Therya

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La portada

Microtus oeconomus, the tundra or root vole, is one of only four Holarctic rodents and the only species of *Microtus* found in tundra and taiga, grass and sedge communities on all northern continents. It has the northernmost distribution of any *Microtus* species in North America, with occurrences to 71° N in Alaska. Tundra vole populations often fluctuate in 3 to 4 year cycles throughout its range, but it is uncertain how climate change will affect its dynamics. It is an important prey item for avian and mammalian predators in northern ecosystems (Photo from Qikiqtaryuk Territorial Park (Herschel Island), Yukon, courtesy of Alice J. Kenney).

Nuestro logo "Ozomatli"

El nombre de "Ozomatli" proviene del náhuatl se refiere al símbolo astrológico del mono en el calendario azteca, así como al dios de la danza y del fuego. Se relaciona con la alegría, la danza, el canto, las habilidades. Al signo decimoprimero en la cosmogonía mexica. "Ozomatli" es una representación pictórica de los mono arañas (*Ateles geoffroyi*). La especie de primate de más amplia distribución en México. " Es habitante de los bosques, sobre todo de los que están por donde sale el sol en Anáhuac. Tiene el dorso pequeño, es barrigudo y su cola, que a veces se enrosca, es larga. Sus manos y sus pies parecen de hombre; también sus uñas. Los Ozomatin gritan y silban y hacen visajes a la gente. Arrojan piedras y palos. Su cara es casi como la de una persona, pero tienen mucho pelo."

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DERECHOS DE AUTOR Y DERECHOS CONEXOS, año 13, No. 1, enero-abril del 2022, es una publicación cuatrimestral editada por la Asociación Mexicana de Mastozoología A. C. Hacienda Vista Hermosa 107, Colonia Villa Quietud, Coyoacan 04960. Distrito Federal, México. Telefono (612) 123-8486, www.mastozoologiamexicana.org, therya@cibnor.mx. Editor responsable: Dr. Sergio Ticul Álvarez Castañeda. Reservas de Derechos al Uso Exclusivo No. 04-2009-112812171700-102, ISSN: 2007-3364 ambos otorgados por el Instituto Nacional de Derechos de Autor. Responsable de la última actualización de este número, Unidad de informática de la Asociación Mexicana de Mastozoología A. C. Dr. Sergio Ticul Álvarez Castañeda. Instituto Politécnico Nacional 195. La Paz, Baja California Sur, C. P. 23096. Tel. (612) 123-8486, fecha de la última modificación 22 enero 2022.

Therya

El objetivo y la intención de *THERYA* es ser una revista científica para la publicación de artículos sobre los mamíferos. Estudios de investigación original, editoriales y artículos de revisión son bienvenidas.

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Editorial

Special Issue in honor of Dr. William Z. Lidicker, Jr.

It is our pleasure to introduce this Special Section of *Therya* in honor of the many professional and mammalogical accomplishments of Dr. William Z. (Bill) Lidicker, Jr. (Figure 1). Bill rocketed through his graduate career. After obtaining a BS from Cornell University in 1953, he began graduate studies at the University of Illinois Urbana-Champaign under the direction of Donald F. Hoffmeister. He completed his MS in 1954 and his PhD in 1957, both under the mentorship of Dr. Hoffmeister. He immediately took up a position as Instructor in Zoology and Assistant Curator of Mammals at the Museum of Vertebrate Zoology (MVZ), University of California, Berkeley, where he remained for his professional career. Influences on Bill's early life leading him towards the study of natural history and mammals can be found in Layne and Hoffman (1994).

Bill must have been a good Instructor because he was subsequently hired as an Assistant Professor at Berkeley in 1959. Most of his publications in graduate school were natural history observations, but he soon focused more on studies of small mammal systematics, including detailed analyses of intraspecific variation (*e. g.*, Lidicker 1960) and cogent discussion of the concept of subspecies (*e. g.*, Lidicker 1962a, reprinted in anthologies in 1970 and 1976). His taxonomic research at this time included descriptions of two new subspecies. During his time as an Assistant Professor, Bill also participated in an expedition to Mexico with other colleagues from MVZ (Figure 2).

Bill's career at MVZ went straight up. He became Associate Professor and Associate Curator of Mammals in 1965, then full Professor and Curator in 1969. Along the way he did terms as Vice Chair of the Department of Zoology and Associate Director of MVZ (Figure 3). Bill's research interests at this time became more focused on population ecology, social behavior, population genetics, and conservation. Starting with a seminal paper on emigration (Lidicker 1962b; see Krebs 2021 in this section), he developed a long-standing interest in small mammal social organization and dispersal, co-editing two books on the latter (Lidicker and Caldwell 1982; Stenseth and Lidicker 1992). Lidicker (1975) introduced the concept of presaturation dispersal. At the time, most ecologists thought of dispersal as increasing with population density, but Bill noted that in many cyclic populations, per capita dispersal actually peaked during the increase (suggesting it was an adaptive behavior), and declined at peak densities when habitats were saturated with individuals.

Bill was (and is) fundamentally a systems biologist, a rare species of scientist in the realm of population biology. Some of his early field studies documenting that populations of California voles (*Microtus californicus*) varied more than two orders of magnitude from year to year impressed on Bill the need to understand the underlying causes of such fluctuations. Bill's interests in this topic developed while broader debates raged among ecologists regarding whether animal populations were regulated by extrinsic factors (*e. g.*, weather), or intrinsic factors (*e. g.*, agonistic behavior), or even at all. To Bill, the answer to these questions was, "yes". Bill defined the phenomenon to be explained – patterns of variation in abundance – in a broad, inclusive way and sought answers in a similar, diverse set of factors (*i. e.*, a multifactorial approach to population dynamics; Lidicker 1988, 1991). He recognized features of the ecological systems in which voles were embedded that later became essential elements of theory on complex adaptive systems, including nonlinear relationships between variables, hierarchical organization, emergent properties, feedback loops, and the lack of equilibria. The conceptual models he described verbally and graphically were criticized as being untestable, yet Bill recognized that empirical tests were valid even if they evaluated only a few components at a time.

Figure 1. Bill and Louise Lidicker at the annual banquet of the 2004 meeting of the American Society of Mammalogists. Photo by Robert M. Timm.

Figure 2. Bill Lidicker in the field in Chihuahua, Mexico in 1961, preparing museum specimens. Photo by Ned K. Johnson, used with the permission of the Museum of Vertebrate Zoology, University of California, Berkeley.

It is not surprising that Bill's interests would turn to landscape ecology and spatial relationships among habitats during his time as Curator of Mammals (along with Jim Patton) in the 1980s (Figure 4). Bill's spatial memory was legendary among his students at the time. Before the advent of personal computers and PDFs, professors tended to accumulate large libraries of reprints. Every flat surface in Bill's office was covered with tall stacks of reprints, some stacks perhaps a meter tall. However, whenever a student stopped by to discuss a scientific problem, Bill could pull just the right reference out of the middle of one of these stacks, a feat that could have stumped Google. We all worried, however, that if there ever was an earthquake (this was the Bay Area after all), we would all have to rush to his office to dig him out from under a mountain of paper.

Bill's contributions to landscape ecology include highlighting the value of landscape approaches for conserving vulnerable mammal species from habitat disruption (Lidicker 1995). His work on mammals has yielded many insights into factors that affect the demography and dynamics of small, vulnerable populations (Lidicker 2002). His interest in dispersal logically led to an interest in the influences of spatial relationships among habitat patches (Lidicker 2000), edge effects (Lidicker 1999), and particularly the ecology of wildlife corridors (Hilty *et al.* 2019).

Although Bill sometimes published synthetic commentaries, after around 2000 he began to publish more frequently on subjects related to the history and philosophy of science (we count at least 11 that could be classified accordingly from a recent CV). One of his most recent papers, for example, warns once again of the likely negative consequences of human population growth from both scientific and social perspectives (Lidicker 2020). Over his career, Bill has published more than 170 scientific papers, including editing or co-editing five books. He has mentored 13 MA students, 24 PhD students, and two postdocs (Figure 5). Bill also played a key role in training students when he co-sponsored Berkeley's first-ever course in conservation biology, beginning in 1987, a popular subject that resonated strongly with young academics.

Bill has had a long-standing association with the American Society of Mammalogists. In addition to serving on numerous standing committees over the years, he has been a member of the Board of Directors since first being elected to that position in 1967. He was elected Vice President in 1974-76, then President in 1976-78. He received the C. Hart Merriam Award in 1986 in recognition of his long-term contributions to mammalian research, and was made an Honorary Member of the Society, ASM's highest honor, in 1995. A few other notable honors include election as a Fellow of the California Academy of Science in 1969, as a Fellow of The Explorer's Club (current members include Elon Musk, Jeff Bezos, and Sir Richard Branson) in 1979, and as a Fellow of the American Association for the Advancement of Science in 1986.

Bill's contribution to international mammalogy has been substantial. Bill attended a symposium in Brno, Czechoslovakia, that preceded the first International Theriological Congress (ITC-1), which took place in Moscow, USSR, in 1974. These congresses were organized by the Steering Committee for the Section of Mammalogy (Theriology) within the International Union of Biological Sciences (IUBS) and take place every four years. Bill has attended all congresses since then. At the 8th Congress in 2001 in South Africa the name was changed to International Mammal Congress (IMC) to better reflect the International

Figure 3. Bill as a faculty member at MVZ in 1967-68. At this time, Bill was Vice Chair of the Department of Zoology, and then Associate Director of the MVZ. From left: R. Bruce Bury, Bill Lidicker, Frank Pitelka. Dr. Pitelka was a strong influence encouraging Bill towards studying ecology and population dynamics. Photo by Elmer C. Aldrich, used with the permission of the Museum of Vertebrate Zoology, University of California, Berkeley.

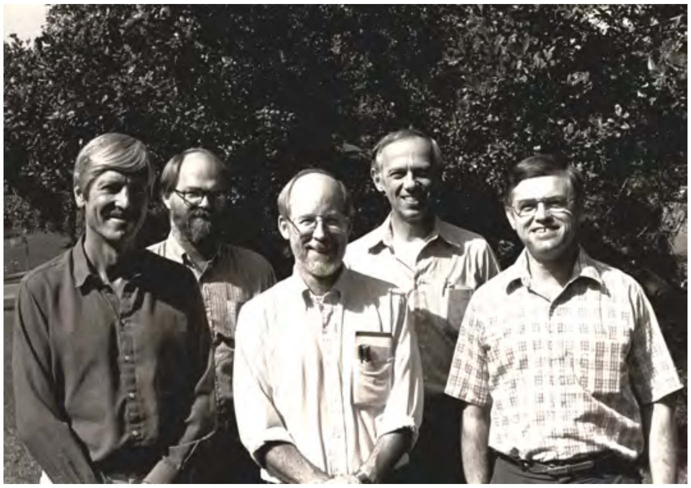

Figure 4. Curators of the Museum of Vertebrate Zoology, 1983. This era was the pinnacle of Bill's career, as his lab in the 1980s included such notables as Rick Ostfeld, Ramone Baccus, David Ribble, Bill Laurance, Ed Heske, and a bit later, Felicia Keesing. All, coincidentally, contributors to this Special Section! From left: Ned Johnson, Harry Greene, Jim Patton, Bill Lidicker, David Wake. Photographer unknown, used with the permission of the Museum of Vertebrate Zoology, University of California, Berkeley.

Federation of Mammalogists (IFM), which was responsible for holding each congress. Bill was elected President of IFM (2005 – 2009), and with Lynne Selwood (IFM Secretary), and Takashi Saitoh (IFM Treasurer), produced the Constitution and bylaws for IFM. Bill also presided over IMC-10 held in Mendoza, Argentina during 2009. Bill published an article describing IFM in the journal *Therya* (Lidicker 2011).

Bill was a key person in the "birth" of *Therya*. When the *Therya* project began, many people thought it was a crazy idea to create a new journal, especially because the Asociación Mexicana de Mastozoología was small, had no budget for such a project, and two previous journals had failed. However, the proponents noted an absence of possibilities for publishing interesting topics about mammals mainly by Latin American authors. Concerns included the need for manuscripts to be reviewed by an "English speaker", publication costs, and the necessity of a double blind evaluation system. At the time, Bill was part of the "Buddy System" of the ASM, a group of volunteers who assist mammalogists for whom English is not their native language improve the writing in manuscripts submitted to the *Journal of Mammalogy*, and agreed with these points among others. *Therya* invited and began to receive manuscripts at the end of 2009, and published its first issue in 2010. Bill was one of the original six editors and a great supporter of the project. *Therya* began as an electronic journal, since the added labor and expense of printing hard copies was a cause of the failure of the previous journals. Bill pushed very hard for the development of *Therya*, and served as an associate editor for seven years. He was Special Editor for the conservation issue (2015 vol. 6:1), which was the first issue of *Therya* that included papers with topics and authors from all continents, and has contributed several articles and letters to the editor himself. Bill has been one of the strong pillars on which *Therya* was been able to depend in order to achieve the growth and development that it has accomplished.

Figure 5. Field trip to Hastings Reservation, Carmel, California, in 1988 to monitor small mammal populations. From left: Back row – Bill Lidicker, Francis Villablanca, Bernie Peyton, Alex Yu, David Ribble; Front row – Susie Peyton, Yulan Chien, Warren Hayes, Marco Salvioni (postdoc from Switzerland). Photographer unknown, photo provided by David O. Ribble.

We would be remiss to fail to mention one of Bill's other interests: international folk dancing. For many summers, Bill and Louise led classes and performed in tours, particularly in Eastern Europe. We've heard it said that he could out-dance others a third his age. He even wrote a paper on dancing by (non-human) mammals, published in *Therya* (Lidicker 2019). Bill was elected a Foreign Member of the Polish Academy of Sciences in 2000, and awarded their 50th Anniversary Medal in 2004. We are sure this was totally based on scientific merit and folk-dancing skills had nothing to do with it.

Congratulations, Bill. Long may you run!

Acknowledgments

Thanks to Bob Timm for Figure 1 and David Ribble for Figure 5. Special thanks to Michelle Koo of the MVZ who helped us gain access to photos in the MVZ archives and arranged to waive user fees! Finally, thanks much to all the contributors in the following Special Section who happily stepped up with manuscripts when contacted about participation.

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How habitat selection, succession, and assembly rules can influence landscape ecology in natural and disturbed areas

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Why should one find a particular set of small mammals at any particular site? This question is at the heart of community ecology, and while no definitive and conclusive answer can yet be provided, this paper does summarize a body of research that has explored, and I think clarified, some of the factors that influence which species occur where and when. The impacts of disturbances such as wildfire and sand mining are examined, along with the regeneration of vegetation and recolonization by small mammals that follow such disturbances in heathland and eucalypt forest in coastal eastern Australia. I describe results from experiments that confirm that these small mammal species do indeed choose or select habitats, rather than just make use of the habitats that are available. Further replicated, experimental removals, as manipulations of each species, one at a time, confirm that interspecific competition between these small mammal species is an important factor determining which species are found where and when, if the temporal aspect of succession is included. Guild assembly rules are examined to illustrate how they may determine which species may or may not become part of a community. Here, my review and synthesis illustrate how the major influences upon the community and landscape ecology of small mammals in the area examined are both spatially variable and temporally dynamic.

¿Por qué debería uno encontrar un conjunto particular de pequeños mamíferos en un sitio en particular? Esta pregunta está en el corazón de la ecología comunitaria, y aunque aún no se puede proporcionar una respuesta definitiva y concluyente, este artículo resume un cuerpo de investigación que ha explorado, y creo que ha aclarado, algunos de los factores que influyen en qué especies ocurren, dónde y cuando. Se examinan los impactos de perturbaciones como los incendios forestales y la extracción de arena, junto con la regeneración de la vegetación y la recolonización por parte de pequeños mamíferos que siguen tales perturbaciones en los brezales y los bosques de eucaliptos en la costa este de Australia. Describo los resultados de los experimentos que confirman que estas especies de pequeños mamíferos sí eligen o seleccionan hábitats, en lugar de simplemente hacer uso de los hábitats disponibles. Las extracciones experimentales, replicadas posteriormente, como manipulaciones de cada especie, una a la vez, confirman que la competencia interespecífica entre estas especies de pequeños mamíferos es un factor importante que determina qué especies se encuentran dónde y cuándo, si se incluye el aspecto temporal de la sucesión. Las reglas del enjambre de gremios se examinan para ilustrar cómo pueden determinar qué especies pueden o no formar parte de una comunidad. Aquí, mi revisión y síntesis ilustran cómo las principales influencias sobre la comunidad y la ecología del paisaje de los pequeños mamíferos en el área examinada son tanto espacialmente variables como temporalmente dinámicas.

Keywords: Assembly rules; Australia; community ecology; dasyurids; disturbances; habitat selection; landscape ecology; rodents; sand mining; small mammals; succession; wildfire.

Introduction

Why should one find a particular set of small mammals at any particular site? This question is at the heart of community ecology and has been investigated by many ecologists following on the ideas set out by MacArthur and Wilson (1963, 1967). While no definitive and conclusive answer can yet be provided, this paper does summarize a body of research that has explored, and I think clarified as my research matured, some of the factors that influence which species occur where and when. The important role that assembly rules might play in restricting which sets of species actually co-occur was first examined by Jared Diamond (1975), using the distributions of bird species in New Guinea and adjacent islands to study how they were assembled into communities. Diamond observed combinations of species of birds, existing in nature, which he termed 'permitted' combinations, and others that have not been found to exist in nature, which he termed 'forbidden' combinations. He said as part of his summary "Much of the explanation for assembly rules has to do with competition for resources and with harvesting of resources by permitted combinations so as to minimize the unutilized resources available to support potential invaders" (Diamond 1975:345). Although there has been much controversy, these views were supported a decade later by many chapters in an edited book on community ecology (Diamond and Case 1986). Bob M'Closkey elegantly demonstrated one mechanism that could explain how Diamond's assembly rule might operate, making use of information on the diets of seed-eating rodents in the Sonoran Desert to describe in detail both their habitat niche and food niche (see M'Closkey 1978, 1985). Morris and Knight (1996) later provided a theoretical derivation for assembly rules as a probabilistic consequence of MacArthur-Tilman models of consumer resource competition (Tilman 1982).

Many factors that have been related directly to mammal species richness at local scales (*e. g.,* Fox and Fox 2000) could also be related to landscape ecology (see Lidicker 1995). Lidicker (2008) proposed the term "ecospace" for a fourth level of ecology, to replace "landscape ecology", rather than other possible terms such as "spatial ecology" or "ecosystem ecology." Lidicker (2008) suggested "ecospace" after writing a review (see Lidicker 2007) for a book that assembled 37 foundational papers ranging from 1915 to 1990 that led to the emergence of landscape ecology as a discipline. Corridor ecology examines animal movements and is a subdiscipline of landscape ecology, which examines species distributions. Bill Lidicker co-edited two books of contributions to the subdiscipline of corridor ecology (see Hilty *et al.* 2006, 2019).

This paper explores in detail several factors, such as habitat selection, ecological succession, species interactions, and species assembly rules, which can have an impact upon small mammal communities. My focus here is on insights into these factors that can be gained by examining a series of studies initiated from a main study site at Big Gibber, a specific location within Myall Lakes National Park (MLNP), almost 300 Km north of Sydney, New South Wales, Australia (see Figure 1). 'Gibber' in this sense is an Australian term meaning a stone, so this location really means 'big stone'. The natural disturbance of wildfire upon heathland and open eucalypt forest sites is compared to the disturbance caused by sand mining on these same landscapes, and the regeneration that follows these disturbances. Comparisons with other studies in similar landscapes illuminate how these factors influence the landscape ecology of small mammals.

Materials and methods

Study site. Sand dunes are important components of Myall Lakes National Park (MLNP; 32° 28' S and 152° 24' E; see Figure 1) located 300 Km, by road, north of Sydney in New South Wales, Australia. Outer barrier sand dunes up to 100 m high support 25-m high eucalypt open forest, whereas low-relief inner barrier sand dunes support wet and dry heathland. The four to five meters of relief provided by these low inner barrier dunes permit gradation from swamp to tall dry heath (Osborne and Robertson 1939; Carolin 1970). Such a gradation occurs on this Big Gibber main study site, part of a former lagoon that now supports swamp and wet heath in some areas, with a low transverse dune supporting dry heath and a patch of eucalypt woodland with a dense, tall, dry heath understory, thus including the full range of habitats available. Names for types of vegetation (macrohabitat) used in this paper and other papers cited follow the protocol established by Specht (1970, 1981). The main study site (approximately seven ha, adjacent to a gravel road constructed by the sand mining company) near Big Gibber (see Figure 2) is located in coastal heathland that had not been burned for a long time.

This paper is a synthesis of many studies by the author and colleagues and full details of methods are included in the references cited, with a representative summary of those methods included here. A trapping grid with 20-m trap spacing was established in May 1974 and topography was mapped using a theodolite and staff to measure and record elevation above an arbitrary datum (see Figure 2). The grid was trapped at monthly intervals using collapsible aluminum Elliott small mammal traps (330 x 100 x 90 mm; Elliott Scientific Equipment, Upwey, Victoria, Australia) placed singly on the ground at each of 176 trapping stations, baited with a mixture of oatmeal and peanut butter. For each trapping session in May, June, and July of 1974 trapping was carried out on four successive nights with no pre-baiting. All but approximately one ha of this main Big Gibber study site was burned during an extensive wildfire in August 1974, which burned in total more than 2,000 ha of MLNP. Post-fire trapping sessions were carried out at intervals of two months on this site, as for several months there were no small mammal captures at all. More complete details of methods used on this site have been published (see Fox 1981, 1982).

To study vegetation regeneration and recolonization by small mammals following sand mining that occurred nearby,

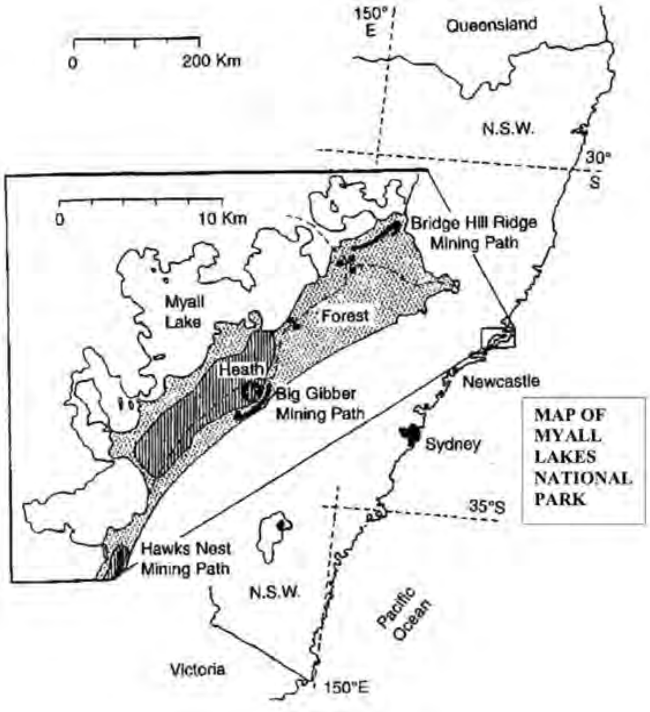

Figure 1. A location map of Myall Lakes National Park, almost 300 Km by road north of Sydney, in coastal New South Wales (NSW) with latitude and longitude lines shown. The main study site at Big Gibber is shown as a star. Mining paths are shown as heavy dark lines at Hawks Nest, Big Gibber and Bridge Hill Ridge. Areas of heath (shading) and forest (stippled) are shown together with larger solid dots in the forest representing trapping plots used by Fox and McKay (1979). This figure has been adapted from a figure published by Fox (1996).

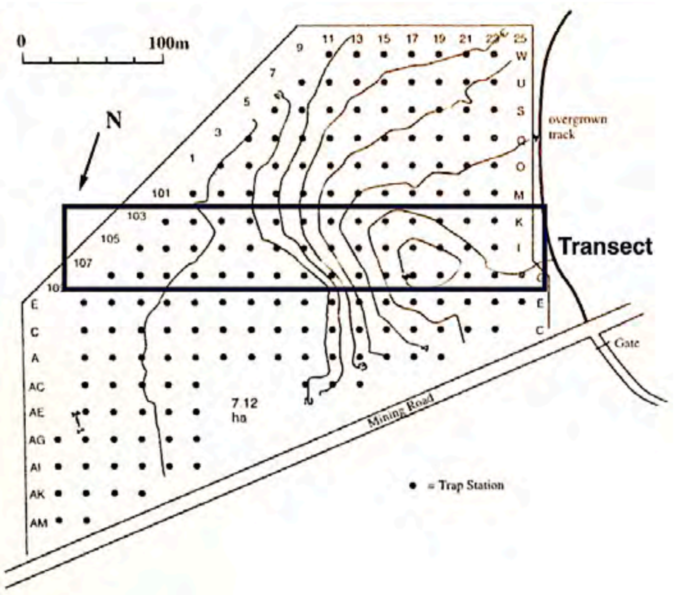

Figure 2. Topography on the Big Gibber study site in Myall Lakes National Park (MLNP) showing contours with a 0.5 m interval. The site is adjacent to a gravel road constructed by the sand mining company and an overgrown sand track used by four-wheel drive vehicles. Trap stations are shown as solid dots together with the position of a belt transect (three trap stations wide) rising 4 m from the swamp and wet heath on the left up the vegetated old dune to dry heath and woodland on the right. This figure is adapted from Fox (1981, 1982).

a number of 1-ha study plots were established, each with 25 traps set on a square grid with 20-m spacing between trap stations. Plots were established along a mining path at positions of known age since regeneration began. Such use of chronosequence analysis has since been validated for sand mining paths through eucalypt open forest (Twigg *et al.* 1989). To study heathland that had been sand mined, eleven study plots of known regeneration age were established along a sand mining path through heathland near Hawks Nest at the southern end of MLNP (see Figure 1). Three additional control plots were also established at adjacent unmined sites (see Fox and Fox 1978). Collection of vegetation survey information and small mammal trapping information was standardized across all of these study plots to be the same as for the studies that had already been undertaken on the main Big Gibber site. For a study of forest that had also been sand mined, we established a total of 20 study plots of known regeneration age (see Fox and Fox 1984). Eight were on one mining path (Big Gibber mining path) and twelve were on another (Bridge Hill Ridge mining path; see Figure 1). For more complete details of all methods used in these two studies, see Fox and Fox (1978, 1984). Control plot information for sites not mined came from 16 forest sites, near Seal Rocks (see Figure 1), within MLNP (see Fox and McKay 1981). This information allowed direct comparisons of results for the regeneration of vegetation and the recolonization by small mammals following wildfire and following sand mining.

Cluster analysis and factor analysis were used with vegetation density measurements (microhabitat) from different vertical layers, from ground level to 2 m above ground level, to identify vegetation types present on each site. Multiple regression analyses using a standard step-wise process were used to identify which variables contributed most notably to the abundance and biomass of small mammals present. In every case, appropriate statistical tests were used to measure significance to a level of at least $P < 0.05$. These tests were identified and explained in the publications cited for the data used from these various studies. Complete and detailed methods for all of these techniques, used on species in both wet and dry heath habitats as well as open forest habitats have been published (Haering and Fox 1995, 1997; Knight and Fox 2000; Ross *et al.* 2004).

Results and discussion

Topography on the Big Gibber study site rises 4 m from swamp and short wet heath up the vegetated old dune to tree heath (or woodland) and a belt transect along this moisture gradient was used to assess how small mammals used these trap stations (see Figure 2). Using Specht's (1970) classification of vegetation, seven vegetation types (macrohabitats) were identified and mapped on the Big Gibber study site (see Fox 1981; Fox and Fox 1981). Six of these vegetation types were found on the belt transect shown in Figure 2, and in order from wettest to driest they are: swamp; short wet heath; tall wet heath; short dry heath; tall dry heath; tree-heath. These terms will be used in the remainder of this paper.

Eight species of ground-dwelling small mammals were commonly trapped on the Big Gibber site. Although the peramelid marsupial *Isoodon macrourus* (northern brown bandicoot) was present, the adults were too large to be regularly caught in the collapsible live traps used. However, they did not unduly impact the availability of traps for other species. Consequently, bandicoot captures have not been included in any of the analyses. Each of the seven remaining species comprised more than 5 % of the total captures and all were included in the analyses. These species were: the native murid rodents *Rattus lutreolus* (swamp rat), *R. fuscipes* (bush rat), *Pseudomys novaehollandiae* (New Holland mouse), and *P. gracilicaudatus* (eastern chestnut mouse); the introduced murid rodent *Mus musculus* (house mouse); together with the dasyurid marsupials *Antechinus stuartii* (brown antechinus) and *Sminthopsis murina* (common dunnart).

Distribution of species along this habitat gradient. Figure 3 illustrates how the four most abundant small mammal species were distributed along this single moisture gradient (habitat resource) before the August 1974 wildfire. The habitats range from swamp and wet heath at the wet end to dry heath and woodland at the dry end, and the graph uses data derived from Fox (1981). The four most abundant small mammal species show a replacement sequence as the moisture levels change along the transect. Each species appears to select habitat according to which type best meets its requirements, but this needs to be tested (see below), although where the house mouse was captured

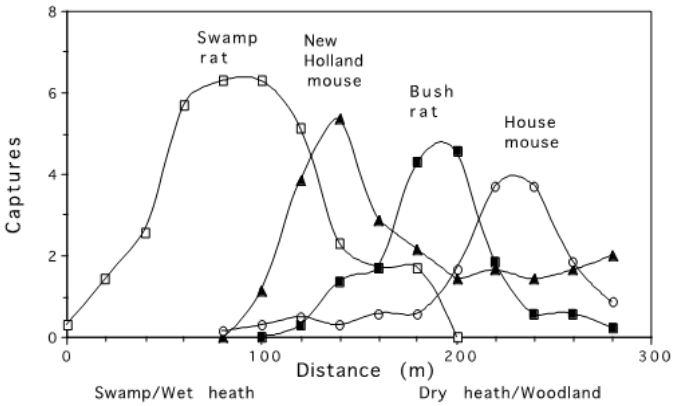

Figure 3. Distribution of the four most abundant species of small mammals, Swamp rat, (*Rattus lutreolus*) New Holland mouse (*Pseudomys novaehollandiae*), bush rat (Rattus fuscipes) and house mouse (*Mus musculus*), along a moisture gradient from wet to dry habitats (in terms of number of captures in May, June and July 1974, before the August 1974 wildfire). Captures along a belt transect (three trap stations wide, shown on Figure 2) were used with a three-point weighted average smoothing (1:2:1) applied to the raw data. Figure adapted from Fox (1981), with full methodology that was used and maps of habitat patches.

was more than likely to be determined by interactions with the other species. Significant interactions have already been well demonstrated for these species with replicated, controlled removal experiments (see Fox and Pople 1984; Fox and Gullick 1989; Higgs and Fox 1993; Thompson and Fox 1993; Luo and Fox 1995; 1996; Fox and Luo 1996; Luo *et al.* 1998; Morris *et al.* 2000).

Post-fire succession brings a temporal scale to when each species may occupy a site. Five years of post-fire trapping results for the Big Gibber site are shown in Figure 4, with wet habitats shown in the upper panel and dry habitats shown in the lower panel for greater clarity and simplicity. There were only three individuals of *Pseudomys gracilicaudatus* (eastern chestnut mouse, early successional species) on the long-unburned Big Gibber site before the fire (hence they were not included on Figure 3). However, their abundance increased in the post-fire period as shown in Figure 4.

Testing for habitat selection versus habitat use. Do these species in fact select habitat, or are they relegated to suboptimal habitat by a dominance hierarchy, or do they merely use habitat in the same proportions in which it occurs? This has been tested using the two species of rodents that were most commonly captured in wet habitats (swamp rat and chestnut mouse) during the post-fire period. This test included all trap stations over the entire study grid, not just the trap stations from the transect shown in Figure 2. Both species showed a much higher proportional use of the wet habitats and a much lower proportional use of the dry habitats (see Figure 5) when measured against the availability of habitats over the entire study grid (*i. e.*, the number of trap stations in each habitat type). The percentage use of wet habitats varied from 35 to 82 % whereas for dry habitats it ranged from 0 to 20 %. In this analysis the macrohabitats were defined using cluster analysis (for detailed methods used see Haering and Fox 1995) and are similar but not identical with those used in Fox (1981, 1982), although the differences are only slight in terms of where the habitat boundaries were drawn. While both species overlapped substantially in habitat requirements, they have been demonstrated to exhibit significant habitat partitioning when measured at the scale of the local trapping grid (Haering and Fox 1995).

For each species, the frequency distribution of where they were captured across the six habitats differed significantly from the availability of trap stations in those habitats (*P. gracilicaudatus,* $X^2 = 26.8$, $P < 0.005$, 5 d.f.; *R. lutreolus* $X^2 = 29.3$, $P < 0.005$, 5 d.f.). Both species clearly most commonly occupied macrohabitats 1 to 3 (wetter heath) in comparison with much reduced occupation of macrohabitats 4 to 6 (drier heath). Captures at stations from each of the first three macrohabitats (see Haering and Fox 1995) provide a separate analysis, as they are the more used habitats. The presence or absence of each species from each trap station and the availability of trap stations in each macrohabitat provide the marginal totals for a X^2 test. The distribution of captures for *P. gracilicaudatus* did indeed differ significantly from availability in habitats ($X^2 = 8.96$, $P < 0.05$, 2 d.f.), showing strong positive selection of macrohabitat 1 (short dense wet heath) and choosing macrohabitat 3 less than expected, whereas macrohabitat 2 was not chosen significantly more than its availability would indicate. The distribution of captures in these three habitats for *R. lutreolus* did not differ significantly from the habitat availability ($X^2 = 1.87$, $P > 0.5$, 2 d.f.).

Longer-term succession in wet heath habitats. Here, I concentrate upon the wet heath habitats occupied by chestnut mice and swamp rats to take a closer look at the impact of wildfire on this part of the small mammal community (see Figure 6). A similar case has been well supported for the dry heath habitats (see Haering and Fox 1997) and has been well documented already in analyses of long-term study sites (see Fox 1996). The Big Gibber study site had been monitored before the August 1974 wildfire so that an estimate of population density for each species before the wildfire was available. This site had two such fires (August 1974 and August 1980) in the time it was monitored (1974 to 1996) and analyses of the long-term results of this and other related studies has been published (Fox 1996); for full details of the site and methods used see Fox (1982). In both fire cycles there was a continuing replacement of the chestnut mouse by the swamp rat with increasing time since fire.

Do these animals respond to changes in the vegetation succession rather than to time *per se*? This has been demonstrated conclusively on different sites with similar wet heath macrohabitat by Monamy and Fox (2000) using microhabitat measurements of horizontal vegetation density in different layers, most significantly for the layer 0 to 20 cm from the ground level. Two high-intensity wildfires 20 years apart at two different sites, but with very similar wet heath vegetation, produced very different patterns of succession when measured against time since fire. The early seral stage specialist *P. gracilicaudatus* (eastern chestnut mouse) appeared after one year at the first site but appeared after only three months at the second site. The late seral stage

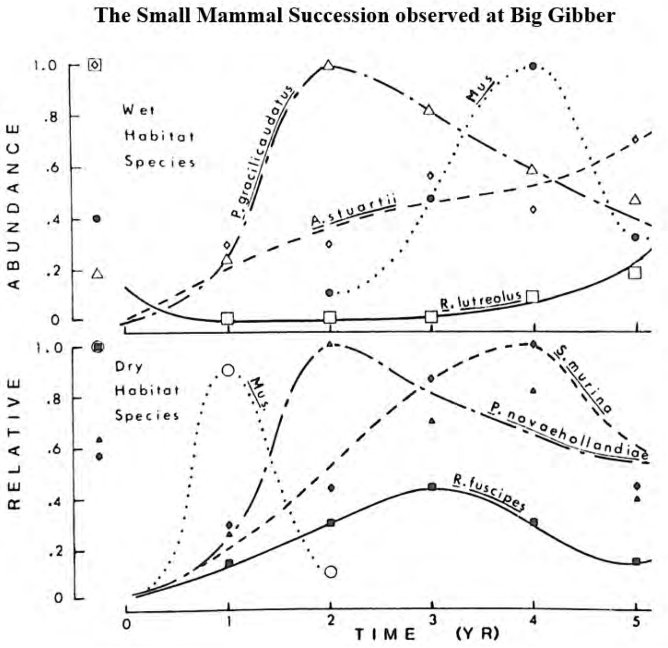

Figure 4. The succession for small mammals regenerating post-fire. The upper panel shows species from wet habitats, *Pseudomys gracilicaudatus* (eastern chestnut mouse), *Rattus lutreolus* (swamp rat) and *Antechinus stuartii* (brown antechinus). The lower panel shows species from dry habitats, *Pseudomys novaehollandiae* (New Holland mouse), *Rattus fuscipes* (bush rat) and *Sminthopsis murina* (common dunnart). Relative abundance of each species is shown as the proportion of the maximum abundance reached by that species. Values for each species before the fire are shown adjacent to the left axis. The house mouse (*Mus musculus*) appeared in both wet and dry habitats, but at different times in the succession. Figure is adapted from Fox (1982).

specialist *R. lutreolus* (swamp rat) took 3.6 years to recolonize at the first site but appeared after only four months at the second site. However, when these responses were graphed not against time, but against a vegetation recovery index (a measure of how rapidly vegetation returned), the trajectories for a species following each of the two fires were concurrent for that species, although for each species the trajectory was different (see figures 4 and 5 in Monamy and Fox 2000:584). The vegetation recovery index was derived from horizontal vegetation density measurements made for different layers of vegetation, from ground level to 2 m.

The role interspecific competition plays in small mammal succession. Does interspecific competition play any role in this species replacement, in relation to the expression of habitat selection that was demonstrated in Figure 5? Similarly, does interspecific competition play any role in relation to regeneration time for this succession? Although graphs of the abundance of species are generally presented on a time scale, these graphs of the abundance of species would be better represented on a scale reflecting changes in the vegetation density as indicated above (see also Monamy and Fox 2000). Experimental analyses of these questions were carried out using replicated, removal experiments (see Higgs and Fox 1993). Figure 7 represents a summary of the results of an experimental removal of swamp rats from five 0.5-ha plots, each with 12 trap stations, in wet heath macrohabitat, when compared to five 0.5-ha control plots in adjacent similar habitat. On all plots each trap station was trapped for three nights in each trapping session. Two pre-removal trapping sessions (23 to 25 January and 8 to 10 February 1989) were undertaken to measure initial mean abundance, then five three-night trapping sessions were conducted (between 13 February and 11 March) during which all swamp rats captured on experimental plots were removed. Post-removal trapping sessions (five) were conducted between 22 March and 30 August 1989. This study concluded that there was very significant interspecific competition from the dominant swamp rat upon the chestnut mouse as seen in Figure 7. The reciprocal removal experiments (Thompson and Fox 1993) had already demonstrated how interspecific competition played an important role in these wet heath habitats. In summer, removal of the chestnut mouse demonstrated a significant competitive release in the abundance of the swamp rat, but in winter (by which time juvenile swamp rats had grown into adults) no significant competitive release was observed. "The different outcomes of such competition are determined by the size class structure of the larger species, thus producing seasonally variable interspecific competition" (Thompson and Fox 1993:264).

An experimental vegetation clipping project (Fox *et al.* 2003) carried out on wet heath habitats in 1993 demonstrated conclusively that physically removing 60 to 70 % of the vegetation significantly reduced the abundance of *R. lutreolus* (swamp rat), whereas the abundance of *P. gracilicaudatus* (eastern chestnut mouse) remained relatively unchanged, thus producing a retrogression of the small mammal succession and demonstrating that the change in vegetation density was causal. This outcome clearly linked small mammal succession to vegetation density, instead of just successional time, by experimentation, in contrast to the observational link reported by Monamy and Fox (2000). A further experimental clipping project (Monamy and Fox 2010) carried out on plots adjacent to each of these same plots in wet heath habitats in 1994 physically removed 85 % of the vegetation. This experiment produced an even

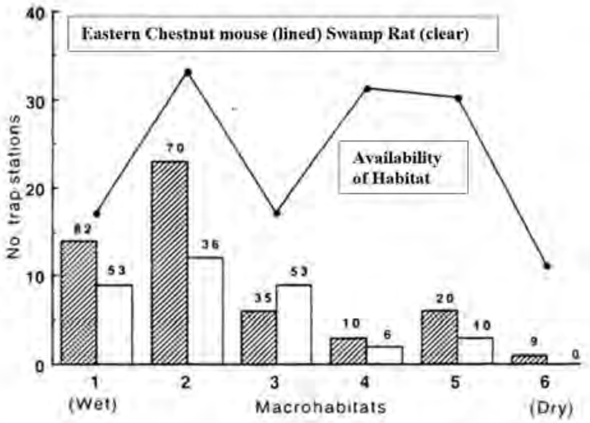

Figure 5. Macrohabitat use by each species shows that both the eastern chestnut mouse (*Pseudomys gracilicaudatus*) and the swamp rat (*Rattus lutreolus*) choose or select wet habitats and avoid dry habitats, in relation to the number of stations of each habitat type available. The percentage of trap stations used by each species in each habitat is given on top of each bar (data from Haering and Fox 1995).

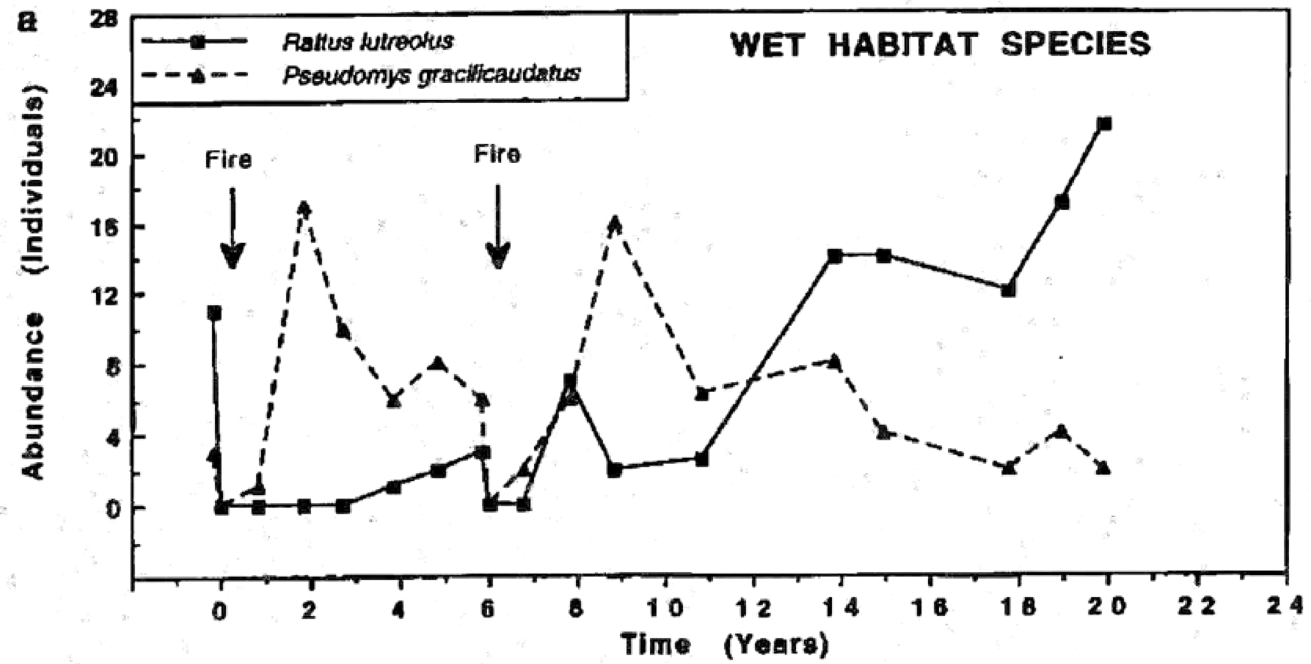

Figure 6. Number of *Rattus lutreolus* (swamp rat) and *Pseudomys gracilicaudatus* (eastern chestnut mouse) individuals captured on the 7-ha Big Gibber study site following wildfires in August 1974 and August 1980 with zero time set to the time of the first fire. This figure is adapted from Fox (1996).

greater retrogression of the small mammal succession, with significant reductions in the abundance of both *R. lutreolus* (swamp rat) and *P. gracilicaudatus* (eastern chestnut mouse). The dry habitat species *P. novaehollandiae* (New Holland mouse) made an appearance, together with the more cosmopolitan *M. musculus* (house mouse), on plots where vegetation density had been made similar to that for vegetation supporting an early seral stage of this small mammal succession.

Experimental support for the habitat accommodation model. The vegetation removal experiments of Fox *et al.* (2003) and Monamy and Fox (2010) that produced a retrogression of the small mammal succession clearly provide experimental support for the habitat accommodation model, first proposed in Fox (1982) that followed from the earlier work of Connell and Slatyer (1977), which described both habitat facilitation and habitat tolerance models. The habitat accommodation model incorporates elements of both the habitat facilitation and tolerance models; small mammal species do not modify local physical conditions, as these are changing in response to external factors (vegetation regeneration following wildfire). Small mammal species enter the post-fire succession when the changing local physical conditions (regenerating vegetation) first meet their specific requirements (habitat facilitation model). This has been experimentally demonstrated with transplantation of *P. novaehollandiae* (New Holland mouse) onto differently aged early seral stages of vegetation regeneration following sand mining. These introductions showed that this species was not able to colonize sites that had been regenerating for less than 4.9 years (see Fox and Twigg 1991:281). However, when vegetation conditions move out of the optimal range for the small mammal species, the animals leave or are reduced in numbers (habitat tolerance model). The reductions in abundance may be caused by these species no longer being able to obtain an adequate share of the resources they need, as their competitive ability becomes reduced. The significant impact of interspecific competition for small mammal species in this succession has been demonstrated experimentally for wet heath species with replicated, reciprocal, removal experiments (Higgs and Fox 1993; Thompson and Fox 1993). The significant impact of interspecific competition for dry heath small mammal species in this succession has also been demonstrated experimentally (Fox and Pople 1984; Fox and Gullick 1989). The habitat accommodation model accounts for all species in this Big Gibber post-fire succession, as well as small mammal successions following sand mining (Fox and Fox 1978, 1984; Fox 1990 a, b; Fox 1996).

Even more support for this model was demonstrated when longer time scales for post-fire succession became available. For the Big Gibber site supporting both wet and dry heath habitats, the common dunnart (*Sminthopsis murina*) was not captured during the last three years of 14 years of post-fire trapping (see Fox 1996). Local extinction was confirmed with an even longer period of post-fire trapping on that same site, as noted by Fox and Fox (2000:30) "… with *Sminthopsis murina* now locally extinct for 6 years, although it has been captured within 3 km (those sites support an earlier successional stage). The eastern chestnut mouse (*Pseudomys gracilicaudatus*) has also now been absent for 2 years (Figure 5)."

The replacement sequence in small mammal succession. Here, I have examined the post-fire succession in coastal heathland, however, elsewhere (Fox and Fox 1978) we described a small mammal succession in similar coastal

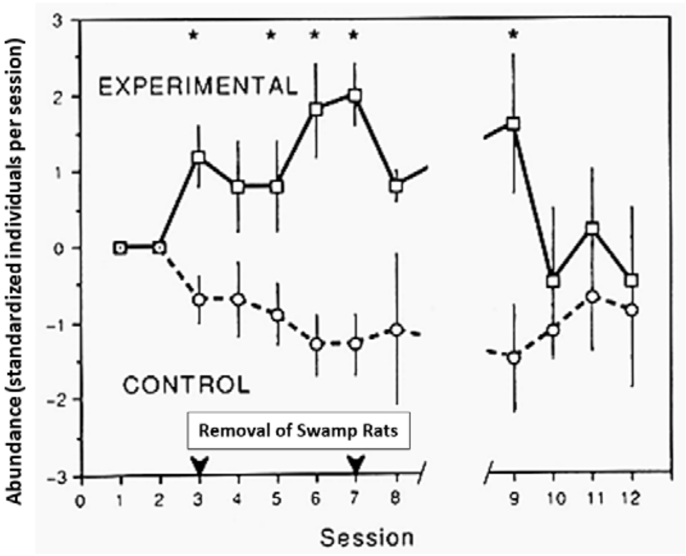

Figure 7. Mean standardized abundance (± SE) for the eastern chestnut mouse during each trapping session, using mean data for five replicates where swamp rats were removed from experimental plots for trap sessions 3 to 7. Abundance is shown as the departure from zero where zero represents the mean pre-removal abundance. Asterisks denote trapping sessions where both the Mann-Whitney U-test and Student's t-test demonstrate significant differences between control and experimental treatments ($P<0.05$). This graph is based upon data published by Higgs and Fox (1993).

heathland regenerating following sand mining. Similar successions for open eucalypt forest near Seal Rocks in MLNP were described following disturbances by wildfire (see Fox and McKay 1981) and sand mining (see Fox and Fox 1984).

The more extensive succession demonstrated for this open forest post-fire, with species reaching their peak abundances before they were replaced, follow the order**:** house mouse (*Mus musculus*), New Holland mouse (*Pseudomys novaehollandiae*), common dunnart (*Sminthopsis murina*), brown antechinus (*Antechinus stuartii*), bush rat (*Rattus fuscipes*), as illustrated in Figure 8 (adapted from Fox 1996). In areas remaining undisturbed for very long periods, even the late successional bush rat decreased in abundance as the understory vegetation began to senesce. This senescence meant the vegetation became more open at ground level, which allowed an increased amount of light to reach the ground beneath the understory vegetation. Hence, vegetation succession became reinvigorated, as dormant seeds from early seral stage plants germinated and appear again in the understory. The mammalian succession also began again, when early successional species (house mouse, New Holland mouse) reappeared in the community at the same time that bush rat abundance had decreased (see Fox 1996:478 Figure 2). The habitat accommodation model for animal succession (Fox 1982; Fox 1990a) recognizes that animals enter the succession when their specific habitat requirements are met, and that they lose dominance in the succession through competitive interactions when species entering the succession outcompete them. One conclusion to be reached from this, relevant to habitat regeneration, is recognition that the species that can occupy any site will be largely determined by the habitat variables at that site, and that there are both spatial and temporal scales to these habitat variables.

This same eucalypt open forest has also been subjected to sand mining (Fox and Fox 1984; Twigg *et al.* 1989), and it is possible to illustrate a similar small mammal succession for the early successional species (see Fox 1996). Some of these data (from 1982, 1987, 1992) have been redrawn in Figure 9 and show three species entering the succession in the order**:** house mouse, New Holland mouse, common dunnart. This pattern reflects the post-fire succession, but on a more drawn-out time scale as the vegetation regeneration proceeds much more slowly after sand mining than after fire. Later trapping in 1997 revealed the presence of brown antechinus and bush rat for the first time on these regenerating sand-mined sites, which had been sampled every five years (1982, 1987, 1992, 1997). Because regeneration following sand mining is so much slower than regeneration following wildfire, it is only the early part of small mammal post-fire succession that has yet been observed on any regenerating sand mining path, even though these have been trapped for more than fifteen years on sites that have been regenerating for up to 25 years. The similarity with the post-fire succession is strong and is in agreement with the comparisons made for vegetation succession reported from three types of disturbance (fire, clearing, and mining) in similar forest/woodland habitat at Tomago, near Newcastle in NSW (Fox *et al.* 1996). Factors influencing plant species richness on these same sites at Tomago have been studied in detail (Ross *et al.* 2002), while the interaction of multiple disturbance types has also been shown to play an important role in regenerating and rehabilitating areas (Ross *et al.* 2004).

How various factors can have influence upon parameters such as mammal species richness at any one spot has been examined (Fox and Fox 2000). Behavioral interactions between species have also been shown to play an important role in determining how species may co-occur at any one place (see Righetti *et al.* 2000). As well as considering species richness, however, it is also necessary to consider which combination of small mammal species might be found assembled into any one community at any one spot in the landscape.

Guild assembly rules. Taking these ideas and applying them to the data accrued from my years of field work in MLNP (Fox 1980, 1981, 1982, 1985) led me to propose what would become a guild assembly rule (Fox 1987) for the small mammals that had been encountered at any one site. This assembly rule was first stated this way: "There is a much higher probability that each species entering a community will be drawn from a different functional group (genus or other taxonomically related group of species with similar diets) until each group is represented, before the cycle repeats" (Fox 1987:201).

My guild assembly rule was developed in an empirical manner from my observations of the structure of small mammal communities occupying different patches of habitat (see Fox 1980, 1981, 1987) but lacked any theoretical derivation. However, in a later publication (Morris and Knight 1996), Doug Morris demonstrated this guild assembly rule was a probabilistic consequence of adding guild structure to MacArthur-Tilman models of consumer resource competition (Tilman 1982). This provided the theoretical underpinning for my empirically derived rule (Fox 1987). I included this theoretical derivation when I dealt with the genesis and full development of this guild assembly rule (Fox 1999). Later, Doug Morris was able to come from Canada and visit my study sites to test out his models on these same wet heath habitats in MLNP (see Morris *et al.* 2000). This guild assembly rule has been applied to a wide range of species and landscapes including shrews in northeastern USA (Fox and Kirkland 1992), rodents from multiple sites in Valdivian rainforests in southern Chile, South America (Kelt *et al.* 1995), lemurs from Madagascar (Ganzhorn 1997) and desert rodent assemblages from North America and Asia (Kelt *et al.* 1999), all far distant from, and quite different to the coastal heathlands and eucalypt forests in eastern Australia where this rule had been empirically derived. A stringent test of this rule was reported when I applied it from data that Jim Brown had compiled for seed-eating rodents from the species-rich southwestern deserts of North America (Fox and Brown 1993). That data set came from 202 sites, widely distributed over an area of approximately 640,000 km^2, including all of the Chihuahuan, Sonoran, Mojave, and Great Basin Deserts north of the U.S.-Mexican border (see Brown and Kurzius 1987), where interspecific competition had already been confirmed from a long-term experimental study (Heske *et al.* 1994). Further analyses of this guild assembly rule have also been undertaken in these southwestern deserts (see Brown *et al.* 2002 and references therein).

Factors such as habitat diversity, disturbance, species interactions, and guild assembly rules have all been shown to influence mammal species richness at any one site (Fox and Fox 2000). These factors and others have also been examined as linkages to landscape ecology and responses to climate change (see Hilty *et al.* 2019).

From the information contained in the studies reviewed and synthesized here, I conclude that:

> Small mammal species do actively choose or select, rather than just use, habitat along a moisture gradient ranging from swamp through dry heath into tree heath (or woodland);
>
> Small mammal species display a sequential replacement series as part of the successions observed in both heathland and eucalypt open forest habitats following disturbance by wildfire and sand mining;
>
> While the small mammal successions that follow wildfire and sand mining are very similar, the latter occurs much more slowly than post-fire succession, reflecting slower vegetative succession after sand mining relative to wildfire;
>
> Replicated and controlled removal experiments have shown that interspecific competition plays a very important role in these small mammal successions and that body size is an important factor in this interspecific competition;
>
> Experimental support has been demonstrated for the habitat accommodation model in small mammal successions following disturbances by wildfire and by sand mining;

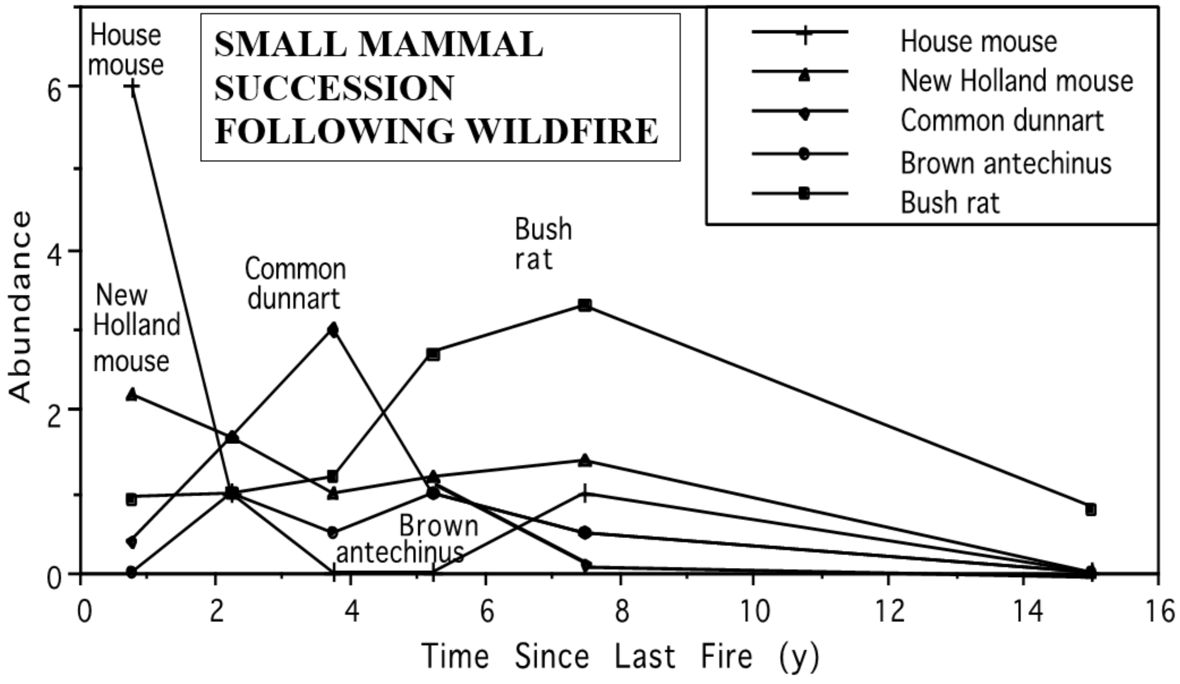

Figure 8. An illustration of the small mammal succession following wildfire in open eucalypt forest near Seal Rocks in MLNP, using composite data from 1982-1994 taken from Fox (1996). Species shown are house mouse (*Mus musculus*), New Holland mouse (*Pseudomys novaehollandiae*), common dunnart (*Sminthopsis murina*), brown antechinus (Antechinus stuartii) and bush rat (*Rattus fuscipes*). Abundance (as individuals captured on each 1 ha trapping grid) is shown as a function of the time since last fire in years.

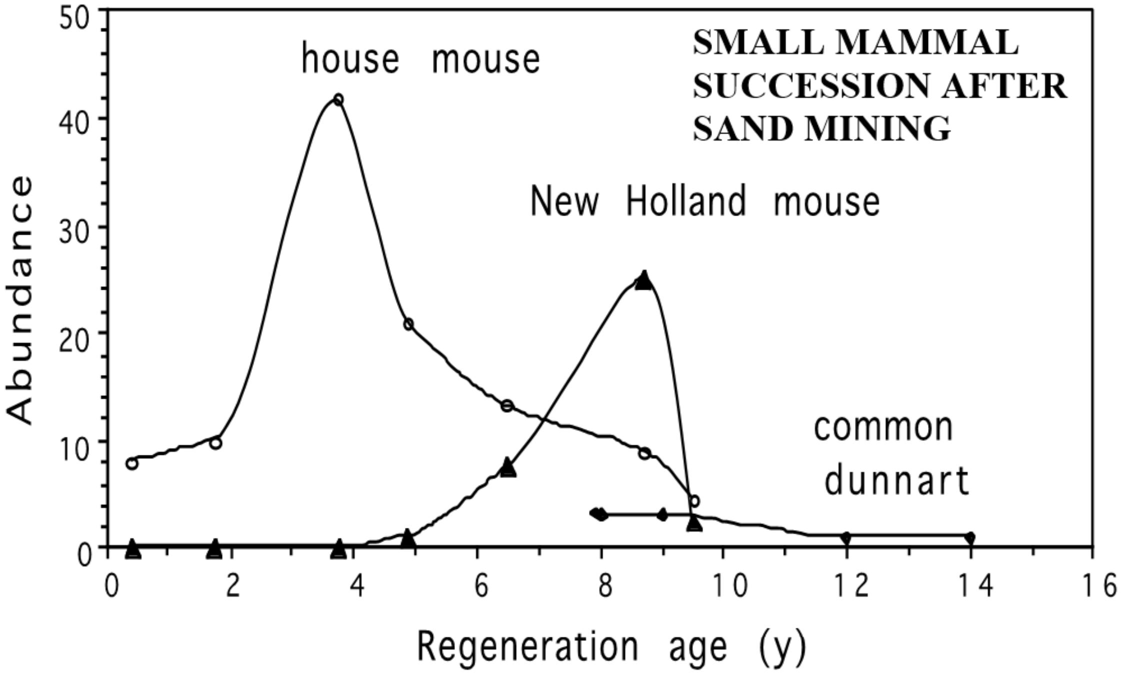

Figure 9. The small mammal succession following sand mining along Bridge Hill Ridge, through eucalypt open forest, similar to forest near Seal Rocks MLNP shown in Figure 8, using composite data taken from Fox (1996) for trapping periods in three separate years, 1982, 1987, 1992. Abundance (as individuals captured on each 1 ha trapping grid) is shown as a function of regeneration age in years, for house mouse (*Mus musculus*), New Holland mouse (*Pseudomys novaehollandiae*), and common dunnart (*Sminthopsis murina*).

> A small mammal guild assembly rule that operates in these communities (as well as in a diverse range of landscapes on different continents) is a probabilistic consequence of adding guild structure to MacArthur-Tilman models of consumer resource competition.

All of these can be major influences upon the community and landscape ecology of small mammals. The particular combination of small mammal species that may be observed to occur at any one place can be influenced by a suite of factors that vary spatially and temporally.

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In praise of emigration and Bill Lidicker's classic 1962 paper

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In 1962 Bill Lidicker, a budding young biologist at Berkeley's Museum of Vertebrate Zoology, published a short paper on the possibility that emigration might be involved in population regulation. He discussed this possibility largely with respect to small mammals and the possibility that genetic differences might be involved in emigration behavior. The paper contained no data, but it generated much interest in both the ecology and the genetics of emigration. I review in this paper how this stimulus to study emigration developed in the 60 years since Bill Lidicker opened this door for mammalian studies. The first attempts to analyze emigration involved removal experiments, carried out mostly on small rodents, which showed that many individuals could be attracted to an empty habitat via experimental removals. This finding influenced both important issues in pest control and theoretical questions about the quality of emigrants in natural populations. The idea that emigrants might be genetically distinct from resident individuals was gradually abandoned since studies of social organization and in particular territoriality and infanticide focused on social interactions over space in small rodents. Further studies of emigration blossomed in behavioral ecology as more and more studies were carried out on interactions over resources in many other vertebrates. Some generality has been achieved by a focus on the simple questions put forward in this short paper by Bill Lidicker in 1962.

En 1962, Bill Lidicker, un joven biólogo en ciernes del Museo de Zoología de Vertebrados de Berkeley, publicó un breve artículo sobre la posibilidad de que la emigración pudiera estar involucrada en la regulación de la población. Discutió esta posibilidad en gran medida con respecto a los pequeños mamíferos y la posibilidad de que las diferencias genéticas pudieran estar involucradas en el comportamiento de la emigración. El documento no contenía datos, pero generó mucho interés tanto en la ecología como en la genética de la emigración. En este artículo repaso cómo se desarrolló este estímulo para estudiar la emigración en los 60 años desde que Bill Lidicker abrió esta puerta a los estudios sobre mamíferos. Los primeros intentos de analizar la emigración involucraron experimentos de remoción, llevados a cabo principalmente en pequeños roedores, que mostraron que muchos individuos podrían ser atraídos a un hábitat vacío a través de remociones experimentales. Este hallazgo influyó tanto en cuestiones importantes en el control de plagas como en cuestiones teóricas sobre la calidad de los emigrantes en las poblaciones naturales. La idea de que los emigrantes pudieran ser genéticamente distintos de los individuos residentes se abandonó gradualmente, ya que los estudios de organización social y, en particular, la territorialidad y el infanticidio se centraron en las interacciones sociales sobre el espacio en pequeños roedores. Otros estudios sobre la emigración florecieron en la ecología del comportamiento a medida que se llevaban a cabo más y más estudios sobre las interacciones sobre los recursos en muchos otros vertebrados. Se ha logrado cierta generalización centrándose en las preguntas sencillas planteadas en este breve artículo por Bill Lidicker en 1962.

Keywords: Carrying capacity; immigration; individual differences; population regulation; selection for dispersal.

Introduction

During the 1950s there was much discussion of population regulation both in a theoretical sense and in field populations. Among vertebrate ecologists most studies featured birds and mammals, and the ideas of how a balance of nature and population limitation were achieved were argued extensively. Density-dependence was the key to understanding. For mammals, the primary focus was on limitations set by the food supply and by predation. Everyone knew that population changes were specified by changes in reproduction, mortality, emigration, and immigration but in practice movements were ignored because everyone assumed that immigration equaled emigration, so they cancelled each other. Laboratory studies by John Christian and David E. Davis (1955) in the early 1950s, however, pointed to the fact that pests like house mice and Norway rats had a social organization centered on aggression and territoriality. Territoriality might prevent immigration at high density, or conversely aggressive behavior might inhibit emigration, as suggested later by Hestbeck (1982). One might have thought at the time that field work on territoriality in birds would have led to more consideration of movements and aggression, but David Lack (1954) in his influential book had concluded that food supplies were primary regulators of bird populations and dispersal was of little consequence. Dispersal was discussed in a genetic framework in *Drosophila* and in a colonization framework for plants and animals on islands. Lidicker's short paper (Lidicker 1962) was critical because he bridged these two mindsets and asked the simple question of whether emigration could limit population density under some circumstances. There was no field data for mammals that he could devote to this question, however.

The Museum of Vertebrate Zoology at Berkeley was at the time a bastion of research on speciation in vertebrates and their ecology in both North and South America. It had a distinguished faculty working on birds and mammals and the predominant belief was the Lackian view that food supplies could explain most population changes. While there was much innovative research, for example on the use of cameras on rodents (Pearson 1959), there was little history of experimental field ecology; however, this began to change when I went to Berkeley in 1962 on a postdoctoral fellowship. I will depart now from this capsular history to follow the development of small mammal population ecology and how Lidicker's thoughts on emigration blossomed over the next 60 years, particularly regarding the ecology of small mammals.

Phase 1: Emigration surprises. The first change that emerged strongly in the 1960s was the experimental outlook. Small mammal ecology began to adopt the experimental paradigm of stating clear hypotheses and predictions and testing these in field populations (Platt 1964). This was not easy and continues so. One prediction Dennis Chitty made in discussion was that if one cropped a cyclic population severely, you could prevent the normal three to four year population cycle from occurring. I did this for two years in Tilden Park just east of Berkeley, California, and was unable to test this idea because even with a 60 % cropping rate of adults every two weeks, I could not hold the experimental population down to low numbers (Krebs 1966). Immigration completely overwhelmed the area. Immigrants from somewhere must be emigrants from somewhere and the result showed that there were exceptionally large numbers of "floating" voles looking for a place to settle. Such high immigration would confound any attempt to study genetic changes in a population, so I had to change my approach. Davis and Christian (1958) had attempted to reduce a Norway rat population in city blocks of Baltimore and found that it was difficult to achieve a population reduction by cropping. Consequently, there was already a suggestion that cropping would not work in pest control. These experiments turned our attention to dispersal and a new experimental design.

Phase 2: Fenced populations. We knew we could not study the consequences of dispersal in the laboratory. Clarke (1955) had shown that voles in a small enclosure would increase to densities much above normal field densities (*ca.* 900 times) so we were warned that to study dispersal in the field would require very large plots. We fenced three blocks of 0.8 ha grassland in southern Indiana USA with 6.3 mm wire mesh that was buried 0.6 m into the soil and extended 0.6 m above ground level, with an inverted V of aluminium on top to prevent voles' climbing. In one fenced grid we left all voles as unmanipulated controls and observed within one year what we called "the fence effect": a complete devastation of the grassland and thus starving voles (Krebs *et al.* 1969, photos in Krebs 1996). No such overgrazing and starvation was ever observed in voles in unfenced areas, and this fencing experiment was the first validation of Lidicker's (1962) suggestion that emigration could regulate population size.

My students and I repeated the fence experiment with other *Microtus* species in grasslands – Boonstra and Krebs (1977) on *M. townsendii*, Tamarin *et al.* (1984) in *M. pennsylvancus*, B. L. Keller (unpublished) on *M. montanus*, Gaines *et al.* (1979) in *M. ochrogaster*, Nelson *et al.* (2002) in *Mus musculus* – but others questioned the generality of the fence effect (Wolff *et al.* 1996). The key point is that the study of the immigration and emigration effects on population changes were stimulated by all this research (Lidicker 1985).

The use of enclosures to study the dynamics of small rodent populations has gone through several phases. Lidicker (1979) studied the dynamics of two enclosed populations of *Microtus californicus* for one year in small enclosures and recognized that even at the extreme density of 24,000 voles per ha there was evidence of some social subdivision. Beacham (1980) was one of the first to demonstrate that if you provided dispersal from a fenced vole population, you could eliminate the fence effect in *Microtus townsendii*. Tamarin *et al.* (1984) showed that one could achieve the same thing by a cleverly designed field experiment.

Some of the findings from fenced vole and mouse populations have led to important new avenues of how social behavior can impact population dynamics. The earliest insights came from the work on stress begun in the 1950s by Christian and Davis (1955), which showed that crowding could cause stress in individuals, measured via the adrenals. Unfortunately, studies of wild populations of voles and lemmings failed to find this adrenal size change observed by Christian in his studies (Chitty 1961; Krebs 1964). It was only in the 1990s that new methods of measuring chronic stress were developed that could be used on field populations of mammals (Boonstra and Boag 1992).

Phase 3: Social behavior. Further studies of fenced populations by Lidicker (1979) on *Microtus californicus* showed that reproduction could be curtailed at high density, in keeping with the observed reproductive changes seen in field populations of voles, so there were clearly some important inferences that came from short studies of both crowded rodent populations in the laboratory and wild populations. An insightful attempt to pull together the many points of view about rodent ecology was a symposium on "Populations of Small Mammals under Natural Conditions" (Snyder 1978). These discussions helped to push the study of rodent ecology into behavioral ecology. Lidicker (1978) proposed a multifactorial model for the regulation of rodent numbers that attempted to bring together all the different views of population regulation on rodents. His views came under critical discussion from John Christian and Robert Tamarin, which led to an exchange of views in the literature (Christian 1978; Gaines *et al.* 1991; Lidicker 1988; Lidicker 1991; Tamarin 1978).

About this time social behavior was beginning to be taken seriously in small mammal ecology. The dominant view in the earlier years was that social behavior in rodents was interesting but it had little to do with demography because changes in numbers were driven by food shortages and predation. The early studies of Lidicker (1979) came during a greater interest in the role of dispersal in dynamics and much discussion of how dispersal might be a regulatory factor. Wolff (1997) pulled together a synthesis of views that social regulation of rodent populations could be achieved if female infanticide was an important part of the social life of the species involved. This blend of the many ways in which rodent sociality has implications for rodent population dynamics has been well reviewed in the book by Wolff and Sherman (2007).

Infanticide by females is difficult to study in field populations, and it has been the least studied of all the social factors impinging on social dynamics. An important early finding was research on the role of kin groups in vole reproductive research. Lambin and Krebs (1993) found that female kinship had a strong effect on improving survival of nestlings of *M. townsendii* (Lambin and Yoccoz 1998). This insight has resulted in much later interest in how relatedness can affect population dynamics.

Dispersing individuals might be genetically different from residents, as suggested earlier by Chitty (1960), but during the 1960s genetic investigations with allozymes were crude by modern standards, and we were unable to relate genes directly to dispersal behavior of individuals. Current research in behavioral ecology recognizes "personalities" in individuals (Lantová *et al.* 2011; Schirmer *et al.* 2019) and raises new questions about dispersal, behavior, and genetics in small rodents.

Conclusion. If you go back to Lidicker (1962) you will find threads of all these more recent developments in the study of dispersal. A simple list is:

1. Emigration, dispersal, and population regulation.
2. Social and genetic consequences of dispersal.
3. Adaptive advantage of dispersal.
4. Selection for dispersal tendency.
5. Frustrated emigration.
6. Lack of food limitation.

In conclusion, I quote Lidicker (1962):

"*Obviously considerably more sophisticated field investigations are required before the extent to which this mechanism actually operates under natural conditions can be determined.*" (page 32)

I think Bill should be highly pleased that his thoughtful paper in 1962 has generated so many interesting and valuable insights into the role of emigration in population ecology. We may not all agree on the conclusions about rodent population dynamics even yet, but by working together we have helped to develop the methods to answer the questions still poised.

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Reproduction, relative abundance, and variability in North American arvicoline rodent populations

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The ecological and life history characteristics of North American arvicoline rodents vary greatly. A general model suggests that changes in reproduction, as a response to changes in climatic harshness and habitat type, likely affect variation in relative abundance of arvicoline populations. Previous work indicated that variability in abundance does not always increase with mean litter size or with latitude, but litter size does tend to increase as the length of the breeding season decreases. I therefore propose the reproductive potential (RP) hypothesis which states that under favorable conditions, populations with higher reproductive potential can grow more rapidly and can reach higher densities during the breeding season, which leads to greater variability in abundance because very high populations eventually decline to low densities. I define reproductive potential as the maximum number of offspring a typical female could produce during a year and calculate it as the product of mean litter size (m) and length of the breeding season in weeks (b) divided by 3 (RP = mb/3). I then review the problems associated with estimation of the necessary parameters and indicate my criteria for accepting data. To test the RP hypothesis I correlate RP to a measure of variability in abundance for populations with at least 10 years of data, and I compare populations of the same or different arvicoline species at the same and different sites. Most results did not support the RP hypothesis. However, three species had different litter sizes in habitats with different vegetation, and all three reached higher maximum densities where reproductive potential was greater.

Las características ecológicas y del ciclo de vida de los roedores arvicolinos de América del Norte varían enormemente. Un modelo general sugiere que los cambios en la reproducción, como respuesta a los cambios en la dureza climática y el tipo de hábitat, probablemente afecten la variación en la abundancia relativa de las poblaciones de arvicolilidos. Estudios anteriores indicaron que la variabilidad en la abundancia no siempre aumenta con el tamaño medio de la camada o con la latitud, pero el tamaño de la camada tiende a aumentar a medida que disminuye la duración de la temporada de reproducción. Por lo tanto, propongo la hipótesis del potencial reproductivo (PR) que establece que en condiciones favorables, las poblaciones con mayor potencial reproductivo pueden crecer más rápidamente y pueden alcanzar mayores densidades durante la temporada de reproducción, lo que conduce a una mayor variabilidad en la abundancia porque las poblaciones muy altas eventualmente disminuyen a bajas densidades. Defino el potencial reproductivo como el número máximo de crías que una hembra típica puede producir durante un año y lo calculo como el producto del tamaño medio de la camada (m) y la duración de la temporada de reproducción en semanas (b) dividido entre 3 (RP = mb / 3). Luego reviso los problemas asociados con la estimación de los parámetros necesarios e indico mis criterios para aceptar datos. Para probar la hipótesis de RP, correlaciono RP con una medida de variabilidad en abundancia para poblaciones con al menos 10 años de datos, y comparo poblaciones de la misma o diferentes especies de arvicolina en el mismo y diferentes sitios. La mayoría de los resultados no apoyaron la hipótesis de RP. Sin embargo, tres especies tenían diferentes tamaños de camada en hábitats con diferente vegetación, y las tres alcanzaron densidades máximas más altas donde el potencial reproductivo era mayor.

Keywords: Breeding seasons; litter sizes; population variability; reproductive potential; variability in abundance.

Introduction

Rodents in the subfamily Arvicolinae (lemmings, voles, and muskrats) have attracted a great deal of scientific attention for several reasons. They are widespread and abundant in the Northern Hemisphere; many species have dramatic population fluctuations; they often strongly affect the structure and function of ecosystems owing to their impact on vegetation, soils, and predators; and they can have substantial economic impact, both negative (damage to crops, orchards, and reforestation efforts) and positive (use of muskrat pelage for furs). Arvicolines fascinate population biologists because they often show multiannual patterns of alternating high and low densities (3- to 5-year population cycles). Charles Elton (1924) first brought population cycles to the attention of ecologists after learning about the phenomenon from a book on Norwegian mammals (Collet 1911-1912). Stenseth and Ims (1993) provide historical details.

Later studies of the cyclic fluctuations of arvicolines have stimulated an extraordinary number of explanatory hypotheses. Three decades ago I found 22 of them in the literature (Batzli 1992), and several more have appeared since. Many species do not appear to cycle, however, and even within species some populations cycle whereas others do not (Hansson and Hentonnen 1985a; Stenseth *et al.* 1996; Boonstra and Krebs 2012). A clear statistical demonstration of cyclic behavior requires a long time series of annual densities (3 to 4 times longer than the period of the cycle), however, and few such records exist, so we do not know if cycling occurs in many populations (Turchin 2003). As a further complication, some populations appear to go through cyclic and noncyclic phases in their long-term dynamics (Mihok *et al.* 1985a; Krebs 2013, Chap.1). Thus, it seems clear that the dynamics of arvicoline rodent populations differ dramatically within and between species, and this paper seeks to link this variability in abundance to differences in reproduction.

Given that there are about 160 species of arvicolines that occur throughout the Northern Hemisphere, mostly in temperate and arctic regions (they reach subtropical latitudes only at high elevations), it comes as no surprise that species also differ widely in their habitat preferences, food habits (even though all species eat mostly plants), and life history characteristics (Wilson *et al.* 2017). Of course, differences in life history characteristics of populations, such as age at first reproduction, litter size, and survivorship, result in differences in rate of population growth. In an analysis of available life table data for 138 mammalian species, including two arvicolines, Oli (2004) divided mammals into fast, medium, and slow life histories based on the ratio of fertility rate to age at first reproduction. In addition to high reproductive rates and early ages of first reproduction, fast species had smaller body size, lower survival rates, and greater potential rates of population growth compared to slow species. These trends in life history continued even after removal of the effects of body size and phylogeny. Changes in the age at first reproduction and fertility (litter size and frequency of litters) strongly influenced rates of population growth of fast species, but not slow species; whereas comparable changes in survival had strong influence on population growth in slow species, but not fast species.

In a review of reproduction Hasler (1975) found that most arvicoline species (those that shelter in burrows and forage on the ground-level plants in grasslands or forests) have short gestation times (18 to 21 days), rapid growth to weaning (12 to 14 days old), quick maturation to reproductive maturity (15 to 30 days old), postpartum estrus with induced ovulation (which results in simultaneous pregnancy and lactation and produces multiple litters for females within a single breeding season), and large litter size (usually means of four to eight young per litter). Nonconforming species in North America include highly specialized species that favor aquatic (larger body size and slower maturation), subterranean (smaller litter size and a diet including many roots and rhizomes), or arboreal habitats (smaller litter size and a diet consisting of needles of coniferous trees), and poorly known montane species at subtropical latitudes (small litter size). See Wilson *et al.* (2017) for further information on these exceptional species. With such high potential rates of reproduction, most arvicoline rodents must also have relatively low survival rates, if not the world would be awash in arvicolines. Further, because they are at the fast end of the continuum, population growth in most arvicoline rodents should respond more to changes in reproductive output than to changes of similar magnitude in survival.

In light of their fast life history, it's not surprising that many arvicolines have episodic outbreaks in abundance, exponential increases during favorable times (relatively mild weather, good food supply, and few enemies) followed by steep declines (weather deteriorates, resources dwindle, and/or enemies increase). But even within the fast group some populations and species of arvicolines have later ages of first reproduction, fewer litters per breeding season, fewer young per litter, and slower potential rates of population growth than others. These populations should have fewer or no outbreaks, and that leads to the prediction that variability in density of arvicoline populations should be positively correlated with potential reproductive rates. Further, insofar as environmental factors that influence reproduction show geographic patterns, the variability of populations should show similar patterns.

Two environmental factors clearly influence the reproductive output of arvicolines, viz., physical conditions and food availability. The actual physical environment that an individual encounters depends not only on the local climate at its geographic location, but also on the shelter that its habitat provides. Latitude, elevation, and proximity large bodies of water all influence seasonal weather patterns (climate) and habitat type (vegetation and the substrate). The resultant shifts in vegetation and substrate change the nature of available food and shelter. As discussed below, these factors can influence the reproductive output of arvicolines, which suggests that a synthesis of geographical factors, reproductive characteristics, and population fluctuations of arvicoline rodents might be possible.

To develop the synthesis described above, I first review the complex of functional factors and evolutionary factors influencing arvicoline reproduction and population growth using a box and arrows model. Then I embark on a more detailed consideration of the factors that cause the considerable variation in reproductive traits within and between arvicoline populations. Next I consider previous work on reproduction of arvicolines, particularly litter size, in relation to geographic patterns. Finally, I test the reproductive potential (RP) hypothesis which states that under favorable conditions, populations with higher reproductive potential can grow more rapidly and can reach higher densities during the breeding season, which leads to greater variability in abundance because very high populations eventually decline to low densities. To do this I correlate the reproductive potential, which incorporates length of the breeding season as well as litter size of an average female, with the long-term (at least 10 years) variability in relative abundance for a series of North American populations for which I could find appropriate data. I also conduct comparisons of reproductive potential and variability in abundance for populations of the same and different arvicoline species in different habitats at the same site or in similar habitats at different sites.

A model of factor interactions. The series of functional and evolutionary relationships that link the geography, physical environment, habitat, nutrition, life history, and variability in abundance of arvicoline rodents are shown in Figure 1. Climatic harshness, including colder temperatures and a shorter growing season, increases at higher elevations and latitudes. This should reduce survival unless the rodent can compensate in some way, for instance by finding refuge from predators and by storing adequate food for winter (arvicoline rodents do not hibernate). The shorter growing season usually produces a shorter breeding season because winter imposes a less favorable nutritional regime and more severe physical conditions. This likely reduces the number of litters that can be produced in a year, which without compensation reduces recruitment. For the population to succeed, this decrease in reproduction must be balanced by adjustments that increase survival or that increase fertility, either by more rapid production of litters or by increasing litter size or both. One way to increase the survival of young might be to make them larger at birth, thereby also reducing time to maturity, but any increase in the size of the young without reducing litter size might strain the mother and reduce her survival. The number of young could be increased without requiring more resources by making them smaller, but any decrease in the size of the young might also reduce the survival of the young. Thus, some sort of balancing act between number and size of offspring seems likely, and much depends on the availability of resources. Both theoretical and empirical analyses of this trade-off have been examined for decades (Smith and Fretwell 1974; Charnov and Ernest 2006).

Habitat type (substrate and vegetation) also changes with latitude and elevation, though not necessarily positively or negatively. Whether the change improves or reduces habitat quality depends on the nature of the changes. Habitat type determines the availability and quality of food because arvicolines depend on plants, and increased availability of high quality food can increase both the frequency of litters and litter size (Batzli 1985). As noted above, the nature of the substrate affects the quality of shelter available, which also influences survival and breeding success.

Increased reproductive success leads to an increased rate of population growth, which leads to greater densities and ultimately to greater declines, so populations seem likely to show increased variability of abundance in higher quality habitats. Such a straightforward relationship is not a given, however. Survival and dispersal also influence rate of population growth and contribute to population variability, and increased reproductive effort and population growth can lead to increased dispersal and reduced survival. Predators, parasites, and disease also reduce survival, and the abundance of enemies may increase as the arvicoline population increases. Even though mortality and dispersal may play an important role in population fluctuations, they can be difficult to measure, and reliable quantitative data on patterns of survival are even less available than those for reproduction. Predation can account for a large portion of estimated mortality (Pearson 1964, 1966, 1971), but separating mortality from dispersal remains a difficult problem in natural populations. In fact, more seems to be known about the causes of dispersal than about the effects of dispersal on population dynamics (Krebs 2013), and I include dispersal within mortality to simplify Figure 1.

Other factors, such as changes in social behavior with increased population density or increase exposure to predation, both of which might reduce reproductive output indirectly because of stress responses (Krebs 2013), could be included in Figure 1. I have not included them or others because the model is not meant to show all factors that influence reproduction and population dynamics. Rather it elucidates the links between the environment, reproduction, and population variability that I used to develop and test the RP hypothesis. Litter size and length of the breeding season were the only aspects of reproduction for which I could find adequate data to compare with long-term data on relative abundance.

In addition to functional relationships among factors, evolutionary patterns also occur, and those that influence litter size are particularly germane to this paper (Figure 1). Several proposals link the evolution of reproductive rates, particularly to explain the frequent pattern of increasing litter sizes with increasing latitude among birds and mammals. Errington (1946, 1951), drawing on his

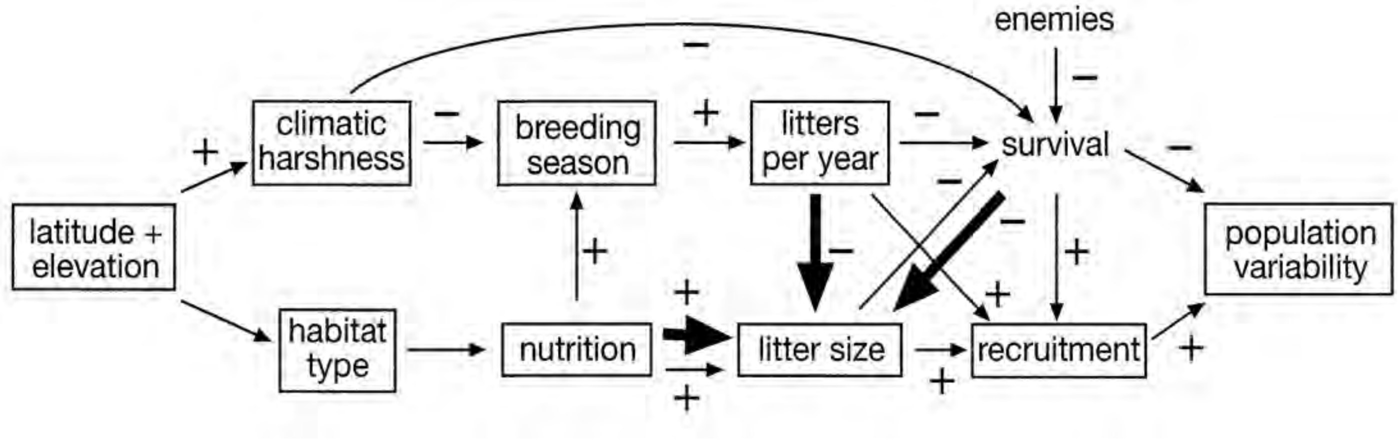

Figure 1. This model summarizes the interrelationships of geography, physical and biological environment, demography, and variability in abundance of arvicoline rodent populations. The thin lines represent patterns of functional relationships, and the heavy lines represent evolutionary influences.

extensive experience with muskrat populations, argued that intercompensation allowed populations to maintain themselves. He observed that changes in mortality and fertility compensated for one another; higher mortality led to greater reproduction as densities declined, and greater reproduction led to higher mortality as densities increased. Although he seemed to be emphasizing phenotypic plasticity in response to short-term environmental changes, he is also associated with the balanced mortality hypothesis: if increased climatic harshness results in increased mortality at higher latitudes, then natural selection favors individuals with more offspring. Of course, adequate resources must exist to support greater fertility if the population is to persist in a given habitat.

Lack (1954) countered with the maximal fecundity hypothesis and argued that selection will always favor individuals that produce additional viable offspring when adequate resources exist. For birds, he argued that more daylight hours for foraging during the breeding season at higher latitudes results in greater food availability, and this accounts for larger clutch sizes with increased latitude. Arvicolines forage day and night so daylength seems unlikely to be a critical factor for them, but the principle of selection for larger litter size with improved nutritional conditions remains. Lack also acknowledged that evolutionary trade-offs between the quality (size) and quantity (number) of offspring could occur.

In 1968, Spencer and Steinhoff explained increasing litter size with latitude or elevation as an evolutionary response in rodents to the decreased length of the breeding season. Increased litter size without increased resources likely reduces female survival thereby curtailing future reproduction. In moderate climates with long breeding seasons, females can balance less current reproduction (smaller litters) with greater survival, which allows for increased future reproduction. But as the length of the breeding season declines, with less prospect of future reproduction, particularly in rodents that only survive for one breeding season, the value of increased current reproduction (increased litter size) outweighs the value of future reproduction (Williams 1967). In their review of life histories of *Microtus* and *Myodes*, however, Innes and Millar (1994) pointed out that seven studies in four species at a variety of latitudes and elevations differed only slightly in the average number of litters per breeding season, from 1.6 to 2.2, which they argued left little scope for the influence of length of the breeding season on reproductive output. Still, the maximum in that range is nearly 40 % greater than the minimum, a rather substantial difference.

Another evolutionary hypothesis, based on a fairly elaborate mathematical model, states that greater population fluctuations in general will favor larger litter size, which turns my previous arguments on their head (Stenseth and Framstad 1980). A later paper extended this model and reexamined this hypothesis in the context of two Swedish species of arvicoline rodents that have increasing population fluctuations (likely population cycles in the north) and larger litter sizes as latitude increases (Stenseth *et al.* 1985). The authors concluded that both population variability and nutrition influence the evolution of litter size. However, even if this evolutionary theory is correct, it begs the question: why are some populations much more variable than others in the first place? Increased litter size in response to increased variability requires a prior gradient in variability.

Of course, some factors could influence the evolution of litter size without regard to latitude. For instance, high variability in mortality and frequent population declines could favor greater litter size, whatever the latitude, because of the offspring of individuals with rapid reproduction could coopt more of the available resources, an argument used by Smith (1988) to explain reproductive patterns in pikas (*Ochotona* spp.). Similarly, species that inhabit temporary habitats created by disturbance likely would experience selection for high reproductive rate because production of larger numbers of dispersers would increase success in finding new suitable habitat, an explanation for the large litters of taiga voles (*Microtus xanthognathus*) by Wolf and Lidicker (1980).

Because of the variety of evolutionary possibilities and the lack of empirical information regarding the evolution of life history for specific arvicoline populations, I concentrate on functional relationships. Even so, using the argument that differences among species in the same habitat more likely reflect evolutionary differences than differences within the same species in different habitats, one might try to evaluate the role of at least some of the functional and evolutionary factors.

Variability in reproductive traits. Body size and reproductive characteristics can be linked to one another and may change with shifts in the environment, because of both phenotypic plasticity and natural selection. In his reviews of the adaptive features of mammalian reproduction Millar (1977, 1981) first cited 100, then 250 studies of mammals, including 13 species of arvicoline rodents (three from Europe). He concluded that offspring size and growth rates show relatively constant relationships with adult size, whereas litter size and time to weaning are less tightly linked to adult size and more likely to adapt to environmental conditions. Age at weaning varies only slightly and generally occurs around 15 to 20 days old in the species that we are considering, and mean litter size appears to be more variable and easier to relate to environmental conditions.

Determining a representative litter size for a population presents difficulties because arvicolines generally show an increase in litter size associated with increasing size, age, and parity of the breeding female (Keller 1985; Krebs 2013). That all three of these factors influence litter size in the same way should not be surprising because they are positively correlated; older females generally have greater body size, greater parity, and larger litters. Although, mean litter size may only increase by one in each step from juvenile to subadult to adult, such differences can lead to significantly different population growth with different population structure. Because mean litter sizes of populations are not comparable if their age structure is not similar, comparisons of litter sizes among populations can be misleading.

Different investigators report data summarized in different ways, often lumping data across age categories and seasons, which complicates comparisons among populations and species if sampling is not extensive. For instance, many studies lump a wide range of adult body sizes for a given population or species because they consider any breeding female as adult. Although female arvicolines can breed shortly after weaning, at that age they are normally considered to be juveniles. As young voles continue to grow the likelihood of breeding generally increases, as indicated by the increasing frequency of pregnancy in older females. Arvicolines have several molts as they mature, and three age/size classes can be defined after weaning by molting patterns, viz., juvenile, subadult, and adult. But even females in the adult class continue to grow, and older adult females can weigh three times more than breeding juveniles and over 50% more than young adults. Even defining adult size as the average for the adult age/size class can be misleading because mean/median body size depends on the distribution of ages within the class, and some investigators simply report a range of body sizes for adults.

Seasonal trends present another problem for comparisons of litter size. Litter size often decreases as the breeding season progresses. While this can reflect deteriorating physical or nutritional conditions, it often reflects the age structure of the population. Females breeding early in the season have survived over winter (overwintered females), and, assuming little winter breeding, are relatively mature. However, most of the breeding females late in the season are young females, the progeny of the overwintered females. When the more northern arvicolines breed under the snow, the winter breeding season may be longer than during summer, but the litter sizes are generally smaller, which likely reflects the colder temperatures and less abundant food in winter (Pitelka and Batzli 2018). Figure 2 shows an example of both the age/size and seasonal trends, in this case for the brown lemming (*Lemmus trimucronatus*) near Barrow, Alaska.

Another important influence on body size and litter size is nutrition. Studies of population dynamics and life history rarely include information on the quality of available forage. However, the diet of arvicolines shifts in different habitats as availability of preferred forage changes, and sympatric arvicoline species favor different plant species because of different abilities to tolerate secondary compounds, high fiber, and low nutrient concentrations (Batzli 1985). Thus, nutrition may often explain differences in fertility among populations of the same species in different habitats and of different species in the same habitat.

At least three studies that indicate a significant effect of nutrition on litter size in populations of the same species, and probably on reproductive potential. First, Cole and Batzli (1979) reported that two populations of prairie voles (*Microtus ochrogaster*) residing in adjacent fields, one in an old alfalfa field with abundant legumes and the other in an old pasture dominated by bluegrass, had different diets, growth rates, body weights, and litter sizes. Those in the alfalfa old field ate mostly legumes (alfalfa and clover) that had high digestible energy, protein, and mineral content, whereas those in the bluegrass old field could not maintain their weight on bluegrass alone and relied on less abundant, non-legume forbs to complete their diet. Mean litter sizes equaled 5.1 in the alfalfa oldfield and 3.7 in the bluegrass oldfield ($P < 0.001$). The litter size in bluegrass oldfield resembled estimates of mean litter size for prairie voles in oldfield grasslands at similar latitudes from Indiana (Keller and Krebs 1970) to Kansas (Fitch 1957), which varied from 3.1 to 3.6.

In California, Krohne (1980, 1982) studied two populations of *Microtus californicus* in two different habitats, one at a site dominated by perennial grasses and the other at a site dominated by annual grasses. Voles in annual grassland, where the preferred grass dried and became unpalatable from May to October, only had litters over five months during which mean litter size varied from 4.2 to 5.5. At a site dominated by less preferred perennial grasses that remained green all year round, the voles had significantly smaller litters (monthly mean litter sizes between 2.0 and 3.4 during all months except April when the mean was 5.5). When brought to the laboratory and fed the same diets mean litter sizes for voles from the two populations did not differ.

A similar pattern occurred for two populations of two brown lemming (*Lemmus trimucronatus*). In wet tundra near Barrow, Alaska the lemmings had larger mean litter size during summer than they did in drier tundra near Atquasuk, 100 km to the south. Litter sizes averaged 5.4, 6.5, and 8.0 for juveniles, subadults, and adults, respectively, at Barrow (Figure 2) and 4.3, 5.5, and 7.1, respectively, at Atquasuk (Batzli *et al.* 1980; Batzli and Jung 1980). The drier tundra at Atquasuk had little of the favorite food of lemmings at Barrow, and the lemmings primarily foraged on less-preferred plants.

Nearly all aspects of life history show variability within a population from season to season and year to year, often associated with changes in age of a cohort or changes in the density of the population (Krebs 2013). Given all this variability, how can one reliably choose the appropriate values to represent any particular population? Most previous authors seem to have chosen mean values for species or populations based upon the largest number of relevant studies that they could find, often using results based on rather small sample sizes (as low as 6). I shall set rather more stringent criteria. I required substantially larger samples ($n > 20$, most much larger, some by over an order of magnitude) taken across ages, seasons, and years with the hope that such values are more representative of the average reproducing female.

Estimation of a representative length of the breeding season can also be problematical. The breeding season can start and end quickly, but often a few females continue breeding when others have stopped. As a result a criterion such as half or more of the population in breeding condition is often used to delimit the breeding season, but determining breeding condition has its pitfalls. Live trapping studies present several lines of evidence for breeding based on the condition of females or the presence of juveniles in traps. Unless they are born in the traps, the latter requires back calculating to the birth date depending on size, and presumably age, of the young. Condition of the female also presents uncertainties. Those with a perforate vagina can breed, but do not necessarily do so successfully. The occurrence of a pregnant female provides clear evidence of breeding, but pregnancy is not always obvious from external examination. Separation of the pubic symphysis and enlargement of the teats for lactation begin shortly before the birth, but they take varying amounts of time to regress after birth. In the late stages of pregnancy the embryos can be palpated, but necropsy can detect much earlier pregnancy based upon swellings in the uterus. Even with necropsied females, however, early in pregnancy the tiny embryos cause no swelling in the uterus. As a result pregnancies can be missed during the first four to five days (about 20 to 25 % of the gestation period). Relying on the expertise of the authors, I used the occurrence of at least 35 to 40 % of females with signs of pregnancy to determine when the breeding season began or ended.

Even with the problem of determining the actual rate of breeding by females, obvious differences occur between years, usually associated with weather patterns or density of the populations (Krebs 2013). When different years showed different beginnings and ends of breeding seasons, I used mean values for the length of the breeding season.

Of course, the best set of data for calculation of reproductive potential would include the proportion of breeding females and litter size throughout the breeding season, including the differences associated with the age of the females and the age structure of the population. However, few long-term studies give such data, and I have settled for a simplified version of reproductive potential.

Population variability and geography. Most of the geographical analyses of life history have centered on two aspects of reproduction, viz, litter size and length of the breeding season. Lord (1960) reviewed the relationship of litter size to latitude in North American mammals and reported an increase of litter size in vole (*Microtus*) populations associated with increased latitude. Although he separated the analyses of different taxonomic groups, he sometimes lumped the results for multiple populations of individual species with single populations for other species, thereby introducing taxonomic bias. For instance, for meadow voles (*Microtus* spp.), three of the ten species had data for more than one population. He did find that latitude accounted for 48 % of the variability in litter size of meadow voles, but his results appeared to depend largely on very low litters sizes for two subtropical montane spe-

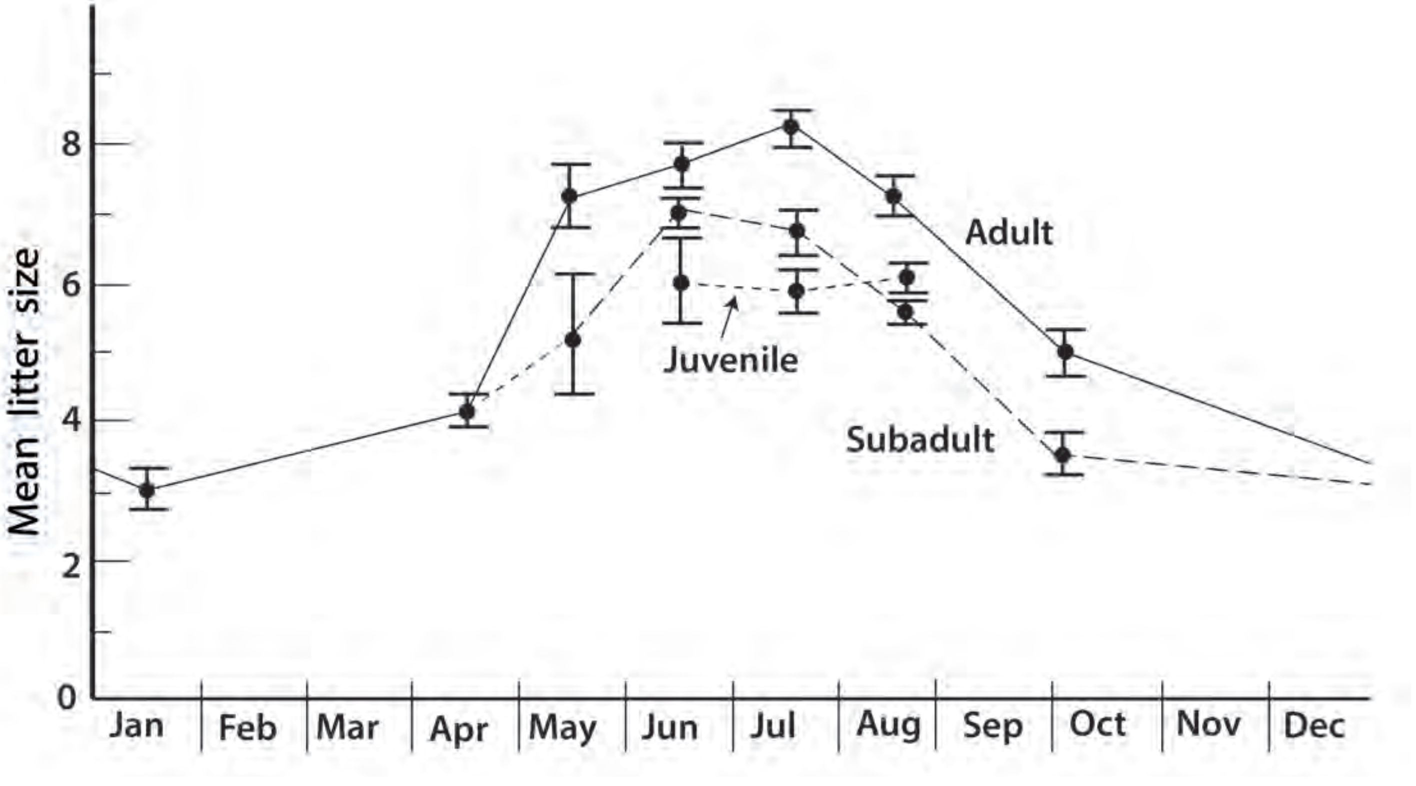

Figure 2. Mean litter size ± 1 SE for brown lemmings (*Lemmus trimucronatus*) at Barrow, Alaska in three age categories during the summer and winter breeding seasons (Batzli *et al.* 1980).

cies (20 to 25° N) and a very high litter size for one high-latitude population (60° N) of *M. pennsylvanicus*. The rest of the data referred to populations between 35-50° N and appeared scattered. Apparently Lord had no particular criteria for accepting data on litter size other than it being based on embryo counts.

Innes (1978) examined the relationships between mean litter size (embryo counts or live births with a sample size of six or greater), latitude, and elevation in the genera *Microtus* and *Clethrionomys* (now *Myodes*) in North America. Using data for 42 populations of *Microtus* distributed across 10 species (up to 18 populations in one species) and 16 populations across two species of *Myodes*. He found fairly strong positive correlations between latitude and litter size (r = 0.66 for *Microtus* and r = 0.73 for *Myodes*). Addition of elevation as an independent variable produced a bit larger correlations of 0.77 and 0.81, respectively. Using just the populations within a species produced no significant correlations within any of the four species of *Microtus* with multiple populations, but there was little variation in latitude and few replicates within a species except for *M. pennsylvanicus*. *Myodes gapperi*, which had 12 populations, did maintain a significant correlation (r = 0.65) of litter size with latitude. However, Innes discussed some deficiencies of the data set, like those I have pointed out above, and he noted inconsistencies in litter size for different species at similar latitudes. This led him to suspect the latitudinal patterns. Instead, he suggested that habitat differences (particularly resource availability) and predation regime (balanced mortality hypothesis?) more likely influenced litter size.

In 1994 Innes and Millar reviewed life history information for five species of *Myodes* and 28 species of *Microtus* using mean values for species with data for more than one population (up to 45 populations for *Myodes glareolus* and 47 for *Microtus pennsylvanicus*). Among the several correlations among traits, was one of particular interest; length of the breeding season had a significant, negative correlation with litter size even after the removal of any effect of female body weight (r = -0.46, $P < 0.01$). Since increased latitude and elevation tend to shorten breeding seasons, this could help explain any relationships of geography with litter size, although the authors again point out that because of low survival of mature females, the mean number of litters per season may not differ much.

Hansson and Henttonen (1985b) examined the relationship of litter size to variability in abundance of four widespread species of European *Myodes* (then *Clethrionomys*). They found no relationship and argued that reproductive output depended more on age at maturation, proportion of reproductive females, and length of the breeding season, all of which differ between the growth and peak phases of cyclic populations and with density in non-cyclic populations. Furthermore, the pattern of increasing variability in abundance moving along a south-to-north transect in Fennoscandia did not occur elsewhere. Later, Boonstra and Krebs (2012) reviewed long-term studies of *Myodes* in North America and found no relationship between latitude and variability in abundance. I conclude that there appears to be no consistent relationship between geography or litter size and population variability, and it seems likely that if reproductive output influences population variability, at least the length of breeding season also needs to be considered. More sophisticated estimates of reproductive potential, including age at reproductive maturation and proportion of breeding females at different times, require more data than generally available for populations with long-term estimates of relative abundance. So, I calculated the reproductive potential of a typical female based on litter size and length of the breeding season as shown below.

Calculating reproductive potential. Reproductive potential (RP) for a population can be defined as the average number of offspring that can be produced per breeding female over a year (usually one breeding season) assuming that it survives. Therefore, RP is a function of the frequency of reproduction, mean litter size, and the length of the breeding season. Because arvicolines generally have post-partum estrous and induced ovulation, I assume that females can continuously produce litters during the breeding season (a potential, even if unlikely, output). My simplifying assumption means that only two measured parameters are needed to calculate RP, viz. mean litter size (m) and length of the breeding season in weeks (b). Because the minimum time between litters is about three weeks, the maximum number of litters produced in a breeding season is b/3. As a result, RP = m(b/3). Of course, females rarely achieve this rate of reproduction in the field, but even if I assumed some standard length of time between litters, it would not change the relative difference in the number of offspring produced under different combinations of m and b.

A few more northern populations may regularly breed during winter, with hiatuses as the seasons shift before and after summer, and for those populations we need to add potential reproduction in winter to that for summer. For these populations $RP = m_s(b_s/3) + m_w(b_w/3)$.

The data set. My data set consists of information on the variability and reproductive potential (litter size and length of breeding season) for particular populations. If the reproductive potential hypothesis is correct, there should be a positive relationship between the two. For the measure of variability I use Heath's (2006) measure (H) because it does not respond as dramatically to non-normal distributions as do the two more frequently used measures, coefficient of variation and standard deviation of the log of abundance. $H = (S(x_i - x_j/x_i))/n$ where x_i is the larger and x_j the smaller value for all possible pairs of estimates of abundance, and n is the number of different pairs. Thus, H is the mean of relative differences in abundance across all possible pairs.

I only used data for populations for which there were consistent annual estimates of relative abundance (number captured per unit effort) or absolute density (number per hectare) during the same season and which had been followed at the same site for at least 10 years so that more representative expressions of variability occurred. For populations that were sampled repeatedly during each year, I used a single estimate for the season with the highest densities (sometimes spring and sometimes fall). In addition, I needed estimates of litter size and length of breeding season for that population, or one in a similar habitat at a similar latitude, to calculate RP. Because these life history data vary from year to year and with other factors as discussed above, I used mean values across years, seasons, and demographic categories. Not surprisingly, nearly all data were for the two genera of voles that are most widespread in North America (*Myodes* and *Microtus*).

Results and Discussion

Overall pattern. Using the data in Table 1 with one entry for a site where a species has two populations (that with more typical habitat), the relationships between litter size, breeding season, and latitude produced mixed results. Litter size tended to increase with latitude (r = 0.706, *n* = 17, *P* = 0.002), length of breeding season tended to decrease with latitude (r = - 0.661, *n* = 14, *P* = 0.010), and litter size tended to increase with decreased length of breeding season (r = - 0.796, *n* = 13, *P* = 0.001). Thus, my data supported a positive relationship between latitude and litter size, contrary to some earlier studies, but agreed with earlier studies that supported a negative relationship between litter size and latitude. I do not claim that my results for latitude and litter size are definitive, however, because I only looked at populations that had at least 10 years of data on relative abundance. Consistent with previous studies, I found no relationship between litter size and variability in abundance (r = 0.079, *n* = 16, *P* = 0.771).

The variability in abundance of arvicoline populations in this study ranged from a low of H = 0.327 for *Microtus breweri* to a high of H = 0.744 for *Lemmus trimucronatus*, a greater than two-fold difference (Table 1). These populations also had reproductive potentials at the top (RP = 58 for *L. t.*) and bottom of the scale (RP = 27 for *M. b.*), again over a two-fold difference. I was unable to complete the table for all of the populations for which I found data that met my criteria for calculation of variability because of missing data required for the calculation of reproductive potential (mostly on length of the breeding season). Nevertheless, the data for the 16 populations indicated substantial differences among populations within the same species. For instance, the variability of four populations of *Myodes gapperi* that occurred in coniferous forest at latitudes from 48 to 61° N had H = 0.409-0.524, the largest almost 30 % greater than the smallest, and the four populations at latitudes from 40 to 45° N in mixed hardwood/conifer or hardwood forests had H = 0.447-0.726, the largest over 60 % greater than the smallest. The population of *M. gapperi* studied by Fryxell *et al.* (1998) occurred in a variety of forests from all hardwoods to a mixed forest to all conifers, and so was not comparable. For *Microtus ochrogaster*, a population in grassy oldfield in Illinois had a variability (H = 0.726) over 30 % greater than a population in grassy oldfield in Kansas (H = 0.548).

Given the lack of consistency within and among species, it comes as little surprise that only a small positive correlation between H and RP occurred among all 16 populations (r = 0.291, *P* = 0.274). This provided little support for the RP hypothesis, which predicts increasing variability with increasing reproductive potential.

Intraspecific comparisons. The study of Cole and Batzli (1979) on the influence of nutrition on local populations of the prairie vole (*M. ochrogaster*) in central Illinois provided the data necessary to calculate reproductive potential and population variability for local populations in alfalfa old field (higher quality diet) and bluegrass old field (lower quality diet). Over the five years of their study, the voles in alfalfa had a 38 % larger mean litter size than those in bluegrass (5.1 and 3.7, respectively) and 43 % greater reproductive potential (RP = 60 and 42, respectively). The populations had synchronous populations cycles, but, as mentioned above, the population in alfalfa reached peak densities that were twice those in bluegrass. We did not evaluate the population in tallgrass prairie, which had much lower densities. Meadow voles (*M. pennsylvanicus*) invaded the bluegrass habitat in 1975 and the alfalfa habitat in 1976. After that the population dynamics of the prairie vole became somewhat different, populations appeared to have double peaks that occurred over two successive growing seasons. Nevertheless, over a 25-year span both populations of prairie voles had H = 0.726, a remarkable coincidence (Table 1). These results did not support the RP hypothesis.

Getz *et al.* (2001) also reported on long-term data the meadow vole (*M. pennsylvanicus)* at the same sites as for prairie voles. Meadow voles generally occurred in much lower densities in alfalfa, so I only compare populations in bluegrass oldfield and tallgrass prairie. Over the years the trapping sites in tallgrass shifted among locations that were separated by a road and about 500 meters of oldfield and second-growth forest, and I only analyzed the data for the 10 successive years during which trapping in tallgrass occurred at the same location. Meadow voles showed a greater preference for monocots than did prairie voles (DeJaco and Batzli 2013), and the quality of the meadow vole diet probably did not differ much between the two habitat types. I therefore assumed that the litter sizes did not differ either, in which case their reproductive potentials would be equal. Given this assumption, the very similar variability of populations in the two habitats (H = 0.495 for tallgrass and H = 0.468 for bluegrass, the former only 6 % higher) supported the RP hypothesis. Although the meadow vole populations did not appear to cycle, densities in the tallgrass averaged about twice those in the bluegrass, in this case apparently reflecting greater cover and survival rather than higher quality food and reproduction (Getz *et al.* 2001).

Mihok *et al.* (1985b) monitored the meadow vole in old-field grasslands by live trapping and snap trapping in Manitoba, Canada. Although the authors do not present separate data on litter size for the two populations, they occurred in similar habitats (grassy old fields) at the same site, and it seems reasonable to assume that their reproductive potential would be similar. Nevertheless the populations had rather different variability; snap trapping (H = 0.733) produced 20 % higher variability than did live trapping (H = 0.610). Again, these results do not support the RP hypothesis, and they raise questions about how differences in local populations in similar habitats and differences in technique influence measurements of variability.

Although separated by hundreds of miles, the populations of *M. ochrogaster* in grassy oldfields in Illinois and Kansas occured in similar habitats at similar latitudes (Table 1). Reproductive potential was higher in Illinois (RP = 43) than in Kansas (RP = 33), and in agreement with the RP hypothesis, population variability followed the same pattern (H = 0.726 in Illinois and H = 0.548 in Kansas). A similar long-distance comparison of *M. gapperi* populations in coniferous forests, again separated by hundreds of miles but at different latitudes (50° N and 61° N) produced the opposite result, higher reproductive potential but lower variability at 50° N (Table 1). So three of five intraspecific comparisons did not support for the RP hypothesis.

Interspecific comparisons. Comparison of two species of *Microtus* in the same habitat over the same time period, bluegrass old fields in central Illinois (Table 1), showed that the species with greater reproductive potential (RP = 52 for *M. pennsylvanicus* and RP = 43 for *M. ochrogaster*) had less population variability (H = 0.468 for *M. pennsylvanicus* and H = 0.726 for *M. ochrogaster*). A second comparison of two species at the same site but different habitats (*M. pennsylvanicus* in grassy old fields and *Myodes gapperi* in coniferous forest in southern Manitoba) produced a similar pattern. Although *M. pennsylvanicus* (RP = 29) had a lower reproductive potential than *M. gapperi* (RP = 44), it had much

Table 1. Location, variability in abundance, litter size, length of breeding season, and reproductive potential for North American arvicoline rodents with long-term data on variability in abundance.

Species	**Location (state or province)**	**Latitude (ºN)**	**No. of Years[1]**	**Variability (H[2])**	**Mean Litter Size**	**Breeding (wks.)**	**Reproductive Potential[3]**	**References**
Lemmus trimucronatus	Alaska	71	22	0.744	7.4/3.0*	13/26	58	Pitelka 1973, Pitelka and Batzli 2018
Microtus breweri	Massachusetts	41	15	0.327	3.4	24	27	Tamarin *et al.* 1987, Tamarin 1977 a, b
M. californicus	California	40	11	0.434	5	26	43	Lidicker 1973
M. ochrogaster	Illinois - alfalfa	40	25	0.726	5.1	35	59	Getz *et al.* 2001, Cole and Batzli 1979
	Illinois - bluegrass	40	25	0.726	3.7	35	43	Getz *et. al.* 2001, Cole and Batzli 1979
	Kansas	39	22	0.548	3.4	29	33	Brady and Slade 2004, Fitch 1957, Fitch *et al.* 1984
M. montanus	B. Columbia	51	15	0.647	?	24	?	Sullivan *et al.* 2021
	Wyoming	44	16	0.626	6.3	18	38	Pinter 1986, Negus *et al.* 1977
M. pennsylvanicus	Illinois - tallgrass	40	10	0.495	4.5	35	52	Getz *et al.* 2001, Keller and Krebs 1970
	Illinois - bluegrass	40	10	0.468	4.5	35	52	Getz *et al.* 2001, Keller and Krebs 1970
	Manitoba - live	50	11	0.61	3.8	23	29	Mihok 1984, Iverson and Turner 1976
	Manitoba - snap	50	14	0.733	3.8	23	29	Mihok *et al.* 1985, Iverson and Turner
Myodes californicus	Oregon	44	12	0.655	2.6	34	29	Gashwiler 1970, 1977
M. gapperi	NWT	61	11	0.437	5.6	15	28	Fuller 1969, 1985
	B. Columbia	50	21	0.498	?	?	?	Sullivan *et al.* 2017
	Manitoba	50	14	0.409	6	22	44	Mihok *et al.* 1985a, 1985b; Perrin 1979
	Ontario	48	43	0.529	?	?	?	Fryxell *et al.* 1998
	Minnesota	48	13	0.524	6.1	?	?	Krefting and Ahlgren 1974, Beer *et al.* 1957
	Quebec	45	11	0.726	4.6	?	?	Grant 1976, Wrigley 1969
	Maine	44	22	0.447	4.3	?	?	Elias *et al.* 2006, Patric 1962
	Vermont	44	16	0.694	4.3	?	?	Brooks *et al.* 1998, Patric 1962
	Pennsylvania	40	21	0.494	4.3	?	?	Merritt *et al.* 2001, Gifford and
M. rutilus	Northwest Territories	61	11	0.519	5.7	15	28	Fuller 1969, Fuller 1985, Martell and Fuller 1979
	Yukon	61	23	0.582	6.2	18	37	Boonstra and Krebs 2006, Gilbert and Krebs 1991, Krebs and Wingate 1985

[1] Number of successive annual estimates of relative abundance.

[2] Heath's measure of variability of abundance (see text).

[3] Estimated length of breeding season.

higher variability (H = 0.610-0.733 and H = 0.409, respectively). Fuller (1969, 1985) compared two parapatric species of *Myodes* at the same latitude in taiga, and reported very similar reproductive parameters (RP = 28 for both species) but about 20 % greater variability in *M. rutilus* (H = 0.519) than in *M. gapperi* (H = 0.437). Thus, none of these three interspecific comparisons support the RP hypothesis.

Maximum abundance and reproductive potential. Earlier I cited three cases that suggested an impact of local food availability on litter sizes of arvicoline rodents by comparing populations of the same species in different habitats. *Lemmus trimucronatus* at Atquasuk had a mean litter size of 6.3 in summer about 85 % of the 7.4 for Barrow, and assuming similar winter and summer breeding seasons at the two sites, RP = 49 at Atquasuk compared to RP = 58 at Barrow. Maximum densities at Barrow were two to three-fold greater than those at Atquasuk (Pitelka and Batzli 1993).

In Illinois the reproductive potential for *Microtus ochrogaster* in an alfalfa oldfield (RP = 59 was 37 % greater than in a grassy oldfield (RP = 43), and maximum densities in alfalfa were about two-fold greater (Getz *et al.* 2001). Krohne (1980, 1982) also found greater densities in the habitat with greater reproductive potential. In this case *Microtus californicus* in annual grassland (RP = 45), with a mean litter size of 5.2 and a breeding season of 26 weeks, had greater reproductive potential than in perennial grassland (RP = 37) where it had a mean litter size of 2.9 and a breeding season of 38 weeks. Surveys of runway densities, which were loosely correlated with live trapping results, indicated five-fold greater maximum densities in annual grassland. Thus, although increased reproductive potential alone may not cause increased population variability, it may influence the maximum densities of populations, which opens up a new line of inquiry.

My review of literature and analysis of the data in Table 1 appears to refute the RP hypothesis, and I conclude that no simple relationship exists between variability in abundance of arvicoline rodents and either litter size or reproductive potential. Clearly, other factors must be involved in producing the observed patterns, either those influencing reproductive success (such as variability in the proportion of breeding females, the age at first reproduction, or in the length of the breeding season in response to physical conditions, food supply, and/or population density) or those influencing survival/dispersal (such as changes in physical conditions, food supply, density of the arvicolines, and/or density of their enemies). Indeed some might argue that in light of complex temporal variation in the population dynamics of arvicolines, it's rather naive to expect simple causal relationships.

Of course, my results might differ if all the studies had been based on simultaneous monitoring of abundance and reproduction done at the same season and over the same time interval, but even then the idiosyncrasies of population fluctuations can make the characterization of their variability difficult. Most populations seem to go through sustained periods of unusual densities, either high or low, so measurement of variability for any given population depends in part on the span of years the investigator chooses to document. For instance, in the longest record of abundance in Table 1, the 43 years of observations on *M. gapperi* reported by Fryxell *et al.* (1998), four of the five highest abundances in the whole series came in the last four years of observation. With little difference in minimum abundances, this resulted in H = 0.435 for the first 22 years, and almost a 40 % increase to H = 0.605 for the last 21 years. Still, one possible generalization comes out of this analysis and deserves further study, viz., populations with greater reproductive potential tend to reach higher maximum densities. This generalization, based upon data from natural populations, agrees with experimental results, which show that the reproductive output and density of vole populations increase with improved availability of nutrients (Cole and Batzli 1978; Desy and Batzli 1989; Forbes *et al.* 2014).

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Importance of demography in understanding disease ecology in small mammals

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Small rodents are increasingly used as model animals in disease ecological research. However, many students in the field have an inadequate knowledge of the significance of demographic heterogeneity of reservoir rodent populations and how that affects infection parameters. I summarize here some of the common problems and give a solution, the use of the concept of *functional groups*, to gain more detailed information and avoid common mistakes (*e. g.*, by drawing conclusion from pooled population samples). I emphasize the importance of seasonality and demography (roles of various population functional subgroups) for parasite/pathogen studies and sampling design to cover the essential components of populations.

Los pequeños roedores se emplean cada vez más como animales modelo en la investigación ecológica de enfermedades. Sin embargo, muchos estudiantes en el campo tienen un conocimiento inadecuado de la importancia de la heterogeneidad demográfica de las poblaciones de roedores reservorios y cómo eso afecta los parámetros de infección. Resumo aquí algunos de los problemas comunes y doy una solución, el uso del concepto de grupos funcionales, para obtener información más detallada y evitar errores comunes (*e. g.*, extrayendo conclusiones de muestras de población agrupadas). Enfatizo la importancia de la estacionalidad y la demografía (roles de varios subgrupos funcionales de población) para los estudios de parásitos / patógenos y el diseño de muestreo para cubrir los componentes esenciales de las poblaciones.

Keywords: Demography; disease ecology; functional groups; pathogens/parasites; reservoir population structure.

Introduction

Small rodents are extensively used in ecoepidemiological research ("disease ecology") by people who are not adequately familiar with the ecology and dynamics of the reservoir host populations. This can and has led in the past to misinterpretations of data and hence erroneous conclusions. Small rodent populations, or generally small mammal populations, are by no means homogenous groups. On the contrary, they are heterogeneous, and this heterogeneity changes seasonally, multiannually, and density- and/or phase-dependently. Many infection parameters and processes are related to the dynamics of the functional groups in the populations, *i. e.*, subgroups that differ physiologically, behaviorally, and immunologically. Understanding host population structure and its varying demographic heterogeneity is a key factor in disease ecology, enabling more detailed analyses and drawing of realistic conclusions. In this commentary I will show why it is important to understand this dynamic heterogeneity. My conclusions are mostly based on our studies in high-latitude systems, but no doubt the conclusions can be applied to small rodents in other systems, and for other small mammal taxa as well.

What is a functional group? The idea of the functional group (functional category) as a behavioral/physiological population subunit was introduced to the small mammal literature by Myllymäki (1977a, b). This concept has subsequently been expanded to pathogen/parasite research, *e. g.*, by Haukisalmi *et al.* (1988, 1995), Haukisalmi and Henttonen (2000), and Cattadori *et al.* (2005). The basic idea as it relates to parasite/pathogen research is the division of a small mammal population into subgroups that are behaviorally, physiologically, and immunologically uniform. A particularly important attribute of this concept is that it is dynamic: population structure changes seasonally, multiannually, and density- and phase-dependently. When making comparisons over season and years, functional groups are the level at which parasite/pathogen comparisons should be made among host populations.

In small mammal populations, *juveniles* have two alternatives after they leave the natal nest (Figure 1). They can either mature immediately, with females in some species becoming pregnant at the age 3-4 weeks, or they can delay maturation and breeding to the next summer (*e. g.*, Prévot-Julliard *et al.* 1999). The use of the words summer and winter are here equivalent with other breeding / nonbreeding seasons in other biomes. If juveniles mature immediately, they become *young breeding adults,* either males or females. If juveniles delay maturation, mostly due to late season or high density, they become *subadults*. These animals do not breed, they are clearly smaller than breeding adults, and most importantly, with respect to behavior and physiological immunology, they are "sexless", and tolerated by breeding animals. Usually subadult males and females do not differ in parasite/pathogen infection values, unlike breeding adults either young or old. After overwintering, subadults mature in spring, males earlier than females, and they become *old breeding adults,* males and females. Maturation of subadults affects

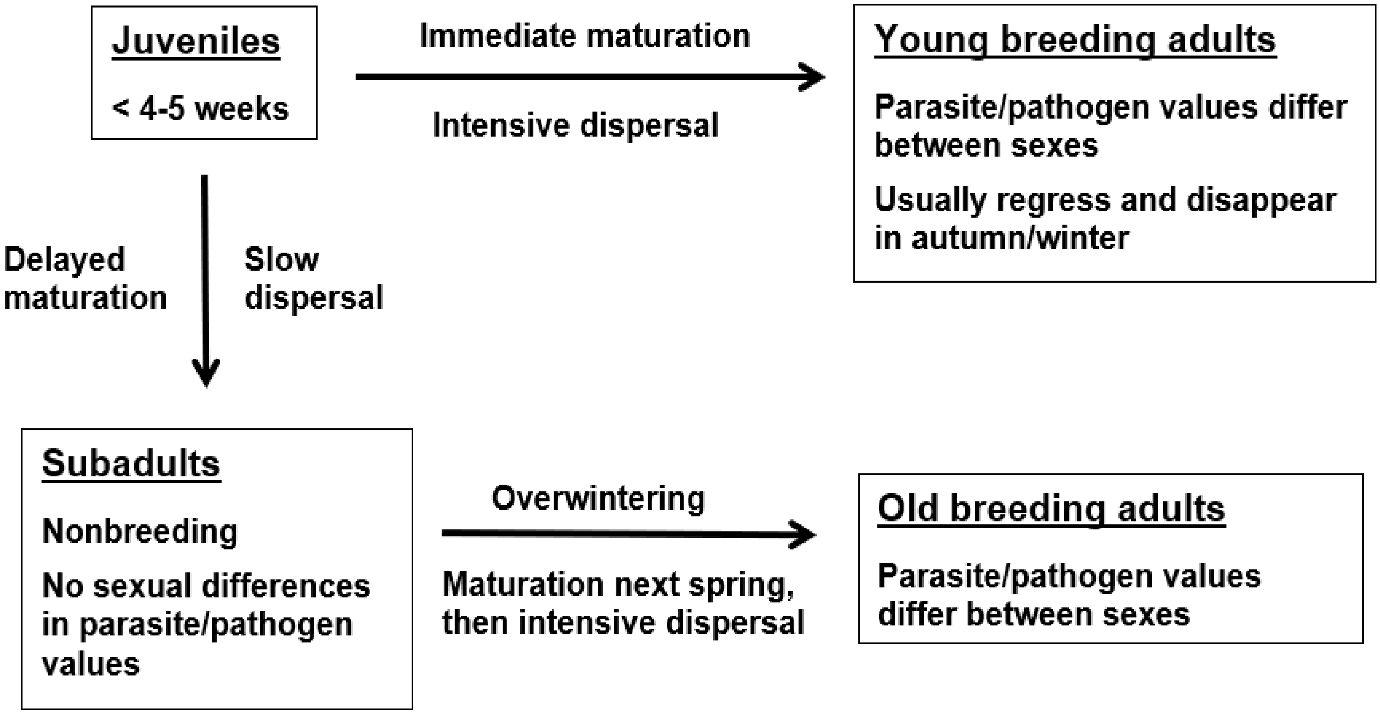

Figure 1. Alternatives for seasonal development in small rodent populations.

their behavior, physiology, and immunology, and leads rapidly to sexual differences in parasite/pathogen values characteristic of those of adults.

It is essential to understand that the functional group is not the equivalent of age. For example, young breeding adults in early autumn can be two months old (and potentially have parasite/pathogen infection values resembling those of overwintered adult breeding animals), but subadults who have delayed their breeding can be eight months old in late winter and still have parasite/pathogen values typical of a nonbreeding animal, with no differences between sexes. Parasite/pathogen infection values are often more closely associated with the functional group of an individual than its absolute age. Still, within a functional group like subadults from autumn to spring, levels of infection with parasites and pathogens can increase with time and age, but without differences between sexes (*e. g.*, for the bank vole and *Puumala orthohantavirus*, see Voutilainen *et al.* 2016).

The seasonality of these events can occasionally vary, for example during phase-, climate- or mast-induced bouts of winter breeding in some rodent species (Tersago *et al.* 2009). Nonetheless, the parasite/pathogen patterns related to functional groups remain.

How to identify functional groups. Defining the functional group is based on the combination of breeding status and age. More detailed information is usually achieved at animal dissection, but many of the aging and breeding parameters can be seen externally in live animals, which helps in categorizing animals without a need to sacrifice them. There are several methods of age determination for small mammals (see *e. g.*, Morris 1972), albeit nowadays often poorly known among modern digital ecologists, and still less known among medical people. Weight is often used as a proxy for age, but weight depends on maturation and breeding status which are density- and phase-dependent.

I detail some aging methods below. Different rodent genera differ with respect to the most appropriate aging methods. Several methods can be used for *Myodes* voles, including growth patterns of molar roots (Tupikova *et al.* 1968; Lowe 1971; Viitala 1971), and pelage (fur) growth patterns (molting) that can be used in live-trapping studies (Zejda and Mazák 1965; Viitala 1981). The fur growth analysis is not very precise for young breeding females over 1.5 to 2 months of age because the energy allocation to pregnancy and lactation delays molting, but it is usable in differentiating juveniles (< 4 weeks) from older animals in summer, and summer-born adults from overwintered adults in late summer – autumn, which is practical in live-trapping. Eye lens development has been used for *Myodes* (Kozakiewicz 1976; Takahashi and Satoh 1997) and also for *Lemmus, Microtus,* and *Apodemus* (Östbye and Semb-Johansson 1970; Adamczewska-Andrzejewska 1971; Hagen *et al.* 1980). Muskrats also have growing molar roots (Pankakoski 1980), whereas *Microtus* and *Lemmus* species have continuously growing ("rootless") molars that cannot be used for age determination, and therefore their age determination must be based on fur growth patterns (Sýkora 1960; Koponen 1970) or eye lens development. *Apodemus* mice can be divided into age groups using, *e. g.*, molar wear (Adamczewska-Andrzejewska 1972).

My own 50-year experience is that methods based on external characters used in live-trapping studies usually work well enough for basic definition of functional groups, though some experience is needed. The problem now seems to be that many scientists do not even know that such methods exist. If animals are sacrificed for tissue sampling and museum specimen preparation, then more detailed information can easily be collected.

The distinction between juveniles and subadults or maturing young adults is rather easy using hair growth patterns. Young rodents have dull thin fur until the age of four weeks and thereafter start to grow their second fur (called, depending on the genus, post-juvenile fur or adult 1 fur). This is externally visible first as new short silky hairs emerging from the skin, first on the ventral side and later on the dorsal side, lasting about two weeks, during weeks 5 to 6 of age. These patterns are visible on the inside of the skin as black pigment figuration. The new emerging fur is eventually clearly longer than the original juvenile fur.

In early summer and/or early in the increase phase of a population cycle the distinction between juveniles and young adults, which then mature and grow quickly, is occasionally more difficult because juveniles can start to sexually mature while still having juvenile fur, *i. e.* even if still having the juvenile fur and being < 4 weeks old, but their behavior changes to that of a breeding type.

The behavior of young small rodent males changes when their testicles reach a length of 5 to 7 mm and they disperse. This coincides with a change in the behavior of adult males towards young maturing males, expelling them from natal sites. Depending on the genus, the same change can occur in young females when the vagina opens. In *Myodes* species, breeding females have exclusive territories, and maturing young females have to disperse whereas in *Microtus* young maturing females can stay in home ranges overlapping those of their mothers. If the maturation is delayed, young subadults can stay at their natal home ranges. Subadults are not territorial and do not induce territorial behavior in adults, and they can usually stay at their natal sites on overlapping home ranges.

Spring maturation is accompanied with intensive dispersal because territories/home ranges of adults are clearly larger than home ranges of subadults. This spring dispersal, which in boreal conditions may already begin under snow, is often forgotten in models analyzing density-dependent dispersal because it takes place before the "summer" field season.

Young maturing voles can be teenager-type runners for a week or two, and depending on the genus and space available, thereafter settle down as breeding adults. These behavioral changes can occur when voles are three weeks old or after overwintering half a year later. Later in summer, live-trapped young and old adults can be distinguished by fur length, or dead animals by molar and fur patterns. When subadults mature in spring, they grow and enter breeding condition, which can be seen externally also in live animals.

Examples of common errors. Seasonality. Many parasite/pathogen values have a seasonal pattern. Prevalence can increase with age. Prevalence is typically low in late summer – early autumn, but can approach 100% in old animals in the next summer (Voutilainen *et al.* 2016). If geographic comparisons are made on the basis of samples collected in different seasons, potential differences are possibly due to seasonality and different age structures, not due to geography or other causes. This is a common, elementary mistake.

Some opportunistic parasites infect only old overwintered voles in their second summer when they are soon to disappear from the host populations (Haukisalmi *et al.* 1988). The proportion of this host functional group in the whole population can be only 5 %, but more than 50 % of these voles are infected. This period in late summer is rather short. Unless there is a concentrated effort on this specific functional group in a specific season, these opportunistic parasites would be missed, or considered rare at the whole population level, leading to a misinterpretation of their role. It is rare to find these parasites in other functional groups. For example, knowing that certain parasite taxa may almost solely occur in old overwintered animals in late summer, researchers must plan the sampling time to detect occurrence in these individuals.

Sampling. Instead of one pooled sample for parasite/pathogen studies, sampling should be designed so that main functional groups with their specific infection values are adequately represented. This, by necessity, increases the total sample size. It may even require extra effort to sample a functional group with low density. Indeed, if one thinks that, *e. g.*, 50 rodents is a good sample, these thoughts may dissipate when this 50 is divided into functional groups: one rodent in the first group, two in a second, 47 in the third, and zero in the fourth.

Population structure. Even if samples are collected in the same season, erroneous conclusions are easily drawn without considering population structure. The same applies to experimental manipulations. Let's take a simple example (Table 1). We can have two different years, or a simultaneous experimental manipulation and its control. The populations to be compared consist of old overwintered individuals and subadults. Total densities are the same in the two populations, but there is a clear difference in population structure. Both functional groups have their specific

Table1. An example of how a parasite/pathogen analysis can give different results depending if it is based on pooled samples or functional groups. Pooled samples seem to suggest a difference between treatments, but it is only because of the different age structures. There is no difference between functional groups, *i. e.* at the individual level. Overwintered (OW), subadults (SUB).

	Control		**Experimental**	
	OW	**SUB**	**OW**	**SUB**
Number of individuals	20	60	60	20
Prevalence/functional group	15.0%	5.0%	15.0%	5.0%
Population mean prevalence	16.3%		38.8%	

parasite/pathogen prevalence, which is the same in experimental and control groups. The common way to analyze this kind of material is to clump all animals together and estimate one prevalence value for the whole population, which in this case seems to suggest that parasite/pathogen prevalence is greater in the experimental group. However, if one analyzes the data per functional group, there is no change in parasite/pathogen prevalence within functional groups, *i. e.* at the individual level. The only thing that has changed is the proportion of functional groups in the sample, not the parasite/pathogen prevalence per functional group. The correct conclusion might be that the manipulation increased the abundance of old animals, but did not affect parasite/pathogen prevalence at the individual level. Or this kind of result could be a typical phase-dependent impact on the population structure between cyclic increase and peak years.

We encounter the same problem when the age of animals is based on proxies, not on real age determination. It is common to use weight as a proxy for age. Weight is sufficient to separate subadult and breeding rodents in late summer – autumn. However, as clarified above, there are two types of adults in late summer - autumn populations of small rodents: young adults born earlier the same summer, and old overwintered animals. They are all breeding adults, above some weight limit, but the young adults typically are 2 to 3 months old, and the overwintered ones are 12 to 14 months old. For example, in cyclic vole populations, adults in the autumn of the increase phase are mostly young individuals due to rapid maturation, while in the peak phase the proportion of old ones is much higher due to the delayed maturation of young animals at high densities (Prévot-Julliard *et al.* 1999). If the functional groups (and real age) have been properly identified, this age difference can have a drastic impact on parasite/pathogen values of young and old adults. If the "age" determination of these adults is based only on a proxy like weight and age groups are pooled, then, *e. g.*, phase-dependent effects on the real parasite/pathogen values in different adult functional groups remain unknown.

Parasite/pathogen infection values can be sensitive to further structuring within young and old adults. Haukisalmi *et al.* (1995) analyzed parasite prevalences in breeding females of two sympatric vole species. Young adults differed from old ones, but prevalences also depended on whether females were pregnant and lactating, or only lactating. In addition, these differences were opposite in young and old females, and they were opposite between species.

Toxicological studies. Understanding population structure is also important in toxicological studies, where pooled population samples are commonly used. A pooled sample can include animals of very different ages, *e. g.* from 1 mo to 16 mo, and depending on the cyclic phase, one sample can be dominated by young animals, another one by old animals. Toxin accumulation certainly depends on age. Still, even though young non-breeding subadults and breeding adults are separated (which is seldom done), the problem of young and old adults remains. In short-lived animals, a difference in age from 2 to 4 mo to 14 to 16 mo makes a difference for accumulation of toxins.

Organ weight. Organ weights, like those of spleen, liver, etc., have often been used as proxies for stress, disease, toxins, and evolutionary processes. However, organ weight does not have a linear relation to animal body size or weight, and there can be abrupt and large differences between functional groups. Therefore, analyses of pooled samples of organ weights without reference to population structure may result in something that depends more on the hidden sample structure than on the biological phenomena being studied.

Season of study. Many, if not most field studies, are performed in "summer" time. Small rodent populations are at that time characterized by intensive breeding and by the presence of all functional groups. However, it is often forgotten that "summer" may comprise only 1/3 of the year, and still most hypotheses on parasite/pathogen transmission are derived from this limited period. These ideas are not wrong as such, but they may not be applicable for periods outside of the breeding season when the population structure is different, *e. g.* during winter when breeding adults are not usually present. The idea that old males with high testosterone values are responsible for most of the parasite/pathogen transmission in the population is popular. But if old males are present in the population only for 1/3 of the year, what happens during the other 2/3 of the year? In addition, seasonality and photoperiod have strong impacts on immunity.

Transmission route of pathogens depends on the functional group. During the breeding season, adult males can be territorial and aggressive, and transmission via biting can be common. Breeding males also are more active and move over larger areas. On the other hand, overwintering subadults are docile, and obviously most transmission in the nonbreeding season takes place indirectly via the environment, as suggested for *Puumala orthohantavirus* (Voutilainen *et al.* 2016).

Dilution. The impact of biodiversity on zoonotic diseases is a rapidly developing field (for a recent review, see Keesing and Ostfeld 2021). Dilution impact is often considered in this context. Transmission routes depend on the behavior of functional groups, and their occurrence is strongly seasonal. Treating the whole population as a homogeneous unit throughout the seasons will lead to omission of important aspects of seasonality in population structure and behavior. Not many studies on direct dilution effects have taken this into consideration. However, Voutilainen *et al.* (2012) analyzed the transmission of *Puumala orthohantavirus* in bank voles in a multispecies small mammal community separately in spring (all voles and shrews were breeding overwintered individuals) and autumn (mostly non-breeding subadults). They found that dilution impact was clear in spring populations consisting of breeding territorial voles and shrews, while in autumn in nonbreeding, non-territorial populations dilution was not observed.

Dispersal. Dispersal in small mammal populations is commonly observed, and has attracted a lot of attention (for reviews, see *e. g.*, Anderson 1989; Lidicker 1995; Bjørnstadt *et al.* 1999; Krebs 2013). Dispersal is strongly seasonal and related to the functional groups; dispersers are not just random subsets of the population. Understanding the roles of dispersing subunits of the population and their potential in parasite/pathogen spread adds to our understanding of relevant patterns in disease ecology. This is relevant for dispersal of rodent-borne zoonotic pathogens, and can be used to predict risk periods, *e. g.*, for rodent-borne pathogens. Dubois *et al.* (2017) and Razzauti *et al.* (2013) analyzed the dispersal of bank voles and *Puumala orthohantavirus* using genetic markers. There are three periods of intensive dispersal: 1) during the maturation and territorial formation in spring when the hantavirus prevalence is approaching its seasonal peak in old overwintered voles, though densities can be rather low at this time; 2) in early – mid summer when maturing young voles disperse from the territories/home ranges of their parents, but at this time virus prevalence in young animals is low, and this event is phase-dependent; and 3) in late autumn with freezing temperatures when subadult bank voles look for overwintering habitats and commonly enter human settlements – and this is the main human epidemic season at high latitudes.

Much more understanding would be gained if disease ecological studies on rodents were based on proper characterization of the dynamic heterogeneity of reservoir populations and identifying the population subunits relevant for the maintenance and spread of zoonotic parasites and pathogens. Using the concept of *functional groups* is a natural way to deal with population subgroups with distinctive physiological, immunological, and behavioral characteristics. Understanding the dynamic demographical background of parasite/pathogen infections and transmission would reduce noise in conclusions and help to avoid misinterpretations stemming from the pooling of materials.

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The ecology of infectious diseases: an homage to multi-factor perspectives

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Decades ago, a multi-factor perspective offered valuable insights into the causes of population cycles in arvicoline (= microtine) rodents. Multi-factor perspectives are also critical for understanding the ecology of infectious diseases. Here, we provide examples of how these perspectives inform our ability to predict variation in disease risk through space and time. We focus in particular on the evidence that many emerging zoonotic pathogens of humans have multiple hosts rather than just one, that most host species harbor more than one pathogen and that these pathogens interact, and that understanding variation in the abundance of species that transmit pathogens often requires deep exploration of the ecological community in which those hosts are embedded.

Hace décadas, una perspectiva de múltiples factores ofreció información valiosa sobre las causas de los ciclos de población en roedores arvicolidos (= microtine). Las perspectivas multifactoriales también son fundamentales para comprender la ecología de las enfermedades infecciosas. Se proporcionan ejemplos de cómo estas perspectivas dan información a nuestra capacidad para predecir la variación en el riesgo de enfermedad a través del espacio y el tiempo. Nos enfocamos en particular en la evidencia de que muchos patógenos zoonóticos emergentes de humanos tienen múltiples hospedadores en lugar de uno solo, que la mayoría de las especies hospedantes albergan más de un patógeno y que estos patógenos interactúan. Comprender la variación en la abundancia de especies que transmiten patógenos a menudo requiere una exploración profunda de la comunidad ecológica en la que están incrustados esos hospederos.

Keywords: Disease ecology; emerging infectious diseases; multifactor perspective; rodent; small mammal; zoonosis.

Introduction

In the 1980s, Bill Lidicker proposed conceptual models to explain the semi-regular population fluctuations (aka cycles) of arvicoline (= microtine) rodents. These models invoked several potential drivers that were extrinsic to the voles themselves, including landscape structure, food supply, and predation, as well as several that were intrinsic, including aggressive behavior, dispersal dynamics, and physiological stress. He called his approach a multi-factor perspective (Lidicker 1988), and predicted that the extrinsic and intrinsic factors he invoked would vary in strength, or even appear and disappear, at different times, both seasonally and between years. The factors were also expected to interact. For instance, variation in aggressive behavior might cause changes in dispersal rates, the effects of which would depend on landscape structure (*e. g.*, the ratio of optimal to marginal patch area, or ROMPA; Lidicker 2000). Lidicker's goal was to explain a type of pattern – population fluctuations with two to five years between peaks – that varies in its specific manifestations both within and between species. The pattern of population fluctuations can vary in magnitude and timing of peaks, as well as the rate of population growth and decline. Thus, his conceptualization of the problem was holistic, in the sense that he defined "cycles" as complex and varying phenomena, and his approach to addressing the problem was also holistic, in the sense that he saw specific mechanisms interacting in complex, hierarchical ways (Lidicker 1988).

Lidicker's approach was criticized by researchers who saw arvicoline cycles as a homogeneous phenomenon rather than a variable but recognizable pattern (Gaines *et al.* 1991; Lidicker 1991). Critics with a simpler, more unitary definition of the problem developed hypotheses in which a single factor (*e. g.,* heritable aggression or specialist predators) by itself explained cycles. Such a focus was more reductionist, and usually neglected the interactions between variables. Hypotheses arising from single-factor, reductionist approaches are simpler, more tractable experimentally, and appealing for many researchers. Although critics were vociferous in the 1980s and 1990s, by the 2000s most research on arvicoline cycles incorporated multi-factor, holistic perspectives (Krebs 2013).

We were both Ph. D. students under Lidicker's guidance, Ostfeld in the 1980s and Keesing in the 1990s. Although we have both focused on the ecology of small mammals, we have paid less attention to the causes of fluctuations in population size and more attention to the consequences of those fluctuations for other ecological phenomena. Changes in the abundance of small mammals through time or across space often affect the transmission of the pathogens and parasites of those mammals. Rodents in particular are important hosts for zoonotic pathogens, those that vertebrate animals share with humans (Keesing and Ostfeld 2021).

Infectious disease ecology has its roots firmly anchored in population biology, just as arvicoline ecology does. A central question in disease ecology is what causes populations of pathogens, and the diseases they cause, to fluctuate through time or across space. As in arvicoline ecology, defining disease dynamics narrowly, *e. g*., by focusing on changes from endemic to epidemic phases, or simply by studying a particular outbreak, often elicits a search for simple explanations or hypotheses. For example, if one defines a disease system as limited to one host species and one pathogen, one will tend to seek answers in a reductionistic way, without reference to a broader context and the interactions that arise from that context. Perhaps what Lidicker called a multifactorial perspective could instead be termed an inclusive perspective, in the sense of broadening the conception of the phenomenon to be explained, as well as of the cause-effect relationships, to include the potential for complex manifestations and contingencies to play important roles. Below we describe three areas of disease ecology that we have addressed in our own research, highlighting the ways a more inclusive perspective, or Lidickerian view, helps advance understanding compared to a more traditional approach.

Replacing the single-reservoir model for most zoonoses. Broadly defined, emerging infectious diseases (EIDs) are those that are caused by pathogens that have recently evolved, recently spilled over into humans, suddenly increased in incidence, or suddenly expanded in geographic range (Morse 1995; Rosenthal *et al.* 2015). Most of the diseases of humans that are classified as emerging are caused by zoonotic pathogens. The vertebrate hosts in which the pathogens originated can be responsible for any and all of these defining aspects of emergence. Identifying the source of the emerging pathogen is expected to increase our understanding of the cause of disease emergence and suggest pathways to disease control and prevention. Consequently, much attention has been paid to determining the vertebrate source of emergence event(s).

The field of infectious disease ecology has traditionally been dominated by the "single-pathogen, single-host" paradigm, whereby it is assumed that pathogens have evolved to infect a single host species. Cross-species transmission, including transmission from a reservoir host to humans, is considered anomalous, as illustrated by use of terms like "spillover" or "species jump" to describe transmission from the focal host to some other host. Consequently, the search for the reservoir for a particular zoonotic pathogen that causes a particular EID typically focuses on identifying a single reservoir host. Such a focus is exemplified by the ongoing search for the reservoir responsible for the initial zoonotic transmission of SARS CoV-2 from some wildlife species to humans.

In reality, pathogens span a continuum of host-specificity, from those that truly infect only a single host species, to those that typically infect few species, to those that are highly promiscuous (Figure 1). Zoonotic pathogens, by definition, must infect at least two species of host – a vertebrate reservoir and humans. Pathogens that undergo a species jump from an ani-

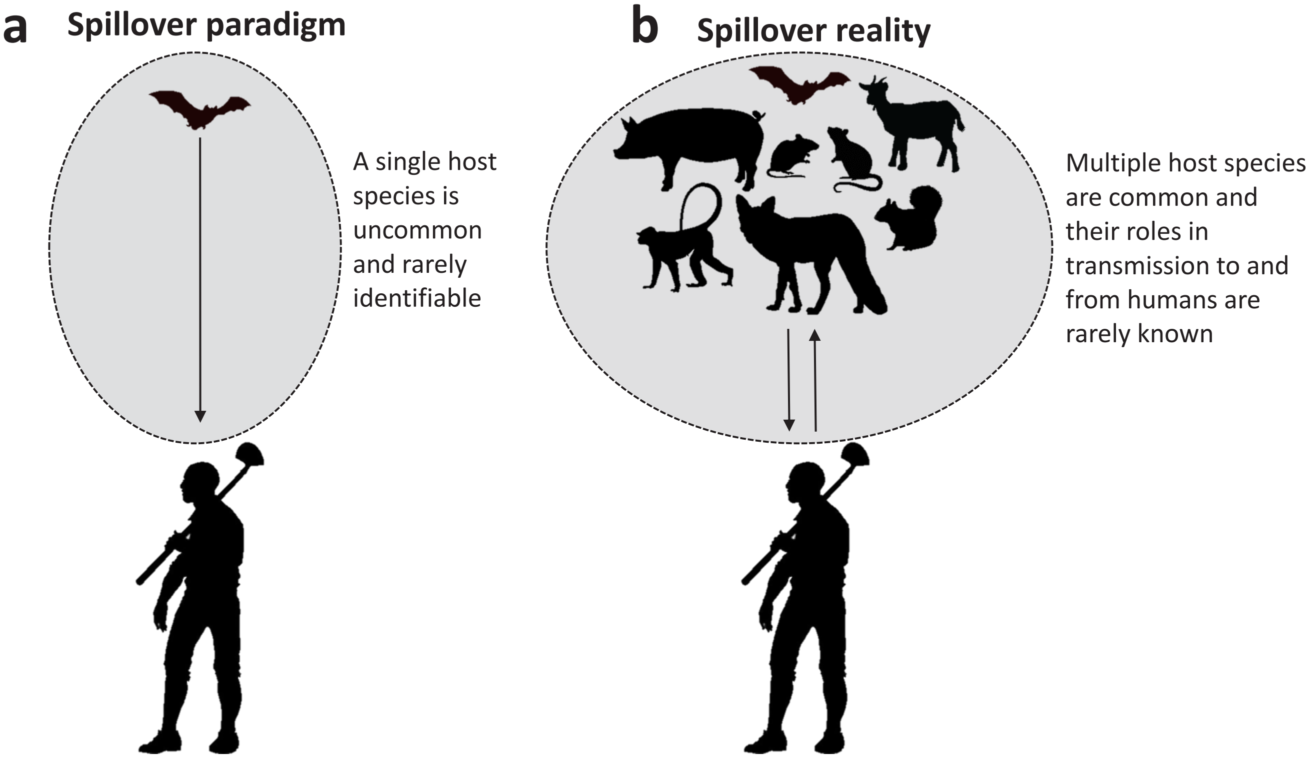

Figure 1. The paradigm (a) and the reality (b) for research on the transmission of zoonotic pathogens from vertebrate animals to humans. (a) The paradigm emphasizes a single animal host species for a zoonotic pathogen and an original spillover event, though the event and the species are rarely identified. (b) In reality, most zoonotic pathogens have multiple host species whose specific roles in transmission to and from humans are rarely known. Adapted from a figure in Keesing and Ostfeld (2021).

mal reservoir to humans tend to be more promiscuous (Keesing and Ostfeld 2021), frequently being shared with numerous host species. After all, these are the "jumpers". Occurrence in multiple species of hosts appears to be a general characteristic of the pathogens that cause EIDs in humans, and indeed, sequential infection of different host species can result in genetic changes that increase transmission to, or virulence in, new hosts, as exemplified by influenza viruses.

Focusing on a single reservoir host for a zoonotic pathogen, although appealingly simple, can be misleading and detrimental to mitigating disease. For instance, attempts to manage a reservoir host may be inefficient or even counterproductive if other reservoirs go unrecognized and unmanaged. Recognizing that multiple vertebrate species are involved in cross-species transmission of a given pathogen, including to humans, raises an inconvenient truth – that identifying pathways of zoonotic spillover involves quantifying transmission from several or many hosts rather than just one. Nevertheless, such research is likely to be critical for predicting and mitigating disease emergence (Keesing and Ostfeld 2021). A Lidickerian expansion of causal pathways is further required by the observation that some hosts play a protective role, reducing transmission rates of zoonotic pathogens by regulating abundance of pathogens (*e. g*., by absorbing but not onwardly transmitting them) or by regulating the reservoir species themselves via predation and competition (Keesing *et al.* 2009; Levi *et al.* 2012; Ostfeld *et al.* 2018; Keesing and Ostfeld 2021).

Broadening the focus to include multiple, interacting pathogens. Just as most pathogens infect more than one species of host, hosts are virtually always infected by more than one species of pathogen. Again, the reductionist adoption of a *one host-one pathogen* framework fails. There is room in such a framework to explore infection dynamics of a given pathogen as a function of a host individual (*e. g*., immune status) or of a host population (*e. g*., density), but there is no room to explore the potential effects of coinfecting pathogens. Two examples from the literature on small mammal populations illustrate the importance of explicit recognition of coinfecting pathogens within hosts.

Telfer *et al.* (2010) studied four fluctuating populations of the field vole, *Microtus agrestis*, in the UK, repeatedly taking blood samples from individual voles to track changes in the presence of the pathogens *Bartonella* spp. (transmitted by fleas), *Babesia microti* (transmitted by ticks), *Anaplasma phagocytophilum* (transmitted by ticks), and antibodies to cowpox virus (transmitted directly between hosts). Despite the potential for pathogen species within a host to interact, either directly via resource competition or indirectly via suppression or activation of immune pathways, the dynamics of pathogens have typically been addressed in isolation from each other (Telfer *et al.* 2010). Telfer *et al.* analyzed the probability of infection occurring between time steps (vole captures) for each pathogen as a function of traditional host and environmental variables, as well as of the presence of the other pathogens in the individual host.

Strikingly, Telfer *et al.* (2010) found that the presence of other pathogens generally had stronger effects on infection risk than did "factors related to exposure risk and host condition, such as age and season" (p. 244). For example, infection with cowpox virus consistently increased susceptibility to the other pathogens approximately two-fold. Voles infected with *A. phagocytophilum* were less likely to become infected with *B. microti*. And, voles infected with *B. microti* showed reduced susceptibility to *Bartonella* spp. but increased susceptibility to *A. phagocytophilum*. Telfer *et al.* argued that these four groups of pathogens (which notably constitute a subset of those infecting these voles) occur as an interaction web, affecting the host's susceptibility to other pathogens with predictably strong magnitude.

Hersh *et al.* (2014) addressed the frequency of coinfection in blacklegged ticks (*Ixodes scapularis*) in the northeastern United States with multiple tick-borne pathogens and sought to determine its cause. Coinfection in ticks with more than one zoonotic pathogen can result in simultaneous transmission of multiple pathogens to humans, with medical and epidemiological consequences. Ticks must acquire these pathogens from blood feeding on wildlife hosts, as the pathogens are not vertically transmitted. Hersh *et al.* found that coinfection of individual ticks with *B. microti* and the agent causing Lyme disease, *Borrelia burgdorferi*, was about twice as frequent as expected if the two pathogens were acquired independently (Figure 2). Moreover, they determined that ticks that had previously fed from specific small mammal hosts, especially white-footed mice (*Peromyscus leucopus*) and eastern chipmunks (*Tamias striatus*), were much more likely to be coinfected than were ticks that had fed from other hosts.

These two examples indicate that less inclusive approaches to pathogen infection in hosts and vectors – those that treat each pathogen in isolation from others – can overlook important factors driving infection risk and disease dynamics. A more inclusive approach that recognizes broader contexts is more accurate and potentially more useful for disease management.

Incorporating concepts from food webs into dynamics of pathogen and vector populations. In his paper arising from the C. Hart Merriam Award from the American Society of Mammalogists, Lidicker (1988) provided a conceptual diagram of the known and suspected factors affecting population size of voles (Figure 2 in Lidicker 1988). An inner, proximate, zone of factors included demographic processes that together produce population dynamics. The outer layers emphasized multiple drivers extrinsic to the vole population, including food resources, predators, competitors, and parasites. His conceptual model therefore subsumed several of the "single-factor" hypotheses that were ascendant at that time, including the hypotheses that time delays in the interactions between voles and their food supply (vegetation) and between voles and their predators were responsible for driving cyclic fluctuations (Krebs 2013). Lidicker's advance was to explicitly recognize that different

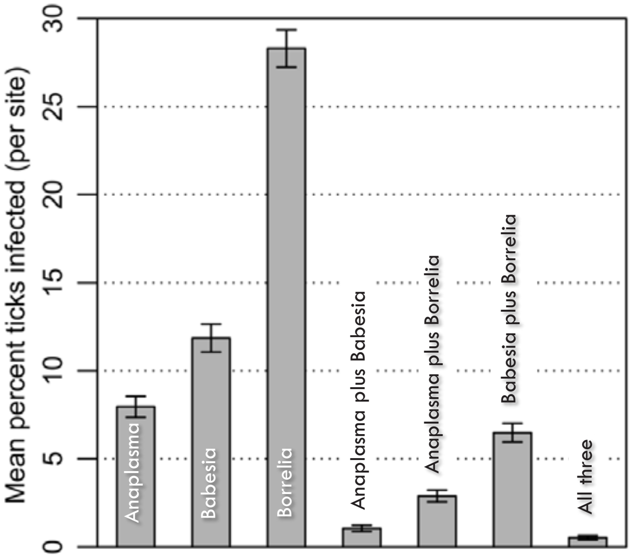

Figure 2. Mean percentage of infection for 4,368 ticks at forested sites. Ticks were coinfected with multiple pathogens more frequently than expected by chance. Each category represents the overall prevalence of a pathogen – for example, the "*Anaplasma*" bar represents not just single infections but also ticks co-infected with *Anaplasma* and either or both of the other two pathogens. Error bars represent standard error. Adapted from a figure in Hersh *et al.* (2014).

extrinsic causal pathways could operate – simultaneously or sequentially – and by acting on one or more intrinsic factors, result in a recognizable population cycle.

Much of our research in disease ecology in recent decades has focused on understanding what causes the risk of human exposure to zoonotic disease to vary in time and space. Many medical entomologists studying tick population dynamics have tended to invoke simple models in which ambient temperature and/or measures of available moisture (*e. g*., relative humidity, vapor pressure deficit) cause patterns of tick abundance by affecting tick mortality (Sonenshine and Roe 2014). These expectations arise from extension of simple, laboratory experiments in which ticks succumb to both high and low temperatures and low humidity (Ostfeld and Brunner 2015) . Other tick experts have focused on the abundance of specific vertebrate hosts for ticks, such as white-tailed deer (*Odocoileus virginianus*), as the primary driver of blacklegged tick abundance. This expectation arises from observations of large numbers of adult blacklegged ticks on hunter-killed deer during the autumn hunting season, followed by the supposition that more deer leads to greater numbers of adult female ticks surviving and reproducing, which consequently drives population dynamics (Ostfeld 2011). Both of these simple conceptual models could be true in theory, but neither is supported by direct evidence (Ostfeld 2011), and basic natural history observations suggests they are likely to be inadequate. For example, blacklegged ticks live in environments in the upper Midwestern United States and Canada, where ambient conditions are more extreme than those that predictably kill ticks in the laboratory (Ostfeld and Brunner 2015). In addition, blacklegged ticks are extreme host generalists, parasitizing dozens of species of vertebrates within local areas, with pronounced variation in host associations between life stages (larvae, nymphs, adults; Ostfeld 2011). Consequently, strong dependence of tick population dynamics on a single host species might not be expected.

We have focused on the abundance of blacklegged ticks that are infected with zoonotic pathogens as a primary indicator of human risk (Ostfeld and Keesing 2000; Allan *et al.* 2003). Thirty years of monitoring the dynamics of blacklegged tick populations in New York State reveals that the abundance of infected nymphs is significantly correlated with the prior abundance of rodents, specifically white-footed mice and eastern chipmunks. The effect of deer abundance is weak or absent (Ostfeld *et al.* 2006, 2018). Furthermore, population density of both of these rodent species is correlated with prior abundance of acorns produced by local oak trees (*Quercus* spp.), which is an important source of food over winter (Ostfeld *et al.* 1996; Jones *et al.* 1998). Such observations lead to a multifactor model dominated by bottom-up forcing, from resources (acorns) to consumers (rodents) to parasites on those consumers (ticks and tick-borne pathogens; Figure 3). More recently, another pathway has materialized as an important contributor to tick and pathogen dynamics. Strong spatial patterns in the prevalence of infection in tick populations, whereby some tick populations have very high and others very low prevalence of zoonotic pathogens, are statistically associated with specific guilds of mammalian predators. Ticks in sites in eastern New York with diverse guilds of predators, including red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), and striped skunks (*Mephitis mephitis*) have significantly lower infection prevalence than do sites with less diverse predator assemblages (Ostfeld *et al.* 2018). These depauperate predator assemblages appear to occur when coyotes (*Canis latrans*) supplant other predators (Levi *et al.* 2012). The diverse group of predators appears to reduce tick infection prevalence by multiple pathways, including reducing the number of rodent hosts responsible for transmitting infection (*i. e*., the reservoir hosts), by deflecting tick meals away from rodents onto the predators, all of which are poorer reservoirs (LoGiudice *et al.* 2003), and by killing ticks directly via more fastidious grooming than occurs with the rodents (Keesing *et al.* 2009). Statistically, neither bottom-up nor top-down forces explain more than half of the variation in human exposure risk, but together they provide a predictive understanding of changing risk in space and time.

Synthesis. These studies have taken a holistic perspective to invoke multiple, interacting factors as drivers of variation in zoonotic risk. Investigating the dynamics of these complex systems sometimes requires exploring factors in isolation, *e. g*. creating an acorn pulse (Jones *et al.* 1998), while recognizing that each factor may interact with others, change in strength, experience feedback, and depend on factors outside the study system. Studying systems with so many interacting components is

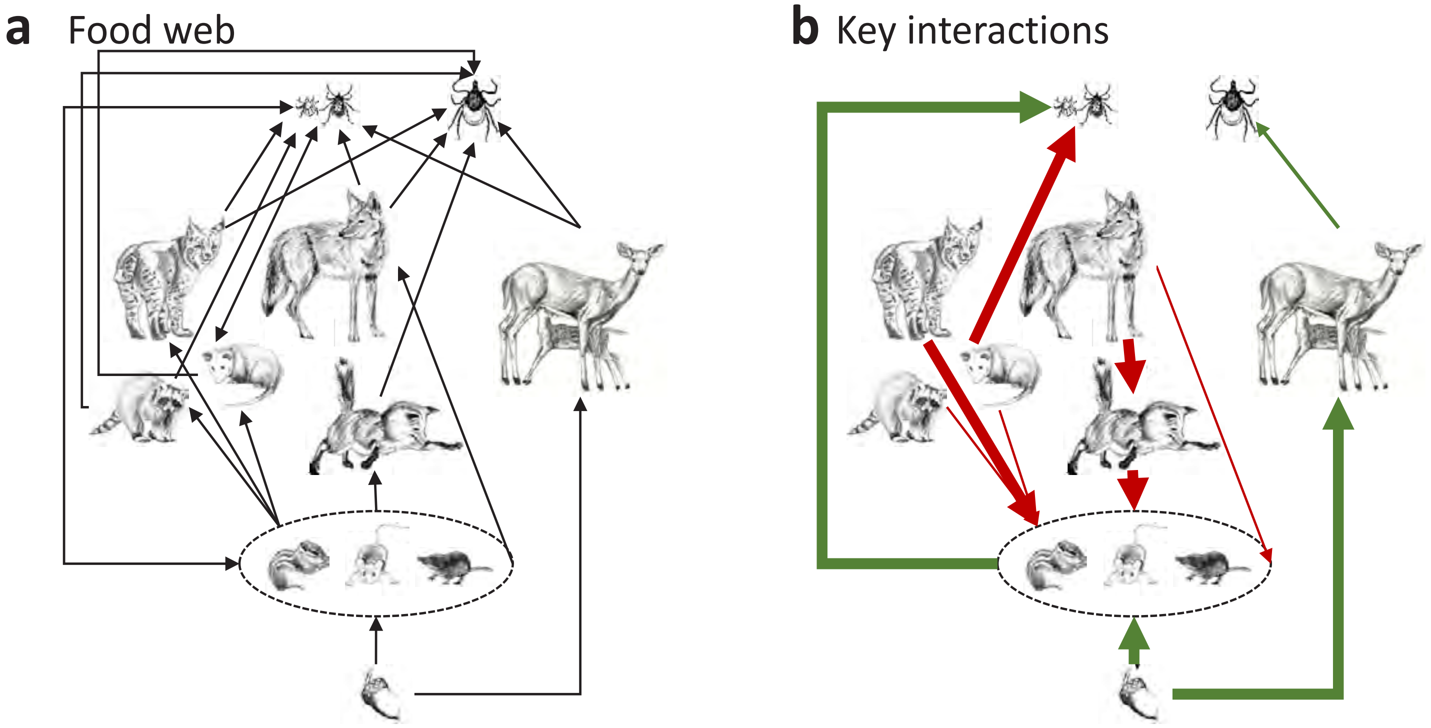

Figure 3. Webs of connections among species in the forests of eastern North America. (a) Trophic relationships, with arrows drawn from resource to consumer. (b) Key interactions, with arrow width representing the strength of relationships, and green and red representing positive and negative effects, respectively. Adapted from a figure in Ostfeld *et al.* (2018).

challenging but not intractable – these systems can be explored using experimentation, comparative or correlative approaches, and modeling. One key acknowledgment is that the very phenomena being explored may in fact be variable, showing similar patterns that are perhaps caused by different underlying processes that vary in space and time. Lidicker's multifactor approach to arvicoline population dynamics continues to inform and enlighten other research areas in ecology, including the study of infectious diseases.

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Ecological corridors for which species?

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Overwhelming evidence points to the importance of maintaining connectivity given rapidly fragmenting habitats and climate change. Many efforts to identify where ecological corridors should be placed are based on estimates of structural connectivity that take advantage of readily available land-cover data. We provide an overview of structural connectivity methodology and review the various limitations of these methods for functional connectivity -- the degree to which corridors facilitate the movement of organisms. These limitations include not accounting for dispersal complexities and specific habitat requirements of focal species, and invisible barriers to movement. Also, to what extent will the resulting corridors serve the most vulnerable species under a rapidly changing climate? We describe several connectivity-modeling approaches designed to be climate-wise. Assessing species for traits that may make them more susceptible to extinction is one way to prioritize which species warrant additional data collection and demographic analyses to improve the likelihood that corridors will function for them. There is substantial evidence that traits such as limited movement or dispersal ability as well as geographic range and habitat restrictions make species more vulnerable. Therefore, we suggest using these traits to guide focal-species selection. Finally, we discuss the importance of employing new technologies to monitor individual movement and species utilization of corridors varying in width and other characteristics to help plan and verify functional connectivity for these species.

La abrumadora evidencia apunta a la importancia de mantener la conectividad dada la rápida fragmentación de los hábitats y el cambio climático. Muchos esfuerzos para identificar dónde deben colocarse los corredores ecológicos se basan en estimaciones de conectividad estructural que aprovechan los datos de cobertura terrestre disponibles. Proporcionamos una visión general de la metodología de conectividad estructural y revisamos las diversas limitaciones de estos métodos para la conectividad funcional-- el grado en que los corredores facilitan el movimiento de organismos. Estos incluyen no tener en cuenta las complejidades de dispersión, los requisitos específicos de hábitat y las barreras invisibles al movimiento. Además, ¿hasta qué punto los corredores resultantes sirven a las especies más vulnerables bajo un clima que cambia rápidamente? Ofrecemos varios enfoques de modelado de conectividad diseñados para ser climáticos. Evaluar las especies en busca de rasgos que puedan hacerlos más susceptibles a la extinción es una forma de priorizar qué especies justifican la recolección de datos adicionales y los análisis demográficos para mejorar la probabilidad de que los corredores funcionen. Hay evidencia sustancial de que rasgos como el movimiento limitado o la capacidad de dispersión, así como el área geográfica y las restricciones de hábitat hacen que las especies sean más vulnerables. Por lo tanto, sugerimos el uso de estos rasgos para guiar la selección focal de especies. Por último, analizamos la importancia de emplear nuevas tecnologías para monitorear el movimiento individual y la utilización de especies de corredores que varían en anchura y otras características para ayudar a planificar y verificar la conectividad funcional de estas especies.

Keywords: Climate change adaptation; conservation science; focal species; habitat connectivity; wildlife.

Introduction

We had the great pleasure of writing the first comprehensive book on biological corridors, *Corridor Ecology,* with William Z. Lidicker in 2006 (Hilty *et al.* 2006) and significantly updating it together in 2019 (Hilty *et al.* 2019). Here we define a corridor as any space that facilitates the movement of populations, individuals, gametes or propagules, and plant parts capable of vegetative reproduction, in a matter of minutes, hours, or over multiple generations of a species. During the earliest meetings, Bill Lidicker urged us to specify who the corridors are for. What are the focal species? After all, species have different habitat preferences, and many species use one habitat type for part of their life cycle and a different habitat type for another. For example, amphibians may require wetlands or rivers during early life stages, upland habitat during the adult stage, and suitable substrate between the two for safe passage (Ribeiro *et al.* 2011).

The introduction of landscape ecology into the study of demography added many new insights for ecologists and conservation biology (*e. g.,* Hanski 1999; Turner 2005). Lidicker's work led to an increased appreciation that the spatially explicit mosaic of habitat patches, edge effects, corridors, and even the proportion of favorable to marginal habitats can all be critically important factors in influencing population dynamics (Lidicker 2002). Hence, habitat-patch configuration and connectivity influences effective population size, density dependence, and growth and decline of species (*e. g.,* Cushman 2006; Lidicker 1994). Clearly, determining if and how habitat patches should be connected is important to prevent species decline. This argues for focal-species based approaches that, if taking climate change into account, rely on modeling current and future species distributions and movements to identify corridors that have the potential to facilitate movement, or help species move to regions that will become suitable for them (*e. g.,* Dilts *et al.* 2016; Wasserman *et al.* 2013).

We (Jodi and Adina) often argued against the importantance of desiging corridors for specific focal species and suggested a need to shift from planning habitat connectivity for a few well-known focal species to an ecosystem approach where the objective is for the entire biota to move through the landscape (Lawler *et al.* 2015). For example, by identifying and designing structural corridors that take advantage of readily available spatially explicit land-cover data, conservation biologists can delineate open space presumed to be permeable from the built environment (Theobald *et al.* 2012). Admittedly, it can seem premature to suggest methods for enhancing connectivity when not enough is known about the requirements of the species presumed to need it. However, in-depth understanding of species habitat and dispersal requirements is difficult to obtain.

Despite this and other debates on the topic, there was a need for a general text on habitat corridors and together we wrote the first book about habitat connectivity science and practice that included structural and focal species approaches to corridor design (Hilty *et al.* 2006). This essay provides a critical assessment of commonly used methods, and where designated corridors fall short for species most in need of connectivity conservation. In essence, we circle back to Lidicker's point about the importance of considering species ecology and population viability.

Structural connectivity designs that meet the needs of many species or whole ecosystems are based on the level of human impact or naturalness and sometimes use graph theory to prioritize connections between habitat patches (Kong *et al.* 2010; Minor and Urban 2008). However, this approach often lacks information on animal ecology. This can lead to corridors that may not work for species with special needs. Hence, fine-filter approaches that are informed by species ecology may be necessary particularly for individual species that slip through the coarse filter employed by structural connectivity measures and may require specific conservation action particularly in the face of climate change (Hunter 2005).

Here, we describe the role of ecological connectivity as a global biodiversity strategy and review widely used structural or coarse-filter approaches, and where they may fall short for species most in need of connectivity conservation. We draw on meta-analyses that reveal species traits which may increase extinction risk and reduce resilience to climate change. Finally, we suggest research directions to fill gaps between structural-connectivity analyses and conservation planning for the most vulnerable species, with a focus on dispersal and movement biology and ecological monitoring. Improved approaches to connectivity modeling and field studies may provide a way forward to help conserve those species that most need it in a rapidly changing world.

Why habitat connectivity? Global estimates of terrestrial and marine species-extinction and population-extinction rates are several orders of magnitude higher than background levels (Ceballos *et al.* 2015; Payne *et al.* 2016) and continue to accelerate (Isbell *et al.* 2017). With even some abundant species on the decline, many local populations going extinct, and massive shifts in ecosystem composition expected due to climate change, it is no surprise there is a strong call for increasing the number and size of protected areas (Ceballos *et al.* 2017; Hallmann *et al.* 2017; Urban 2015). Clearly, ensuring the persistence of biodiversity requires effective protection of a percentage of the Earth's surface, although just how much is debated (Woodley *et al.* 2019). Ecological connectivity is the second key component for biodiversity conservation, because protected areas become increasingly isolated due to surrounding land degradation, and the resident populations become more vulnerable to random genetic and demographic changes, increasing the risk of extinction (DeFries *et al.* 2005; Fagan and Holmes 2006). Even the largest protected areas will lose species due to isolation and external environmental pressures over the long term (Halley *et al.* 2016; Laurance *et al.* 2012).

In addition, even large protected areas may not be climatically diverse enough to retain their set of species with rising temperatures. In fact, with climate change no country is expected to retain the current level of protection for even half of the range of current climatic conditions found in their existing areas (Elsen *et al.* 2020). Therefore, ecological connectivity is one of the top recommendations for building ecosystem resilience around climate change, and is often the only option when surrounding landscapes are heavily modified (Heller and Zavaleta 2009). The importance of connectivity in addition to protection was recognized in the 2010 version of the Convention on Biological Diversity, where the Aichi Target 11 was set to have 17 % of Earth's land surface covered by well-connected PA systems by 2020. There is also increasing recognition of the importance of "climate-wise connectivity", which aims to connect current habitat to future suitable habitat, not just by facilitating daily, dispersal, or migratory movements, but over the generations during which range shifts are likely to occur (Keeley *et al.* 2018).

Many large-scale conservation efforts are actively seeking to identify, restore, and create protected areas and corridors as part of large landscape and seascape initiatives. Examples are Australia's Great Eastern Ranges corridor; Two Countries One Forest in North America's Eastern Appalachian region; Europe's Natura 2000 conservation network; the Yellowstone to Yukon Conservation Initiative; Baja California to Bering Sea in the Pacific Ocean; and the Vatui-Ra Seascape in Fiji (Hilty *et al.* 2012). With ecological connectivity central to the implementation of regional, national, and international conservation efforts, the IUCN produced *Guidelines for Conserving Connectivity through Ecological Networks and Corridors* to provide guidance for governments and conservation practitioners to plan and implement ecological networks consisting of protected areas and corridors (Hilty *et al.* 2020).

Structural connectivity. Designing structural connectivity as a coarse-filter approach that accommodates the need of many species is often recommended as the first step for designing corridors (Beier *et al.* 2011). Here we use the term 'structural connectivity' to refer to methods that rely mostly on land cover information and patch configuration with little or no information on species behavior or habitat preferences. In developed and agricultural areas, remnant vegetation identified as structural connectivity often are de facto corridors, such as fencerows, windbreaks, roadside vegetation, and creeks or ditches that serve as structural elements that may function as corridors (Bennett 1990; Kasten *et al.* 2016; Kubeš 1996). They may harbor optimal habitat or, more commonly, marginal habitat left undisturbed as development progressed, providing vegetative structure that is distinct from the surrounding developed matrix.

Planners attempt to locate corridors to go through areas presumed to offer the least resistance to movement therefore are least costly to move through. Landscape resistance estimates are often at the heart of identifying corridors. Resistance estimates are generally expressed as a spatial raster layer made up of grids of cells where each cell contains a value representing information that represent the hypothesized relationships between landscape features (*e. g.,* land cover, topography) and the ability for organisms to move and influence gene flow (Spear *et al.* 2010).

Several studies use the degree of human modification or level of naturalness to estimate resistance. This approach assumes, for example, that species avoid highly developed areas such as urban or intensive agricultural land cover (Gray *et al.* 2016). Some studies also add elevation, slope, and large rivers into the resistance calculation to account for the tendency of species to avoid steep terrain and crossing large rivers (Dickson *et al.* 2017). Another structural approach aims to find corridors consisting of similar land facets as present in the natural areas to be connected. Land facets are landscape units defined bytopography and soil type (Brost and Beier 2012). This approach is based on the assumption that species are often adapted to particular types of land facets, for example, steep, north-facing slopes, and will preferentially move between protected areas through corridors that reflect this type of physiography. The level of dissimilarity of a landscape cell to the focal facet type is used as a measure of resistance. If the resistance estimates used are inaccurate, the identified corridors may not function as intended. In fact, when a combination of focal species models was compared with structural approaches to identifying connectivity areas, the structural model had greater spatial overlap with corridor networks designed for far-dispersing large-bodied species than smaller-bodied taxa (Krosby *et al.* 2015).

Survey data collected by Keeley *et al.* (2019) from authors of 109 connectivity conservation plans reveals that a majority (79 %) were designed with focal species in mind (Figure 1). Thirty percent of the plans took advantage of one or more species-explicit modeling approaches, 13 % used individually based movement models, 9 % used meta-population models, and 17 % used species distribution models (24 % of plans applied two or all three approaches). Most of the other plans (39 %) incorporated information about the focal species to help estimate the resistance of the landscape to species movement or relied in part on local knowledge or expert opinion around species preferences and movement patterns. Climate gradient information was rarely incorporated (4 %) into the data used to develop these plans. This shows that while some species information is often used when creating connectivity-conservation plans, extensive data requirements on the ecology of focal species are a challenge for developing fully informed species-based approaches.

Structural climate-wise connectivity. Climate change provides an additional motivation for establishing large-scale ecological networks, because such networks would allow for species range shifts (Lawler *et al.* 2015). At the same time, there is concern that areas established to protect particular species will, due to climate change, not be suitable anymore for these species. Instead, the need to protect them will arise in other places that become climate refugia (Alagador *et al.* 2014). Several connectivity-modeling approaches designed to be climate-wise take into account estimates of climate velocity, climate analogs, climate gradients, and climate refugia, combined with structural-connectivity approaches such as resistance estimates based on low human impact.

Today's protected areas can be connected to sites that are forecasted to harbor analogous climate characteristics in the future. Ensuring habitat connectivity between climate analogs does not make any assumption about the effect of climate change on species responses. Therefore, increasing connectivity between climate-analog sites can be a useful strategy for climate-wise structural-connectivity designs intended to facilitate movement for entire communities (Littlefield *et al.* 2017; McGuire *et al.* 2016). Similarly, climate-gradient corridors connect climate-analogue natural areas with corridors that harbor similar temperature and precipitation regimes, avoiding steep climatic gradients along the corridor (Nuñez *et al.* 2013). Forecasting local climate change is inherently uncertain and this uncertainty should be explicitly incorporated when employing climate analogs and other methods that rely on climate models (Mozelewski and Scheller 2021).

Measures of climate velocity, calculated as the rate of change per time divided by the spatial gradient of change (Loarie *et al.* 2009), reveal the rate at which species have to move to maintain constant climate conditions. This measure is regularly used to examine the pressure that species face under rapid climate change (Burrows *et al.* 2014). In combination with other examinations of climate space it can reveal areas that may serve as climate refugia (Carroll et al. 2015; Roberts and Hamann 2016). Climate velocity is an important concept in corridor ecology, because it is assumed that minimizing velocity along a corridor increases the likelihood that species can use it for a longer period of time (Dobrowski and Parks 2016).

Climate refugia refers to places with lower climate velocity relative to the surrounding landscape. These areas can emerge on cooler aspects, areas adjacent to deep lakes or oceans, deep valleys that harbor cold air, streams fed by cold groundwater from deep aquifers, dense canopy cover, and topographically complex terrain with a diversity of microclimates (Morelli *et al.* 2016). Species are expected to persist and reproduce in climate refugia for a longer time than in the surrounding landscape. Populations may not always persist until the climate cools again and they may eventually need to move to more distant sites, but local refugia may afford them more time before longer range shifts will be required. Conserving refugia is now a recommended approach for planning climate-resilient protected area networks (Keeley *et al.* 2018; Keppel and Wardell-Johnson 2015). Shoo *et al.* (2013) further define internal refugia as climatically stable spaces within a species' existing range as compared to external refugia found outside present ranges.

Riparian areas can sometimes serve as local refugia from warmer temperatures and drier conditions due to the cooler and moister microclimates that come with proximity to freshwater streams and wetlands. Riparian corridors are known to serve as movement corridors for many species (*e. g.,* Hilty 2001). Fortunately, in many places stream corridors have some legal protection in part because they provide protection for freshwater quality and quantity as a critical ecosystem service (Fremier *et al.* 2015).

Does structural connectivity equal functional connectivity? Structural connectivity may exist without functional connectivity. Here, we define the latter as the degree to which corridors actually facilitate or impede the movement of organisms. Some of the primary reasons for the disconnect between structuraal and functional connectivity are species' dispersal behavior and abilities, the need for specific habitat requirements, and particular barriers. Some species may have traits that make functional connectivity between patches essential to their persistence. This can be the case for meta-populations that require recolonization from other emphemeral populations nearby especially when their habitat is degraded (Binzenhofer *et al.* 2008).

Dispersal. Dispersal, the process of individuals leaving the place where they are resident in search of a new place to live, is a key process to be considered in connectivity planning, because it greatly influences the demographic and evolutionary dynamics of populations (Stenseth and Lidicker 1992). There are several reasons why dispersal behaviors may prohibit species' use of corridors and other landscape elements that provide structural connectivity. Species with poor dispersal abilities may not be able to move through long corridors that lack adequate water, food resources, and shelter. Behavioral factors such as avoidance of edges and disturbed habitats may limit species movements (St. Clair *et al.* 1998). Tropical forest understory birds especially are known to avoid crossing even narrow gaps in the vegetation (Machtans *et al.* 1996; Castellon and Sieving 2006). Dispersing animals may avoid territorial conspecifics and therefore be unable to use landscape elements that provide structural connectivity. Dispersing juvenile male lions (*Panthera leo*) avoided habitat preferred by adult lions, and instead used areas with high anthropogenic risks (Elliot *et al.* 2014). Mutualistic relationships and antagonistic relationships may also influence corridor use (Lidicker and Koenig 1996). For example, the spread of mistletoe depends on the behavior of mistletoe-eating bird species (Norton *et al.* 1995), and brown-headed cowbirds (*Molothrus ater*) parasitize nests of songbirds especially in edge habitats such as narrow corridors (Hansen *et al.* 2002). The process of dispersal in highly social species can be suppressed by the high risk of individuals moving solitarily and the difficulty of prospective immigrants to integrate into existing social groups. Thus, even in the presence of structural connectivity, habitat patches may remain unoccupied by animal species that are highly social (Cockburn 2003; Laurance 1995).

Habitat requirements. Habitat quality may determine whether structural connectivity equates to functional connectivity. For example, lemuroid ringtail possums (*Hemibelideus lemuroides*) were only found to use primary rainforest corridors of at least 200 m in width (Laurance and Laurance 1999). In highly modified environments, the habitat within a corridor may be disturbed, invaded by exotics, or sparsely vegetated. Non-native vegetation can render low habitat quality. For example, where *Arundo donax* and *Tamarix chinensis* have invaded riparian areas, some native species may avoid moving through the riparian corridor (Boose and Holt 1999; Stromberg 1997). Some arboreal species require corridors to have characteristics of intact forests and avoid them otherwise (Laurance 1995). Thus, what may be a corridor for some species does not fulfill this function for others. In particular, some species will need to reside within large habitat linkages to eventually move through them. If their specific habitat needs are not met they will not be able to persist within the corridor (Doerr *et al.* 2010). This will lead to generalist species, such as those that use multiple habitat types or have broad diets, to pass through, while for specialist species the landscape will still be fragmented (Dijak and Thompson 2000). Protecting wide swaths of land for connectivity and managing them for biodiversity can ensure that the specific habitat needs of specialist species are met. It will also minimize edge effects which can preclude species that primarily inhabit interior habitat from living in or moving through structural connectivity elements (*e. g.,* Mills 1996; Perault and Lomolino 2000).

Less obvious barriers to movement. Modeling and mapping the most likely pathways that species may use to move through a landscape based on structural connectivity is now relatively commonplace. For example, within

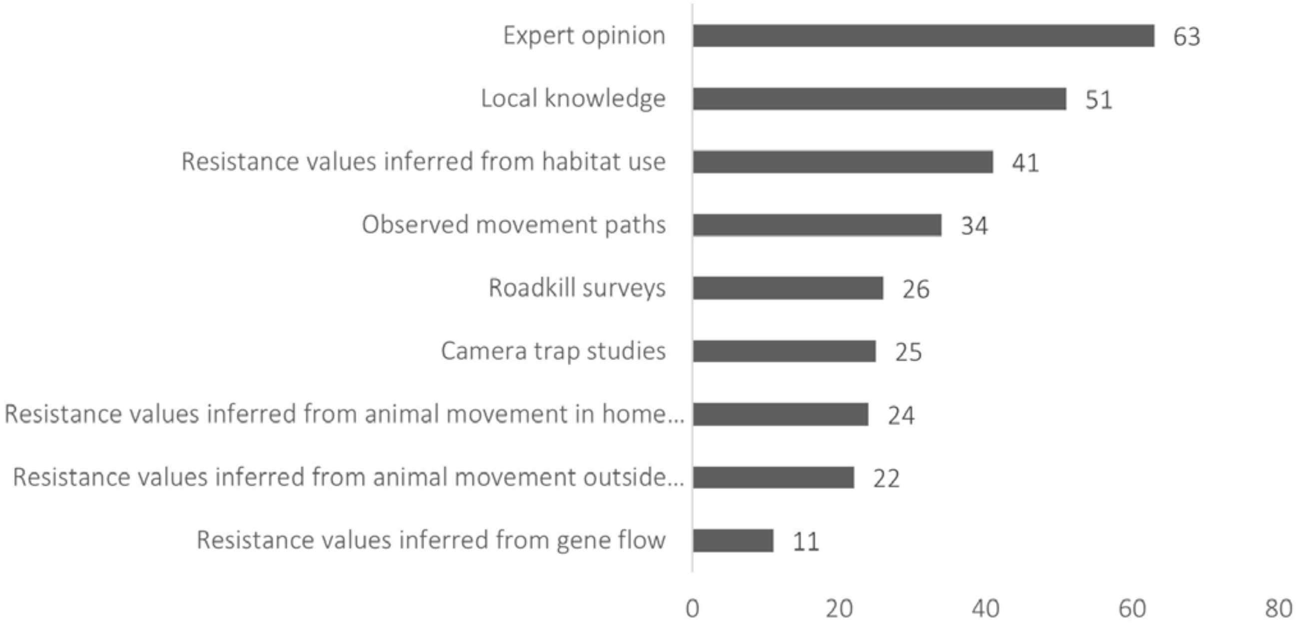

Figure 1. Data sources informing connectivity modeling in 109 connectivity conservation plans; see (Keeley *et al.* 2019) for data collection methods. One plan may use more than one data source.

the GuidosToolbox there is a module called "Reconnect" that can be used to detect stepping stones and quantify connected area gained by including corridors (Vogt and Riitters 2017). However, these models can fail to take into account what may seem like minor structures in the landscape that have enormous impacts on one or more focal species. For example, secondary roads may be a death trap for western toads (*Anaxyrus bufo)* where significant portions of populations may die crossing a busy road (McCrory and Mahr 2016). Other human structures and changes to the environment such as, but not limited to, fencing and canals, light, and noise can also inhibit movement of some focal species (*e. g.,* Tuxbury and Salmon 2005). There are also attractants to consider such as the placement of salt licks that can influence the course of species movements and preditor-prey interactions (Gonzalez *et al.* 2017; Lazarus *et al.* 2021).

Another consideration related to humans is whether their presence and management turns habitat from a source habitat where reproduction exceeds mortality to sink habitat where the reverse is true and populations may become extirpated in areas that a landscape model might predict as providing high-quality habitat connectivity. Just one house per section (square mile) on average transforms that land from source habitat where grizzly bear (*Ursus arctos horribilis*) could reproduce successfully to sink habitat where a bear is most likely to die (Schwartz *et al.* 2012). Rural low-density development creates source and sink dynamics for some birds as well (Hansen *et al.* 2005). Sink habitat can also be created where domestic animals or human-habituated wildlife flourish, causing dynamics like meso-carnivore release, the expansion of a smaller predator following the reduction or removal of a larger predator, that can have an impact on the survival of some native species (Brashares *et al.* 2009). To better predict and understand such scenarios, one requires a detailed understanding of animal behavior related to the built environment.

For some large carnivores, wildlife-human conflict is a threat to movement and species persistence (Primm and Clark 1996). In the Greater Yellowstone Ecosystem, most grizzly bears are killed by people (Haroldson and Frey 2002). To reduce this toll, co-existence efforts are employed that range from removal of livestock carcasses, the use of range riders (humans on horseback to reduce carnivore kills), bear-proofing dumpsters and trash, public education programs, and much more. The theory is that these tools will help humans and carnivores share landscapes, but more research is required to test the efficacy of these various strategies (Eklund *et al.* 2017). Understanding human resistance or fear of different species can help practitioners either choose to advance connectivity areas in places with lower human resistance or advance work seeking to change human values and resistance (Ghoddousi *et al.* 2021).

Methods and Results

Which traits render species vulnerable? Why are some species far more vulnerable than others? There is increasing reliance on trait-based analysis of species and communities in part due to the importance of predicting species loss, how well various interventions may lead to recovery, and the difficulty of obtaining detailed life history information for the myriad species at risk. For example, smaller range size is useful in predicting a species' vulnerability to extinction along with narrow habitat breadth, small population size, and poor dispersal (Beissinger 2000). Species that avoid using or moving through modified habitats have less stable populations as was observed for non-flying mammals in Australia's tripical rainforest (Laurance 1991). A recent meta-analysis of 173 manuscripts examined which well-studied traits may be predictors of extinction risk using any variables that indicated decline of the species over time (Chichorro *et al.* 2019). Mammals and birds were the most commonly studied groups; far fewer studies were done on fishes, insects, and plants. Body size and geographic-range size are frequently associated with rarity and, not surprisingly, these two variables, as well as habitat breadth, were most commonly included in predictive models. While positively correlated, the relationship between the two is not tight enough for one to be a surrogate for the other. While big animals are found in lower densities and generally have larger ranges, the range sizes of small-bodied animals vary from small to large (Gaston and Blackburn 1996). Findings from the meta-analysis reveal that geographic range size and specific habitat requirements are significant predictors of extinction risk. Body size, while most commonly studied, was not clearly linked to extinction risk. Generation length was also commonly included in these studies but found to be significant in only 27 % of the cases. Far less frequently examined was dispersal ability, which, however, was significant in 43 % of the relevant studies. The more common inclusion of body size and geographic range size reflects the fact that these data are easier to obtain than dispersal ability.

These same traits relate to species' abilities to shift their ranges in response to climate change. Dispersal is particularly poorly described for most species and even less is known about long-distance dispersal that can be less frequent but very important in predicting colonization probability and range shifts. However, established demographic analyses of simulated species, parameterized with a wide range of values for a set of traits, are useful for exploring range shifts (Santini *et al.* 2016) and species persistence (Kitzes and Merenlender 2013). In simulations, median dispersal distance turned out to be the best predictor of species-spread rates with little power detected for annual survival rate, age of sexual maturity, litter size, or number of litters per year (Santini *et al.* 2016). The Santini *et al.* (2016) study also examined the utility of body mass, home range area, and population density as a proxy for other trait combinations to model the rate of spread and ability to shift species' range location under climate change. While the rate of spread tended to increase for the first two variables (body mass and home range area) and decrease with the latter (population density), none of the traits proved to be a strong predictor of species' spread rates ($R^2 = 0.3$ for each).

There is strong theoretical support that greater dispersal ability will facilitate future range shifts, which will be necessary for many species to adapt to climate change. However, results from the simulations conducted by Santini et al. (2016) caution that the rate at which most of the virtual species they simulated are estimated to move is slower than the global mean velocity of climate as predicted by Loarie *et al.* (2009). A meta-analysis of empirical research on 26 taxonomic assemblages conducted by MacLean and Beissinger (2017) revealed that historic range limit was the strongest predictor variable (expressed for 60 % of the studies) for limited range shifts. Assemblages found at higher elevations and latitudes demonstrated smaller range shifts than those occupying lower locations. Range shifts increased with habitat breadth when differences in study area size were accounted for and a positive relationship for movement ability (related to dispersal) was observed for 50 % of the studies. No overarching significant effect among these studies was detected that indicated an influence of body size, fecundity, or diet breadth on range shifts.

Reflecting on this work, the most vulnerable species given the pressures of climate change are likely to have limited dispersal capacity, restricted ranges, and strong habitat specificity (or narrow habitat breadth) – traits that make them susceptible to habitat loss and fragmentation especially. To persist, these species likely need special consideration to ensure functional habitat connectivity.

Species viability and persistence. Species persistence is the raison d'être of corridor conservation. Incorporating species persistence into protected-area-network design relates back to metapopulation theory, where groups of subpopulations need to remain linked by dispersal between patches and maintain some gene flow. Measures of persistence include mean time to extinction or probability of extinction within a given timeframe. These measures are generally estimated by modeling species viability based on species-specific life-history information (*e. g.*, birth, death, immigration, and emigration rates). Estimates of species viability rely on measures of life-history, demographic, and ecological information to quantify extinction risk (Beissinger and McCullough 2002; Shaffer 1981). This same approach is also used to estimate the influence of environmental stochasticity and resource extraction or land management on species persistence (Akcakaya *et al.* 2004; Wintle *et al.* 2005).

Improving persistence may result from maintaining or creating corridors that allow for continued dispersal between habitat patches to lower species-extinction probabilities and reduce genetic degradation, yet species persistence measures are very rarely assessed as part of corridor design or planning. Incorporating species-viability analysis into corridor planning requires a spatially explicit approach that combines traditional population-viability analyses with a GIS that includes attributes that influence the model parameters, such as the impact of habitat type on reproductive and dispersal rates. This approach was taken for a tiger (*Pantheris tigris sumatrae*) subpopulation in a region in Sumatra, Indonesia: A population viability analysis was performed to assess the importance of corridors for the persistence of the different populations under different levels of poaching pressure (Linkie *et al.* 2006). Their models indicate that maintaining connectivity between the largest core area and a smaller core area would greatly improve the long-term persistence of tigers in the region.

Maximizing persistence using a persistence-like index based on the probability of occurrence and colonization was used for European mink (*Mustela lutreola*) and a water clover (*Marsilea quadrifolia*; found on the Iberian Peninsula) as one approach to evaluating spatial linkage design outcomes (Alagador *et al.* 2016). One key result from this study is that when implementation cost is not overly constraining algorithms that maximize persistence provide the best-performing model for designing ecological networks for conservation.

The approaches we are advocating here follow Bill Lidicker's perspective on the importance of species ecology and the need to know the role that species corridors are intended to serve before we can design and implement corridors, or assess their effectiveness. However, it does not address the problem we raise about the lack of available ecological information to properly parameterize focal-species movement or connectivity models. Incorporating species viability into corridor planning and assessment requires a good deal of data for a single species, making these methods infeasible for applications to large numbers of species. An important way to address this constraint is to develop spatially explicit, stochastic, demographic metapopulation models that can be parameterized for many species (Nicholson *et al.* 2006).

Discussion

New research directions. Given the lack of readily available species-ecological data and the high cost of obtaining this information, we recommend using species traits, considerations around population persistence, and vulnerability to climate change to identify which species should be studied to determine if a proposed connectivity-conservation plan is likely to function as intended for more vulnerable species.

With new technologies (*e. g.,* Kays *et al.* 2015), collecting extensive movement data for many species is becoming possible. Movement-path data will increasingly become available for planning and justifying costly on-the-ground implementation action. Learning more about how organisms move through landscapes during daily movements, migrations, and dispersal, the cues they use to navigate, and the resources that are critical for their safe passage will improve our ability to design effective corridors. When direct observations of animal movement paths are not available for a planning site, applying statistical models to animal-movement data from nearby can be a good way to link connectivity evaluations to empirical data. Movement data are also ideal for generating public enthusiasm for a corridor project (Keeley *et al.* 2018; Morrison and Boyce 2009). Social-science studies on how knowledge of individual animals' movements influences people's willingness to protect and respect wildlife corridors are needed.

A critical question that has not been answered yet is how wide corridors should be to meet conservation objectives. Beier (2019) gives the rule of thumb that a width of 2 km is appropriate when the corridor is intended to connect protected areas up to 80 km apart in a landscape likely to experience impact from development in the future. However, empirical evidence is needed to help planners and managers decide on the appropriate corridor width in different scenarios.

With climate change, species that are not commonly considered in connectivity plans will need to shift their ranges. Research and monitoring are necessary to determine which species' connectivity needs are not met by structural connectivity and will need special attention (*e. g.,* (Carroll *et al.* 2018). It will also be critical to understand when the velocity of climate change exceeds the dispersal ability of species potentially requiring assisted migration.

Once corridors are established and/or protected, monitoring becomes essential to allow for adaptive management, which is a science-based, structured approach to improving our understanding and reducing uncertainties. Systematic monitoring and adaptive management need to occur to increase the likelihood that ecological corridor projects will meet their objectives, and that we learn from corridors that have been implemented. Monitoring is especially necessary to determine for which species coarse filter corridors do not meet connectivity requirements. In addition to documenting movement paths, camera-traps are an excellent tool for detecting medium- to large-sized animals especially in narrowly vegetated corridors (LaPoint *et al.* 2013) and crossing structures (Ng *et al.* 2004). Roadkill distributions, winter snow or sand-tracking transects, track plates, scat surveys with or without scat-detecting dogs, and bird surveys are other ways wildlife biologists or local naturalists can determine whether focal species are using a corridor (Merenlender *et al.* 1998). Long-term monitoring is essential to understand how species with restricted ranges respond to climate change. Are connected landscapes adequate to allow these species to shift their ranges with climate change? Answering this question will require presence data collected at fine resolution across broad spatial scales over many years. Crowd sourcing can be an efficient approach to obtain these types of data (Fink *et al.* 2014).

Even when habitats are connected structurally, their populations can remain susceptible to local extinction because gene flow and recolonizations cease between habitat patches that are not functionally connected. We discuss several reasons for this, including the complexities of dispersal, specific habitat requirements not reflected in land-cover data, and less obvious barriers to movement. Both theoretical and empirical evidence suggests that movement or dispersal ability, geographic-range restrictions, and habitat restrictions predict the potential for species to shift their ranges. Assessing focal species for these particular traits is one way to determine when to examine functional connectivity using established demographic analyses and modeling.

Rapid climate change is forcing a new approach to ecological connectivity to accommodate longer-term species-range shifts including protecting climatic refugia, connecting climatically analogous areas, and protecting corridors that follow similar climate types. The focus on physical environmental data for climate-wise connectivity including climate velocity, analogs, and refugia is in line with structural connectivity approaches. However, there is little evidence that these structural approaches will lead to functional connectivity for the reasons we outline above. Given the requirement for more detailed species data especially on dispersal, which is difficult to obtain, we suggest prioritizing species-based data collection and modeling on the species most vulnerable to habitat loss and climate change.

Finally, new technologies to monitor individual movement and species utilization of corridors varying in width and other characteristics will help managers plan and verify functional connectivity. Engaging the public in contributing data is a way to improve demographic data collection required to assess persistence and the impacts of protecting patches and linkages across large-scale ecological networks. In sum, research into species with restricted ranges and low dispersal capacity is crucial if we are to design resilient ecological networks that will also serve the most vulnerable species.

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Species composition and abundance of small mammals on forest edge in southern Illinois in summer

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Relationships of mammals to habitat edges is a continuing concern for conservation as habitat fragmentation continues and ratios of edge to interior habitat increase. Mammal species that respond negatively to habitat edges may be at greater risk of extirpation, whereas species that are attracted to habitat edges may cause unanticipated ecological problems such as increased depredation of songbird nests. Proximity of contrasting habitats may also result in unique small mammal assemblages, including components of both habitats or providing opportunities for edge specialists (ecotonal effects). We compared the species composition of small mammals along live-trapping transects in forest edge, forest interior (both 100 m from edge and >1 km from edge), and the adjacent matrix (successional field or old field) in southern Illinois in summer 2003. All forest transects clustered together but differed from assemblages in either matrix type. Thus, we did not find an ecotonal effect on the forest side of the edge. The abundances of the three most common forest-dwelling species did not differ between forest edge and interior. However, there were more reproductive, adult female *Peromyscus leucopus* on transects in the forest interior, suggesting this may be higher-quality habitat at our study site, at least in summer. Edge effects have been reported for a variety of small mammal species, including *P. leucopus* in small (<2 ha) forest remnants and woodlots. We conclude that without supporting data one should not assume that edge effects are a consistent, general feature of small mammal abundance.

Las relaciones de los mamíferos con los bordes del hábitat es una preocupación constante para la conservación a medida que continúa la fragmentación del hábitat y aumentan las proporciones del borde al hábitat interior. Las especies de mamíferos que responden negativamente a los bordes del hábitat pueden tener un mayor riesgo de extirpación, mientras que las especies que se son atraídas a los bordes del hábitat pueden causar problemas ecológicos imprevistos, como una mayor depredación de los nidos de pájaros cantores. La proximidad de hábitats contrastantes también puede resultar en ensamblajes únicos de pequeños mamíferos, que incluyen componentes de ambos hábitats o que brindan oportunidades para especialistas de borde (efectos ecotonales). Se comparó la composición de especies de pequeños mamíferos en transectos con trampas para organismos vivos en el borde del bosque, el interior del bosque (ambos a 100 m del borde y > 1 km del borde) y la matriz adyacente (en la zona de sucesión o campo antiguo) en el sur de Illinois durante el verano de 2003. Los transectos del bosque se agruparon, pero difieren de los ensamblajes en cualquier tipo de matriz. Por lo tanto, no encontramos un efecto ecotonal en el lado del bosque del borde. La abundancia de las tres especies más comunes que habitan en los bosques no difirió entre el borde del bosque y el interior. Sin embargo, hubo más hembras adultas reproductivas de *Peromyscus leucopus* en transectos en el interior del bosque, lo que sugiere que este puede ser un hábitat de mayor calidad en nuestro sitio de estudio (al final del verano). Se han informado efectos de borde para una variedad de especies de pequeños mamíferos, incluido en pequeños remanentes de bosques (<2 ha) y arboledas. Llegamos a la conclusión de que sin datos de apoyo no se debe suponer que los efectos de borde son una característica general y constante de la abundancia de los pequeños mamíferos.

Keywords: Ecotonal effect; edge effect; habitat fragmentation; matrix effect; *Peromyscus leucopus*.

Introduction

As habitat loss and fragmentation became a prominent focus of conservation biology in recent decades, so did the responses of organisms to habitat edges ("edge effects"; Murcia 1995; Lidicker 1999; Lidicker and Peterson 1999; Ries *et al.* 2004). Forests can be fragmented, which creates more edges in a landscape, by timber harvesting, conversion of land to agriculture, urban development, and a variety of other human activities (Fahrig 2003; Haddad *et al.* 2015). In fact, Haddad *et al.* (2015) estimated that 20 % of the world's remaining forest was within 100 m of a forest edge, and 70 % was within 1 km of an edge. Pfeifer *et al.* (2017) examined the global landscape-level abundance of 1,304 forest-dwelling vertebrate species in relation to the amount of forest edge in the landscape. They found that 85 % of the species examined showed edge effects; 39 % showed a negative relationship and 46 % showed a positive relationship with the amount of forest edge. For mammals, the abundance of 57 % of the species examined (n = 519) showed strong declines near forest edges (Pfeifer *et al.* 2017).

Small mammals show a variety of responses to habitat edges (Lidicker and Peterson 1999). One response is an ecotonal effect, where a species typically associated with one habitat type (*i. e.,* forest or matrix in this case) can occupy peripheral areas of an adjacent habitat type, creating greater species diversity in edges, novel assemblages, and perhaps even edge specialists (Lidicker 1999; Lidicker and Peterson 1999). An alternative response is a matrix effect, where a species' distribution does not change, and the species remains in its respective habitat (*e. g.,* remains in either forest or matrix; Lidicker 1999). In this case, assemblages along edges are similar to those in the habitat interior, whether forest or matrix, if all species show matrix effects. A strong matrix effect might indicate species with poor dispersal through the matrix, and thus high sensitivity to isolation and reduction of habitat area caused by fragmentation. Differences in population density or vital rates between edge and interior habitats could occur under either ecotonal or matrix effects, and these differences are what are usually of concern to ecologists and conservation biologists (*e. g.,* Morris 1989; Morris and Davidson 2000; Klein and Cameron 2012; Hannebaum 2017). Species that show a strong avoidance of edges could be especially susceptible to risk of extirpation because as forest becomes fragmented, the edge-to-interior ratio increases, and the amount of core area decreases.

For small mammals, the type of edge effect observed varies by species, and even within species it can vary by habitat type, area of the habitat patch, and season. Mills (1995) reported that *Myodes* (formerly *Clethrionomys*) *californicus* (red-backed voles) showed a negative effect of forest edges on abundance, possibly because the drier and warmer microclimate in these edges were less conducive to the hypogeous fungal sporocarps that the voles feed upon. However, in a later study at the same sites, Tallmon and Mills (2004) could not duplicate the previous findings and suggested that capture probabilities for voles vary over space and time; thus, replication of studies is needed to confirm the generality of findings from a single snapshot. *Microtus pennsylvanicus* (meadow voles) showed avoidance of forest edges in old field habitats, likely due to the possibility that the trees could provide perches for avian predators (Manson *et al.* 1999; Nickel *et al.* 2003). Pardini (2004) found one species with a positive association and three species with negative associations with forest edges out of 20 species of rodents and marsupials detected in Atlantic Forest fragments in Brazil. In contrast, Di Napoli and Caceres (2012) did not find evidence of an edge effect in abundance among 12 species examined in woodland savannah remnants in Brazil. Mazzamuto *et al.* (2018) reported that *Myodes glareolus* (bank voles) were more abundance along forest edges in Northern Italy, but that *Apodemus sylvaticus* (wood mouse, a species morphologically and ecologically similar to North American *Peromyscus*, see below) showed no relationship between abundance and edges. Forest edges in their study also were neutral in terms of species richness, survival, and personality of individual small mammals, although foraging by both species yielded lower giving-up densities (GUDs) in seed trays near edges, suggesting lower perceived predation risk.

In the midwestern United States and southern Canada, studies of the responses of *Peromyscus leucopus* (white-footed mice) to forest edges have yielded a variety of results (Table 1). In general, the density of *P. leucopus* has been found to be higher in small fragments than large fragments or extensive forest (Nupp and Swihart 1996, 1998; Krohne and Hoch 1999; Anderson and Meikle 2006; Wilder and Meikle 2006). Similarly, positive (greater abundance) edge effects have been reported several times, but always in small woodlots (*i. e.*, <2 ha; Cummings and Vessey 1994; Anderson *et al.* 2003; Wilder and Meikle 2006). *Peromyscus leucopus* is known to select areas with more complex vertical structure of the vegetation and greater cover by fallen logs, stumps, and other downed woody debris (Kaufman *et al.* 1983; Barnum *et al.* 1992; Moore and Swihart 2005), and this has been suggested as one reason density might be higher in small fragments and edges (Anderson and Meikle 2006). Habitat quality for *P. leucopus* has been suggested to be both higher in forest interior (Morris and Davidson 2000; Wolf and Batzli 2002, 2004; Moore and Swihart 2005) and higher along forest edge (Wilder *et al.* 2005; Klein and Cameron 2012; Hannebaum *et al.* 2017). Additionally, *P. leucopus* is a primary reservoir of Lyme disease (*Borrelia burgdorferi*; Lane *et al.* 1991) and research suggests a positive relationship between black-legged tick (*Ixodes scapularis*) infection with Lyme disease and fragmented landscapes (Allan *et al.* 2003). *Peromyscus leucopus* also is a reservoir of hantavirus in the United States, which can result in fatal pulmonary failure (*e. g.,* Hjelle *et al.* 1995; Monroe *et al.* 1999). Thus, the relationships between white-footed mice and habitat fragmentation/edges may have important implications for human health.

Studies of edge effects on the other common forest-dwelling species in our study area (southern short-tailed shrew, *Blarina carolinensis*; eastern chipmunk, *Tamias striatus*) are few. Constantine *et al.* (2005) reported no edge effect for *B. carolinensis* (or any of the five rodent species included in their study) in loblolly pine (*Pinus taeda*) forest in South Carolina. Manson *et al.* (1999) found no edge effect on *B. brevicauda* (northern long-tailed shrew), but their study was in an old field rather than forest. King *et al.* (1998) reported a weak trend for more observations of chipmunks near a forest-clearcut edge in New Hampshire, but the relationship was only marginally significant ($P = 0.0876$; King *et al.* 1998:153). Heske (1995) found no difference in captures for all three species (*P. leucopus*, *B. carolinensis*, *T. striatus*) when comparing randomly located transects in forest interior versus forest-agricultural field (corn, *Zea mays*; soybeans, *Glycine max*) edges in southern Illinois. Thus, it has been difficult to come up with generalities given such conflicting or sparse results.

Our goal was to evaluate the generality of the findings of Heske (1995) for southern Illinois. We opted to do this for two reasons: 1) most studies cited above and in Table 1, especially those detecting edge effects in abundance, were conducted in highly fragmented landscapes whereas the study by Heske (1995) was conducted in a moderately fragmented landscape with extensive forest areas remaining, which may yield different results; and 2) given the lack of duplication of results reported by Tallmon and Mills (2004), we wanted to determine if the finding of neutral effects of forest edge reported for these forests was repeatable. In Heske (1995), transects in forest interior and forest-agricultural edge were not associated, and distributed throughout the eastern Shawnee National Forest. Here, we compare numbers of small mammals in forest edges to those in parallel transects in forest interior, which we consider a more rigorous experimental design, and a more natural matrix consisting of adjacent old field or successional field. Both studies were conducted during the late spring - summer months. If the findings of Heske (1995) are general, we expect no differences between forest edge and interior, although differences between forest and matrix may occur.

We had three main goals for this study. 1) We evaluated ecotonal effects by comparing the identities of small mammal species in forest edges, forest interior, and matrix. If ecotonal effects are manifest, assemblages along edges should prove different from those in interior or matrix. 2) We compared abundances of forest-dwelling small mammal species between forest edges and interior. Edge avoidance or attraction by species could indicate species at greater risk from habitat fragmentation, or species that may cause unanticipated ecological problems. 3) Finally, because many studies in Table 1 report differences between edge and interior in aspects of the behavior or reproductive success of females, we conducted separate analyses on numbers of reproductively active, adult female *P. leucopus*. During the reproductive season, females should show the strongest responses to differences in habitat quality, whereas males respond to the distribution and density of females (*e. g.,* Ostfeld 1985). Thus, a difference between forest edge and interior in the abundance of adult females should indicate which habitat provides greater fitness (*e. g.,* Morris and Davidson 2000).

Materials and Methods

We conducted this study from late May through late July 2003 at the Cache River State Natural Area (CRNA; 37° 21′ 44′ N, 88° 57′ 20″ W), Johnson County, in southern Illinois, United States. CRNA comprises 5,793 ha of upland and bottomland forest and Tupelo-cypress swamps. Our survey transects were all located in upland forest or adjacent matrix; dominant canopy trees were maples (*Acer* spp.), oaks (*Quercus* spp.), and hickories (*Carya* spp.). Our study was conducted in extensive forest, avoiding confounding the influences of patch area and edge (Fletcher *et al.* 2007; Banks-Leite *et al.* 2010).

We live trapped small mammals on 500-m transects, each with 50 trap stations spaced 10 m apart. At each station, we set two folding aluminum Sherman live traps (10 x 11.25 x 37.5 cm; H. B. Sherman Co., Tallahassee, Florida USA) approximately 2 m apart, baited with sunflower seeds, for a total of 100 traps per transect. Each transect was trapped once per month (May, June, July), with traps set on day 1,

Table 1. Studies of edge effects on *P. leucopus* in the central U.S. and southern Canada. Positive indicates density or some vital rate (*e. g.,* reproduction) greater in forest edges than forest interior, negative indicates the reverse. No response indicates no significant differences detected between edge and interior. Multiple references in a row indicate related studies (*e. g.,* authors reporting different aspects of a study in different papers).

Reference(s)	Positive	Negative	No response
Morris 1989; Morris and Davidson 2000		Density, litter size, longevity, % reproductive adults not different, but recruitment greater in interior	
Cummings and Vessey 1994	Density higher in edge of small woodlot (2 ha), reproduction greater in forest edge		
Heske 1995			Captures in forest interior and agricultural edges similar
Nupp and Swihart 1996, 1998			No difference in density between forest edge and interior in either small or large patches
Wolf and Batzli 2002, 2004		Higher density in interior, no differences in litter size or survival	
Anderson *et al.* 2003	Higher density in small (<10 ha) vs large (>100 ha) patches, edge effect in small patches only		
Moore and Swihart 2005		Density lower in edges, but positively correlated with downed woody debris	
Wilder *et al.* 2005; Wilder and Meikle 2005, 2006	Density not different between edge and interior in spring and summer, but higher density and reproductive effort in edges of small patches (<2 ha) only in autumn		
Klein and Cameron 2012	Movement distances not different between edge and interior for males, but greater in interior for females, suggesting lower quality habitat		
Hannebaum *et al.* 2017	Transitions from forest interior to edge locations were greater than transitions from edge to interior. Assumed transitions would be to higher-quality habitat (but see text).		

checked and re-set on the morning of day 2, and checked and removed on the morning of day 3. Traps were placed to maximize capture of terrestrial small mammals (*e. g.*, along fallen logs, at the base of large trees, in runways). We identified all small mammals captured to species, weighed them to the nearest g with a Pesola spring balance (Pesola, Schwyz, Switzerland), determined sex, assigned reproductive status (testes descended or abdominal for males; visibly pregnant, lactating, enlarged nipples indicating previous reproduction, or non-reproductive for females), and categorized them as adult, subadult, or juvenile based on size and pelage. We marked each captured animal with a small fur clip to identify recaptures. We did not identify individuals, but animals were marked with a distinctive fur clip (right haunch, left haunch, or top of rump) for each of the three surveys on a transect. *Blarina carolinensis* were an exception to these procedures, as their fur was too short to rely on fur clips for identification, and it was difficult to determine sex or age in the field. All captured individuals were released at their capture site. Animal capture and handling procedures conformed to guidelines approved by the American Society of Mammalogists (Sikes *et al*. 2016) and were approved by the University of Illinois IACUC.

We conducted our surveys along 18 transects. Fifteen transects were arrayed in five groups of three parallel transects each: one in forest edge (< 5 m from edge, under the canopy), one in forest interior (approximately 100 m from the canopy edge), and one in the adjacent field (distance from the canopy edge was constrained by size of the fields, but was always >25 m and usually 50 to 100 m; Figure 1). Four of the adjacent fields (matrix) were in a mid-successional state (dense saplings up to 2 m tall, shrubs, vines, but also with some grassy or weedy patches) and one was an old field (predominantly grass and forbs) that had been released from cattle grazing about 10 years prior to our study. Groups of transects were at least 500 m apart to assure independence. The remaining three transects included a second, nearby old field with a similar history of livestock grazing to obtain a replicate sample of old field small mammals, and two transects deeper in the forest interior (> 1 km from the nearest edge) for samples of small mammals distant from edges. We live trapped six

Figure 1. Photos of the four habitat types included in our study at Cache River State Natural Area, Illinois USA, in May – July 2003. A: Forest interior (at least 100 m from the edge); B: Old field; C: Successional field; D: Forest edge (within 5 m of the tree canopy edge).

transects simultaneously, taking approximately two weeks for a complete series of surveys (the last two weeks of each month), and always included all three transects in a group in each survey.

We used principal component analysis (PCA) to compare the species composition of small mammal assemblages on each type of transect (forest edge, forest interior, successional field, old field) using data from all 18 transects. If forest edges show an ecotonal effect resulting in higher diversity or unique assemblages, we expect edge transects to map distinctly from other habitat types on a biplot of PCA axes. Similarly, PCA should reveal if the two deep-forest interior transects differ in species composition from our transects 100 m from forest edge.

We evaluated edge effects in abundance by comparing the number of individuals of each species captured on each transect, using only the 15 grouped transects and considering three categories: forest edge, forest interior, and "field" combining both successional and old field transects. As each transect was surveyed three times, we used a repeated measures analysis of variance (rmANOVA). Initially, we included month as a factor along with habitat; month was highly significant for all species examined, with fewer captures in May than in June or July, but there were no significant interactions (month*habitat, all $P > 0.10$) so we only report the results for habitat below. Separate analyses were conducted for each species for which there was sufficient data; only *P. leucopus* provided sufficient data for rmANOVA of adult females. When rmANOVA indicated significant differences among transect types, we used Tukey's HSD to identify pairwise differences. PCA was conducted in Stata ver. 9.2 (StataCorp LLC, College Station, Texas, USA). All other analyses were conducted using R ver.2.10.1 (R Development Core Team 2009).

Results

We captured 11 species of small mammals during our surveys: *P. leucopus* ($n = 782$ individuals), *B. carolinensis* ($n = 613$ captures), *Microtus ochrogaster* (prairie voles; $n = 105$ individuals), *T. striatus* ($n = 40$), *Ochrotomys nuttalli* (golden mice, $n = 34$), *Synaptomys cooperi* (southern bog lemmings, $n = 34$), *Microtus pinetorum* (woodland voles, $n = 33$), *Peromyscus maniculatus* (deer mice, $n = 20$), *Glaucomys volans* (southern flying squirrels, $n = 13$), *Zapus hudsonius* (meadow jumping mice, $n = 9$), and *Oryzomys palustris* (marsh rice rats, $n = 3$). PCA yielded 2 axes explaining 37 % and 27 % of the total variation, respectively. Old fields were distinctly separated from the other habitat types along PCA1, and were most strongly associated with *M. ochrogaster*, *S. cooperi*, *P. maniculatus*, and *O. palustris* (Figure 2). Successional fields were distinctly separated from other habitat types along PCA2, and were most strongly associated with *O. nuttalli*, *Z. hudsonius*, and *M. pinetorum* (Figure 2). The deep forest interior transects, forest interior transects, and edge transects clustered together, and were most strongly associated with *P. leucopus*, *T. striatus*, and *G. volans*. *Blarina carolinensis* were associated with both forest and successional habitats (Figure 2).

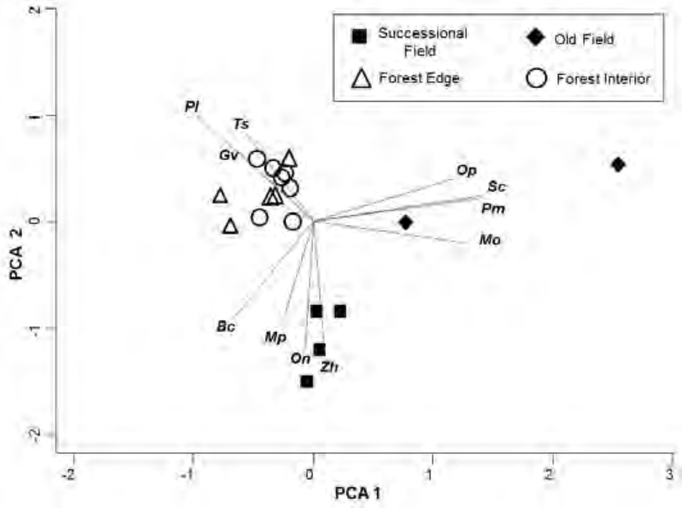

Figure 2. Biplot of the first two axes uncovered by principal components analysis (PCA) of the species composition of small mammals on each transect. Note that edge, interior (100 m from edge), and deep interior (>1 km from edge, same symbol as interior) all cluster together. Species: Ts = *Tamias striatus*, Pl = *Peromyscus leucopus*, Gv = *Glaucomys volans*, Bc = *Blarina carolinensis*, Mp = *Microtus pinetorum*, On = *Ochrotomys nuttalli*, Zh = *Zapus hudsonicus*, Mp = *Microtus ochrogaster*, Pm = *Peromyscus maniculatus*, Sc = *Synaptomys cooperi*, Op = *Oryzomys palustris*.

Peromyscus leucopus differed in abundance among transect types ($F_{2,12} = 46.62$, $P = 0.0001$). White-footed mice were less abundant on field transects (Tukey tests: edge versus field, $P = 0.003$; interior versus field, $P < 0.0001$) but did not differ in relative abundance between transects on forest edge and interior (Tukey test: edge versus interior, $P = 0.59$; Figure 3A). *Tamias striatus* also differed in abundance among transect types. Chipmunks were never captured on transects in fields, but did not differ in relative abundance between transects on forest edge and interior ($F_{1,8} = 0.06$, $P = 0.82$; Figure 3B). *Blarina carolinensis* did not differ in the number of captures among transect types ($F_{2,12} = 0.90$, $P = 0.43$; Figure 3C). There were too few captures of *G. volans* for analysis, and all other species were only captured in the open habitats (old field, successional field) with the exception of a single *M. pinetorum* on a forest interior transect.

The number of adult female *P. leucopus* captured on forest interior transects was greater than that on forest edge transects ($F_{1,8} = 5.34$, $P = 0.05$; Figure 4). Captures of adult females of other forest-dwelling species were too sparse for analysis of edge effects.

Discussion

Species richness and diversity were not greater along forest edge than in forest interior in spite of differences in the species composition of assemblages in forest and matrix (successional field, old field; Figure 2). Forest edge and interior transects (including the two deep-interior transects) were identical in terms of species composition, but differed strongly from both old field and successional field assemblages (Figure 2). Thus, most species captured in the open habitats showed a matrix effect (*sensu* Lidicker 1999), with the forest taking the role of "matrix" in this case. One species, *B. carolinensis*, occurred in both forest and matrix similarly; slightly greater numbers of captures in successional fields and the old field were not significantly different from those in forest edge or interior (Figure 3C). We did not have transects along edges outside of the forest canopy, so we cannot evaluate an ecotonal effect there; however, some *P. leucopus* were captured in successional fields where there was woody cover (Figure 3A; see also Manson *et al.* 1999), so this species likely showed an ecotonal effect wherein the edge was not a hard barrier but density in the matrix was lower. *Tamias striatus* appeared to show a strong matrix effect as no captures of chipmunks were made in the matrix (Figure 3B), but we do not know if chipmunks occupying the forest edge might venture out into adjacent matrix for short distances.

These differences are reflected in the distribution of these species in highly fragmented Midwestern forests: *P. leucopus* and *B. brevicauda* (closely related to *B. carolinensis*) were ubiquitous in forest remnants and woodlots, whereas *T. striatus* were less so (Rosenblatt *et al.* 1999; Nupp and Swihart 2000), and survival of chipmunks was lower in small woodlots (Nupp and Swihart 1998). Although *P. leucopus* is associated with wooded or at least brushy habitats (Lackey *et al.* 1985), it can be found in a variety of Midwestern habitats (*e. g.,* Cummings and Vessey 1994) and is likely very good at dispersing even through highly fragmented landscapes. Similarly, *B. carolinensis* can be found in a variety of habitats (Genoways and Choate 1998; McCoy 2001), and Constantine *et al.* (2004) reported no effects of pine forest edges on this species. In contrast, *T. striatus* is much more strictly associated with closed-canopy woodlands and forests, including forest edges, although it may often occur in residential areas as well (Snyder 1982; Bowers 1995).

We did not detect differences in abundance between forest edge and interior for the three most common species of forest-dwelling small mammals at our study area. Studies comparing relative abundance or density of *P. leucopus* have reported data showing greater abundance in some forest edges (Cummings and Vessey 1994; Anderson *et al.* 2003; Wilder *et al.* 2005; Anderson and Meikle 2006), greater abundance in forest interior (Wolf and Batzli 2002), and no difference (Heske 1995; Nupp and Swihart 1996, 1998). Anderson and Meikle (2006) found density of *P. leucopus* to be positively related to structural complexity of the understory, with structural complexity greater in small forest patches. Our study area was a large, extensive forest. We did not measure cover, but woody cover such as shrubs and bushes did not seem greater along the edges we surveyed; most increased ground cover was due to greater amounts of poison ivy (*Toxicodendron radicans*) within about 5 m of the edge (E. Heske, personal observation). We also did not observe obvious differences in downed woody debris, stumps, or logs; selective logging decades earlier had left many such items scattered throughout the forest (see Figure 1A), and traps could readily be set at the bases of large trees, stumps, or next to features providing cover or travel routes (*e. g.,* Barnum *et al.* 1992). Four of the five edges would be called "soft" given the growth of saplings, vines, briars, and weeds in the successional fields. The forest-old

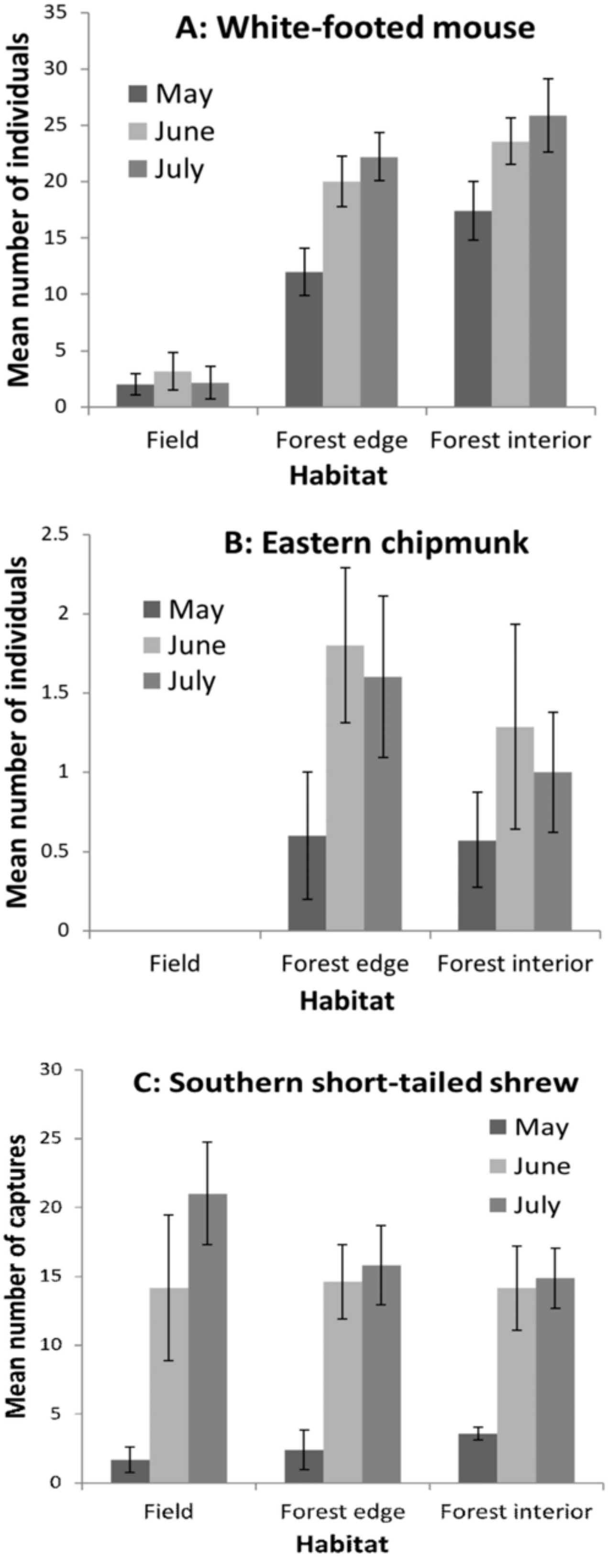

Figure 3. Mean (± SE) number of captures (individuals for *P. leucopus* and *T. striatus*, total captures for *B. carolinensis*, see text) for the three most abundant species of forest-dwelling small mammals on our transects at CRNA in May, June, and July 2003. A: White-footed mice, *P. leucopus*. B: Eastern chipmunks, *T. striatus*. C: Southern short-tailed shrews, *B. carolinensis*.

field edge was more "hard," with grassy habitat transitioning abruptly to an open understory with little structural complexity. The type of edge did not affect the patterns detected, however.

Density can be a misleading indicator of habitat quality (*e. g.,* Van Horne 1983). In most small mammals, the distribution of reproductive females is more likely to reflect habitat quality than that of other demographic categories. As with density, studies of the distribution of reproductive, adult *P. leucopus*, or of reproductive parameters such as litter size, number of litters, and recruitment, have produced varied results. Morris (1989) and Morris and Davidson (2000) did not find differences between forest edge and interior in litter size, proportion breeding, or adult longevity, but did note that the success of recruiting at least one offspring per litter and the number of recruits per litter was greater in forest interior, leading them to conclude that fitness of adult females was greater in forest interior than on forest edge. Wolf and Batzli (2004) did not find any edge effects on reproductive variables, and also noted that the distribution of seeds and arthropods was not related to distance from edge. They instead found higher predation risk and higher rates of parasitism (*e. g.,* from botflies, *Cuterebra fontinella*; Wolf and Batzli 2001) near edges and also concluded that forest interior was the higher-quality habitat. In contrast, Wilder and Meikle (2005) reported a greater number of litters and proportion of females producing litters in edges versus interior, and in small versus large woodlots.

Taking a behavioral approach, Klein and Cameron (2012) found that MSD (mean squared distance from the center of activity, a measure of movements related to home range size) increased for females, but not for males, along a gradient from forest edge to interior. They suggested that greater MSD reflected lower-quality habitat, such as fewer nesting sites or diet items, inducing greater movement. Hannebaum *et al.* (2017) took another novel behavioral approach to the question of habitat quality: transitions of individuals from one habitat type to another (*e. g.,* from interior transects to edge transects). Their analyses showed greater numbers of males than females making transitions, body mass negatively related to the probability of transition, and more transitions from interior to edge than vice versa, although numbers of such transitions were small (*e. g.,* males showed a 0.112 probability of transitioning from edge to interior and a 0.359 probability of transitioning from interior to edge; females showed a 0.037 probability of transitioning from edge to interior and a 0.077 probability of transitioning from interior to edge; Hannebaum *et al.* 2017, Table 3). Females showed higher survival than males and more fidelity to their habitat type. Oddly, hind foot size was positively related to the probability of transition; interpretations of this result can only be speculated upon. Assuming that transitions should be from lower- to higher-quality habitats, Hannebaum *et al.* (2017) interpreted their findings to imply edges were the better habitat. However, an alternate hypothesis is that greater transitions to edge by smaller males suggest this may be less-preferred habitat, as these could be the more subordinate individuals in a population and are more likely to be dispersers (Clobert *et al.* 2012). The approach to assessing habitat quality taken by Hannebaum *et al.* (2017) is intriguing, but motivations for transitions (acquiring better home ranges or coercion out of former ranges) needs further investigation. For example, Mergey *et al.* (2011) concluded that overrepresentation of subadult European pine martens (*Martes martes*) in fragmented forests indicated this was suboptimal habitat. Additional behavioral and demographic analyses to assess habitat quality would be interesting and informative.

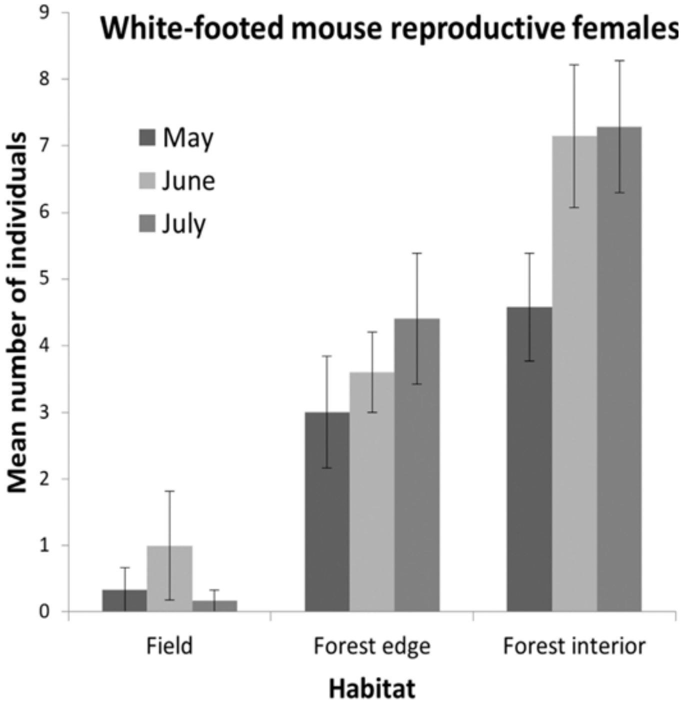

Figure 4. Mean (± SE) number of captures (individuals) of reproductive, adult female *P. leucopus* on forest edge and interior transects at CRNA in May, June, and July 2003.

Our finding of greater abundance of reproductive, adult females in forest interior supports the hypothesis that interior is higher-quality habitat than edges at our study site; the extensive forest at our site more closely resembles the study sites of Morris (1989) and Wolf and Batzli (2004) as well. It is likely that site-specific factors such as understory cover, diameter at breast height of canopy trees (Klein and Cameron 2012), food resources, and predation risk contribute to the variation observed in the studies cited above. At our site, a concurrent study of habitat use by black rat snakes (*Elaphe obsoleta*) and blue racers (*Coluber constrictor*), which are sometimes predators of small mammals, found greater use of edges than either forest or matrix interiors during summer due to the thermoregulatory advantages they offered (either basking or shading sites; Carfagno *et al.* 2006).

Conclusions. Our findings support the pattern of edge effects on abundance of *P. leucopus*, and perhaps other small mammals, only in small (*e. g.,* < 2 ha) forest fragments

(Anderson *et al.* 2003), and perhaps only seasonally (Wilder *et al.* 2005; Wilder and Meikle 2006). *Peromyscus leucopus* is the most abundant and widespread small mammal in Illinois (Hoffmeister 1989), and certainly not at risk of extinction. However, factors influencing the abundance and distribution of small mammals are still of concern for a variety of reasons. These include their potential influence on vegetation as seed predators (*e. g.,* Ostfeld *et al.* 1997), their role as potential predators of songbird nests (Maxson and Orig 1978; Schmidt *et al.* 2001), because they may attract the activity of predators who might then depredate nests incidentally (for reviews of edge effects on songbird nests, see Heske *et al.* 2001; Lahti 2001; Chalfoun *et al.* 2002), and because they are important reservoirs for the human pathogen Lyme disease (Lane *et al.* 1991, Allan *et al.* 2003) and viruses responsible for potentially fatal hantavirus pulmonary syndrome (*e. g.,* Monroe *et al.* 1999).

Edge effects on abundance, particularly negative relationships, have been widely demonstrated (Pfeifer *et al.* 2017) and remain a concern for the conservation of affected species (*e. g.,* Laurance *et al.* 2011). Although we did not detect edge effects on abundance at our study site, resource gradients and idiosyncratic attributes (*e. g.,* biased distribution of downed woody debris) may produce edge effects in forest-dwelling small mammals at other locations. An important caveat of our study is that it was only conducted in one season (summer) of one year (although results supported conclusions of another study in southern Illinois in the same season, Heske 1995). Resource distributions and environmental conditions may change after mast production in fall or during cold periods in winter when edges may be more exposed (Wilder *et al.* 2005). However, without supporting data one should not assume that edge effects are a consistent, general feature of small mammal abundance.

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Why environmental impact assessments often fail

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The environmental impact assessment (EIA) is a nearly universal instrument intended to limit or to offset the environmental tolls of development projects. Here, I describe some of the key shortcomings of EIAs in terms of their real-world application, especially in developing nations that harbor much of the world's imperiled biodiversity. A surprisingly large number of EIAs suffer from major inaccuracies and some are green-lighting projects that will have serious environmental and societal costs. I summarize by proposing eight strategies to help improve the conservation capacities of EIAs.

La evaluación de impacto ambiental (EIA) es un instrumento casi universal destinado a limitar o compensar los peajes ambientales de los proyectos de desarrollo. Aquí describo algunas de las deficiencias clave de las EIA en términos de su aplicación en el mundo real, especialmente en las naciones en desarrollo que albergan gran parte de la biodiversidad en peligro del mundo. Un número sorprendentemente elevado de EIA adolece de importantes imprecisiones y algunos son proyectos de luz verde que tendrán graves costes medioambientales y sociales. Resumo proponiendo ocho estrategias para ayudar a mejorar las capacidades de conservación de las EIA.

Keywords: Biodiversity protection; conservation; environmental threats; habitat loss; strategic environmental assessment; threatened species.

Introduction

Across much of the world, nature is declining apace. Many new protected areas have been established in the past half-century (Jones *et al.* 2018), but in most other ways nature is in broad retreat. For example, the total area of wilderness is declining rapidly worldwide (Watson *et al.* 2016), 70 % of the world's forests are now <1 km from a forest edge (Haddad *et al.* 2105), the rate of tropical forest fragmentation is accelerating sharply (Taubert *et al.* 2018), and half of the world's biodiversity hotspots retain <10 % of their original intact habitat (Sloan *et al.* 2014). As a consequence of such intense environmental disruption, nearly a hundred mammal species have become globally extinct and a quarter of all extant mammals are seriously threatened with extinction (Burgin *et al.* 2018; Richie and Roser 2021).

One of the biggest drivers of environmental change is the tsunami of development projects sweeping our planet (*e. g.*, Álvarez-Casteñeda and Lidicker 2015; Rodriquez *et al.* 2019). The wave of change is in the form of new roads, dams, mines, housing estates, and extractive-industry developments, among others (Finer and Jenkins 2012; Clements *et al.* 2014; Laurance *et al.* 2014). The governments and corporations enabling these projects urge us not to be concerned, as each project is subjected to a rigorous environmental impact assessment (EIA) to ensure there is no lasting harm to nature.

Yet the alarming fact is, many EIAs are of limited value and some are virtually useless (Wang *et al.* 2003; Alamgir *et al.* 2018; Laurance and Salt 2018). As a frontline of environmental protection in most countries, the EIA is usually a legal requirement placed on a developer to measure the impact on nature of their proposed development (Li 2008; Momtaz and Kabir 2018). If that impact includes anything that the government has pledged to protect, such as a threatened species or rare ecosystem, then the development is halted or redesigned to avoid the impact.

That is the idea, anyway. Unfortunately, many EIAs are failing to stop dangerous or otherwise ill-advised projects (*e. g.*, Fearnside and Graça 2006; Goosem 2008; Laurance *et al.* 2015; Alamgir *et al.* 2017). Globally, one sees a growing catalog of cases where EIAs are giving green lights to developments that should never proceed — projects that are destroying irreplaceable habitat or extirpating the last living representatives of critically endangered species (Alamgir *et al.* 2017, 2018; Jamal 2017; Laurance 2018; Arkert 2021).

In Panama, for instance, a remarkably superficial EIA gave a thumbs-up for a large housing project that would be carved out of tropical forest, because the study reported only 12 bird species in the area. Fortunately, a local bird expert repeated the bird survey and in just two hours of searching tallied 121 bird species, including several rare and threatened species, demonstrating just how grossly inadequate the EIA was (Laurance 2007). EIAs can be especially poor in sampling secretive, nocturnal species such as smaller mammals, bats, and amphibians, which require specialized methods (*e. g.*, camera-traps, bat detectors, mist nets) to reliably detect them (Knegtering *et al.* 2006). Surveys of mammals in particular can be labor intensive, requiring different skills and approaches for different taxa (*e. g.*, small mammals, bats, secretive species such as carnivores and some large forest-dwelling herbivores like tapirs), and often requiring longer than the typical surveys for *e. g.*, birds.

Another EIA, for the 870-km-long BR-319 highway slicing through the heart of Brazil's Amazonian rainforest, concluded that the project would cause *no net increase in deforestation*. Yet independent analyses suggest that by 2050 this project will provoke additional forest losses of up to 39 million hectares (Ritter *et al.* 2017), an area nearly the size of Switzerland.

As a final example, the approval of a $1.5-billion hydropower project in North Sumatra, Indonesia was based on an EIA that was so biased and rife with inaccuracies that I and 24 other international scientists wrote directly to Indonesian President Joko Widodo, decrying its serious distortions (Anon 2018; Laurance *et al.* 2020). Nonetheless, today this project is still advancing, cutting across the last remaining habitat of the critically endangered Tapanuli orangutan (*Pongo tapanuliensis*; Figure 1), the rarest great ape species in the world, and causing repeated construction-induced landslides that have so far claimed the lives of 10 local residents in the project area (Jong 2021; Karokaro 2021).

Designed for failure? Of course, not all EIAs are fundamentally flawed. In the most general terms, EIAs conducted in industrial nations tend to be more robust than those conducted in developing nations, which are often dogged by pervasive corruption and limited public engagement in the EIA process (Wood 2003; Fearnside and Graça 2006; Soares-Filho *et al.* 2015; Alamgir *et al.* 2017, 2018; McCullough 2017). EIAs commissioned by some major financial institutions, including multilateral lenders like the World Bank and Asian Development Bank, also tend to be relatively robust (Anon 2013). Rather than relying on an EIA, such lenders may require a broader evaluation known as a strategic environmental assessment (SEA) or strategic environmental and social assessment (SESA), which consider the cumulative effects of a project along with key economic and societal considerations (Lee and Walsh 1992).

Despite such positives, many EIAs are failing to do their job, for at least four reasons:

Inadequate investment. Rigorous environmental assessment takes time, effort, and resources. For example, detecting threatened species, one of the principal things EIAs are supposed to do, is technically challenging and expensive (Raiter *et al.* 2014; Middle and Middle 2010; Garrard *et al.* 2008, 2015; Wintle *et al.* 2012). Limiting EIAs to 'quick and dirty' appraisals, or simply avoiding an EIA altogether (Ward *et al.* 2019), saves money and time and also helps to avoid detecting rare species whose presence might block the development.

Figure 1. In Sumatra, Indonesia, a seriously biased EIA is allowing a major hydroelectric project to slice through critical habitat for the Tapanuli orangutan (*Pongo tapanuliensis*), the rarest great ape species in the world (photo © Maxime Aliaga).

Insufficient scope. The impacts of any development are rarely confined to its planned spatial footprint. Industrial mining projects in the Amazon, for example, have caused sharply elevated deforestation up to 70 km outside of the mine sites (Sonter *et al.* 2017). This is because the mines require new forest roads and those, in turn, promote illegal land encroachment and forest loss.

Similarly, in Malaysia, as elsewhere, few EIAs have considered the chronic increases in poaching (especially on mammals sold in the illegal wildlife trade or used as food, *e. g.*, Figure 2), habitat fragmentation, and other human pressures that occur when a new project slices into a native forest (Gray *et al.* 2016; Alamgir *et al.* 2017, 2018). The situation is comparable in Amazonia, where roads lead to broad 'deforestation halos', with 95 % of all deforestation occurring within 5.5 km of a legal or illegal road (Barber *et al.* 2014). In yet another example, EIAs for large dams in Brazilian Amazonia have markedly underestimated the size of the area that will be flooded by dam reservoirs, by 65 % on average (Cochrane *et al.* 2017).

Vested interests. Why do EIA assessors not simply try harder, do the job properly, and extend their assessment to incorporate all impacts related to the development? In short, vested interests and conflicts of interest (Arkert 2021). Most governments require the developer to pay for the EIA, which is typically undertaken by private consultants. Obviously, the last thing the developer wants is an EIA that stops its project dead in its tracks. If that happens, the EIA assessors involved might be blacklisted by other project developers in the future (Alamgir *et al.* 2018), creating a strong disincentive for the assessors not to favor a particular project.

On occasion, one even sees EIA consultants defending and promoting the project in public. In northern Queensland, Australia, for example, environmental experts were stunned in 2018 to see an EIA consultant publicly defending a major resort development, known as KUR-World (FOE 2019), that he was hired to evaluate objectively.

Figure 2. A poacher selling dead moustached monkeys (*Ceropithecus cephus*) for bushmeat along a Chinese-funded road cutting through a national park in the Republic of Congo. Many large development projects trigger uncontrolled secondary effects, such as wildlife poaching and illegal gold mining, that are not effectively countered by the EIA process (photo by William Laurance).

Poor governance. How do developers get away with such poor outcomes? A large part of the answer is weak or inadequate governance. Governments responsible for ensuring the integrity of the EIA process are failing to ensure it actually happens at the level required (Alamgir *et al.* 2017). Governments have vested interests, too. Development is usually equated with economic growth and jobs, and politicians can turn these benefits into votes. Add to that bribery and corruption, which are rife in many developing countries (Li 2008; Mukul *et al.* 2012; Alamgir *et al.* 2017; Momtaz and Kabir 2018) and common even in some wealthier nations, and it is easy to see how developers can gain an unhealthy hold over political and governance processes (Dupuy and Williams 2016; Laurance and Arrea 2017; Arkert 2021), including EIAs.

Eight ways to improve EIAs. Our planet is experiencing intense development pressures (Figure 3), including the planned construction of around 25 million km of new paved roads (Dulac 2013) and over 3,700 major hydropower projects (Zarfl *et al.* 2015), among others. Assessing such development trends in a way that prevents or greatly limits their environmental impacts is technically doable, as the relevant science is available. A greater challenge, however, is demanding appropriate transparency, accountability, and compliance around assessment efforts (Ward *et al.* 2019). Without those ingredients, we are poorly prepared for the ongoing wave of development.

Here are eight things we can do to help improve EIAs:

1. Insist to government authorities that EIAs be made freely available online, and that anyone be allowed to comment on them. Governments often allow only local residents to comment on EIAs, but many projects have regional or global effects. Limiting comments also excludes top international experts, such as hydro-dam or mining specialists, from providing critical advice.

2. Expect bribery to plague most projects (Laurance 2004; Alamgir *et al.* 2017, 2018), and tailor your strategies accordingly. Many projects that should never be approved move ahead because key decision-makers have been secretly paid off by the project proponent or land developers. These realities need to be communicated to stakeholders, journalists, and the general public, who may not be aware of the potentially serious impacts of corruption in development projects.

3. Insist that the public be allowed to comment on projects *early* in the approvals process, before a project gains momentum. Many developers try to ram projects rapidly through the approvals process (Laurance 2018). Hence, by the time the public is allowed to raise concerns, the project is virtually a *fait accompli* (Jamal 2017).

4. Where financial resources are available, urge that EIAs include funding for a) detailed pre-project surveys of envi-

Figure 3. The Padma Bridge, a US$6.2 billion project, is heavily impacting the world's largest mangrove forest in Bangladesh (photo © Azim Khan Roonie).

ronmental values and biodiversity, b) long-term monitoring and habitat rehabilitation after the project is completed, and c) insurance coverage for unexpected project disasters.

5. Be aware that too many EIAs recommend approving projects with only minor 'tweaks'. Such mitigation or offset measures can make the project seem palatable but are often minimally effective (Alamgir *et al.* 2018; Arkert 2021). Fish ladders around big dams and wildlife underpasses beneath highways are examples of expensive measures that may have only modest benefits for disturbance-sensitive species (van der Ree *et al.* 2007; Brown *et al.* 2012). Highway underpasses in Peninsular Malaysia, for instance, are largely avoided by the most vulnerable mammal species in the area, such as tigers, leopards, and elephants (Clements *et al.* 2014).

6. We need to say "no" to projects far more often (Fearnside and Graça 2006; Laurance 2018). Many proposed projects are simply a bad idea, with serious environmental, economic, social, and reputational risks that exceed their potential benefits. Such projects should be cancelled altogether rather than being allowed to proceed despite having serious flaws.

7. Watch your government closely. Just because a completed EIA recommends certain mitigation measures does not mean the developer will be compelled to do them (Arkert 2021). Government agencies that oversee development are typically overwhelmed and sometimes compromised by big money behind projects. Governments do better when they are closely monitored and scrutinized.

8. Use your expertise to help environmental and social groups opposing ill-advised projects. Most environmental and public-interest groups are stretched thin and in dire need of financial help and volunteers (Lawrence 2018).

The bottom line: Do not trust EIAs. Some are relatively strong and others are passable. But far too many are based on 'boilerplate' documents (standardized text that is re-used with only minor changes) or superficial reports that fall apart on close inspection. Expect many EIAs to be full of holes, and you will not be alarmed or disappointed.

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The role of rodents in the conservation of endangered species in the Ethiopian highlands

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The Ethiopian highlands is the largest Afroalpine habitat on the African continent contributing 80 % of the land above 3,000 masl on the continent. The Ethiopian highlands are part of Conservation International's Eastern Afro-Montane Biodiversity Hotspot supporting a large number of endemic mammal and bird species. In the highlands, rodent species are key for the survival of many species including the endangered Ethiopian wolf (*Canis simensis*) and over 25 species of diurnal raptors. However, increasing agricultural activities and livestock grazing affect rodent density and distribution through degrading their habitat and disrupting their reproductive cycle. As human settlement expands into the Ethiopian wolf range, it also attracts the African wolf (*Canis lupaster*) towards the core area of the Ethiopian wolf. The African wolf was recently reported to affect the survival of the Ethiopian wolf though exploitative and interference competition. Along with all the anthropogenic effects, climate change may further threaten the rodent abundance of the Ethiopian highlands through altering the grassland vegetation cover, the main forage of the rodents. Polices and strategies for the conservation management of the Ethiopian highlands should consider rodents as keystone prey playing a critical role for the survival of a large number of wildlife species.

Las tierras altas de Etiopía son el hábitat afroalpino más grande del continente africano, aportando el 80 % de la tierra por arriba de los 3,000 msnm del continente. Las tierras altas de Etiopía forman parte del Hotspot de biodiversidad afro-montano oriental de Conservation International, que alberga una gran cantidad de especies endémicas de mamíferos y aves. En las tierras altas, las especies de roedores son clave para la supervivencia de muchas especies, incluido el lobo etíope en peligro de extinción y más de 25 especies de rapaces diurnas. Sin embargo, el aumento de las actividades agrícolas y el pastoreo de ganado afectan la densidad y distribución de los roedores, degradando su hábitat e interrumpen su ciclo reproductivo. A medida que el asentamiento humano se expande hacia la zona de distribución del lobo etíope, también atrae al lobo africano hacia el área central del lobo etíope. Se informó recientemente que el lobo africano afecta la supervivencia del lobo etíope a través de la competencia de explotación e interferencia. Junto con todos los efectos antropogénicos, el cambio climático puede amenazar aún más la abundancia de roedores en las tierras altas de Etiopía al alterar la cubierta vegetal de los pastizales, el principal forraje de los roedores. Las políticas y estrategias para la gestión de la conservación de las tierras altas de Etiopía deben considerar a los roedores como presas clave que desempeñan un papel fundamental para la supervivencia de una gran cantidad de especies de vida silvestre.

Keywords: Afroalpine habitat; birds of prey; Ethiopian highlands; Ethiopian wolf; rodents.

Introduction

The order Rodentia is the largest mammalian taxon, encompassing 2,552 species representing 42 % of worldwide mammalian biodiversity (*n* = 6,495; Burgin *et al.* 2018). Rodents produce large litters after a short gestation period and adapt to extreme temperatures that extend from the hot desert sand dunes of Death Valley to freezing cold in the Arctic (Ingles 1967; Nowak 1999; Vaughan *et al.* 2000). Rodents are key components in several ecosystems playing a major role in predator-prey relationships and maintaining ecological balance (Kotler *et al.* 1994; Granjon and Traore 2007; Tschumi *et al.* 2018; Nyirenda *et al.* 2020).

Ethiopia is one of the countries with the highest number of rodent species with a total of 104 rodent species. Within the country, the highest rodent diversity is recorded in the Ethiopian highlands where 43 rodent species are endemic to the country (Bryja *et al.* 2019). In the Ethiopian highlands, rodents feed mainly on forbs and grasses and support a large number of carnivores and birds of prey. The very high density of rodent biomass in the Ethiopian highlands is equivalent to those of ungulates in East African savannas (Sillero-Zubiri and Gottelli 1995). In the Bale Mountains, for instance, the total density of three rodent species, giant mole rat (*Tachyoryctes macrocephalus*), Blick's grass rat (*Arvicanthis blicki*), and the brush-furred mouse (*Lophuromys melanonyx*), is estimated at 8,000 individuals/km^2 (Vial *et al.* 2011). Minimum density estimates ranged between 32 to 89 animals/ha for *L. melanonyx*, 32 to 127/ha for *A. blicki*, and 16 to 60/ha for *Stenocephalemys albocaudata*. The mean monthly biomass of three diurnal rodent species was estimated at 25.7 kg/ha and 23.8 kg/ha in two Afroalpine regions of the Bale Mountains (Sillero-Zubiri and Gottelli 1995).

The Ethiopian highland is the largest Afroalpine habitat on the African continent and part of Conservation International's Eastern Afro-Montane Biodiversity Hotspot with a high level of endemism (Yalden and Largen 1992). Almost 50 % of the African highlands above 2,000 masl and 80 % of the land above 3,000 masl occur in Ethiopia (Siebert and Ramdhani 2004). The isolated Afroalpine mountains have resulted from the great Ethiopian volcanic eruptions *ca.* 30 Ma (Hofmann *et al.* 1997). These unique environmental conditions, complex topography, narrow homothermal elevation zones, and isolated habitats lead to a wide range of speciation processes, making the Ethiopian highland a center of diversification for numerous Ethiopian mammal taxa (Lavrenchenko *et al.* 2014).

Role of rodents in maintaining a healthy ecosystem in the Ethiopian highlands. Rodents play a major role in maintaining the structure and natural functioning of grassland ecosystems of the Ethiopian highlands, which is an important factor for the long-term survival of several endangered species (Hillman 1986; Sillero-Zubiri *et al.* 2008). Through burrowing, rodents increase landscape heterogeneity by creating unique patches of habitat that differ from the surrounding landscape, facilitate resource flow, and enhance soil aeration and component mixing (Davidson and Lightfoot 2008; Galiano *et al.* 2014). Herbivorous rodents also shape plant communities and influence their dynamics through seed predation (Moorhead 2017). The endemic giant mole rat (*Tachyoryctes macrocephalus*) in the Bale Mountains, for instance, digs burrows and maintains the Afroalpine vegetation in a permanent pioneer stage through turning over the soil (Yalden 1985). In the Ethiopian highlands, three rodent species, giant mole rat, Blick's grass rat, and the brush-furred mouse, perform an important role in the Afroalpine as ecosystem engineers, turning over the soil and maintaining the vegetation in a permanent pioneer stage (Yalden 1985; Tallents 2007). The focus of our paper, however, is on the role rodents play as the staple prey for large carnivores in this region.

Rodents as main prey of Ethiopia's endangered carnivorous mammals and birds of prey. Rodents are prey for many carnivores and birds of prey in the Ethiopian highlands. One of the world's rarest canids with less than 500 individuals, the Ethiopian wolf (*Canis simensis*), which is endemic to the Ethiopian highlands, relies on rodents as its main food source (Johnson *et al.* 2010). Currently, the Ethiopian wolf survives in six isolated Ethiopian highland regions (Figure 1). In the Bale Mountains, *Tachyoryctes macrocephalus* represents an estimated 69.1 % of their diet by occurrence (46.6 % by volume), while the murine species *Arvicanthis blicki* and *Lophuromys melanonyx* compose 54.3 % and 39.8 % by occurrence (26.7 % and 15.5 % by volume), respectively (Sillero-Zubiri and Gottelli 1995). In the Guassa Mountains, giant molerats (*Tachyoryctes macrocephalus*), the main prey for Ethiopian wolves in Bale Mountains, are not found, and hence the Ethiopian wolf population in Guassa feed on nine rodent species that accounted for 88 % of prey volume (Ashenafi *et al.* 2005). Rodents of the Ethiopian highlands also serve as the main prey base for several birds of prey inhabiting the region. The Afroalpine moorlands of the Bale Mountains alone support a large guild of at least 25 species of diurnal raptors that depend on rodents as their main prey (Clouet *et al.* 2000). These raptors include the vulnerable tawny eagle (*Aquila rapax*) and migrant species such as the endangered steppe eagle (*Aquila nipalensis*) and vulnerable greater-spotted eagle (*Clanga clanga*) as well as the near-threatened pallid harrier (*Circus macrourus*) (Clouet *et al.* 2000; Shimelis 2008).

The only breeding population of the golden eagle (*Aquila chrysaetos*) in sub-Saharan Africa is located in the Bale Mountains, an area representing the world's largest continuous extent of Afroalpine habitat (Shimelis 2008). While not endangered, there are also several additional raptors of interest including black eagle (*Ictinaetus malaiensis*), augur buzzard (*Buteo augur*), common kestrel (*Falco tinnunculus*), long-legged buzzard (*Buteo rufinus*), pallid harrier (*Circus macrourus*), and red-chested sparrow-hawk (*Accipter rifiventris*; Clouet *et al.* 2000).

The conservation implication of declining rodent densities in the Ethiopian highlands. The Ethiopian Afroalpine highland, which used to be less preferred for agriculture due to low productivity, is now increasingly being used for agriculture and livestock grazing, and new villages are increasingly being constructed (Stephens *et al.* 2001; Alemu *et al.* 2012). The increased human activity and livestock grazing affect rodent density, which in turn affects the survival of Ethiopian wolves and other wildlife species that rely on rodents as their main food source (Marino 2003). Afroalpine habitats in Ethiopia are geographically fragmented and facing rapid ecological change due to continuous pressure from human activities and climate change (Mezgebu and Workineh 2017; Kidane *et al.* 2019). The loss of ground vegetation leads to loss of cover and food supply for small mammals thereby decreasing rodent diversity but increasing predation risk (Hoffmann and Zeller 2005). Alteration of habitat can also destroy burrows and increase soil compaction, which affects rodents' reproductive cycle and survival (Ashenafi *et al.* 2012). Loss of critical prey resources resulting from increased human activities are especially concerning for the Ethiopian wolf in light of the fact that it represents the large carnivore that has experienced the greatest range contraction (Wolf and Ripple 2017).

Ecological specialist carnivores with limited dietary plasticity are sensitive to impacts of competition, which depend on their specific diets, habitats, and activity patterns (Segura *et al.* 2007; Colles *et al.* 2009). The Ethiopian wolf is particularly vulnerable to the effects of habitat alteration, which affects the rodent prey base of the Ethiopian highlands due to their habitat and diet specialization. The Ethiopian wolf is one of five carnivore species reported to depend on prey species declining in density by the IUCN (Wolf and Ripple 2017). The density of diurnal rodents was found to be correlated with the density of Ethiopian wolves revealing the importance of rodents in the survival and reproduction of this species (Sillero-Zubiri and Gottelli 1995). Rodent density in Ethiopian wolf territories is an important predictor

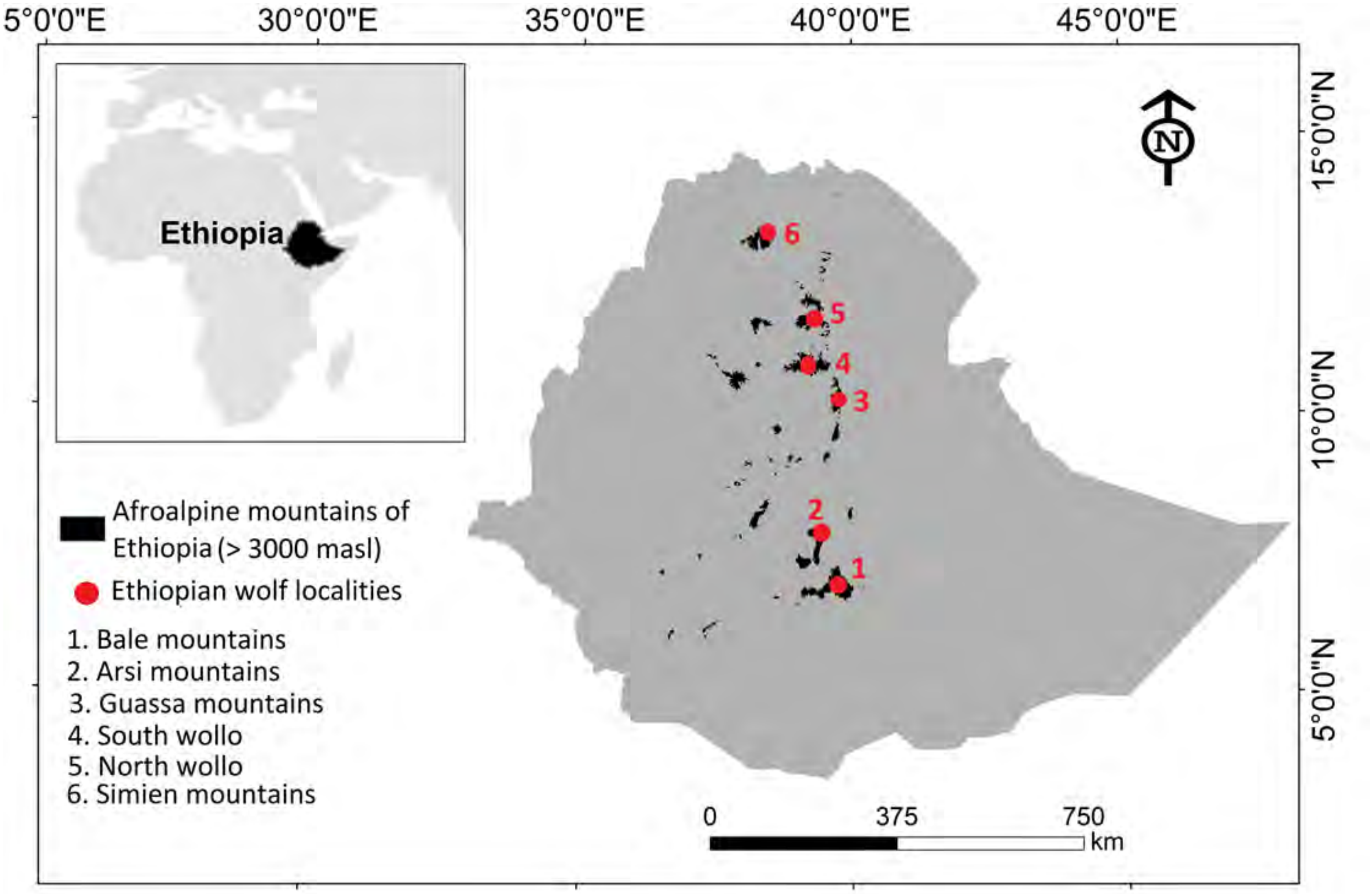

Figure 1. Locations of Ethiopian wolf (*Canis simensis*) populations in the Ethiopian highlands.

of the rate of the survival of pups (Tallents 2007). The Bale Mountains have much higher density of rodents and giant molerats (*Tachyoryctes macrocephalus*), which is endemic to the Bale Mountains, compared to the Guassa Mountains, Simien Mountains, and mountains in the North and South wollo (Figure 1). This enables the Bale Mountains to be home for the largest Ethiopian wolf population compared to the other respective sites (Ashenafie *et al.* 2005; Sillero-Zubiri *et al.* 1995; Yihune and Bekele 2014).

Threats to the Ethiopian wolf due to a decline in rodent density may worsen by exploitative and interference competition from the African wolf (*Canis lupaster*; Guetema *et al.* 2018, 2019). The African wolf is one of the most recently discovered large mammals of Africa in the central Ethiopian highlands as it was previously classified as the golden jackal (Rueness *et al.* 2011; Viranta *et al.* 2017). The expansion of human settlement intensifies the competitive interaction between the Ethiopian wolf and the African wolf due to two different mechanisms. First, as the Afroalpine area shrinks, and the available space for the two sympatric carnivores diminishes, spatial interactions leading to increased interference competition between the wolves is expected to occur. Second, as human settlement expands towards the Ethiopian wolf range, more African wolves will be drawn to the Ethiopian wolf range. The African wolf is attracted to human settlements as they feed on garbage dumps and sometimes prey on livestock (Guetema *et al.* 2018, 2019).

The Ethiopian wolf went extinct in Mount Choqa several decades ago (Yalden and Largen 1992), and about two decades ago in the central highlands of Gosh Meda and Mount Guna (IUCN 2011). The current increasing impact of humans may further lead to extinction of some of the Ethiopian wolf populations. Sixty percent of the landscape of the Ethiopian highlands above 3,200 m has been converted into farmland (Marino 2003). The effect of climate change on the vegetation and animals in the Afroalpine mountains of Ethiopia is also very well documented (Chala *et al.* 2016; Razgour *et al.* 2021). Protecting the Ethiopian highlands' Afroalpine area will enable rodent populations to maintain their normal cycle of reproduction, a key factor for the conservation of the endangered Ethiopian wolf and several raptors.

Conclusions. The Ethiopian highland is the largest area of alpine habitat remaining in the African continent, representing a center of endemism. The presence of glaciers and the spatially largest Afroalpine ecosystem are important factors promoting the evolution of endemic biodiversity in the landscape. The highlands support 60 percent of Ethiopia's rodent fauna (n = 104). Rodents are an important component of the Afroalpine community playing a key role as prey for the endangered Ethiopian wolf and many raptors. As one of the world's rarest canids, the Ethiopian wolf's survival therefore is directly tied to the persistence of high densities of these highland-adapted rodents. While the dependence on these same rodents by raptors in these areas has not been fully studied, the Afroalpine moorlands of the Bale Mountains alone maintain 25 species of diurnal raptors thought to prey on rodents. The current increasing human population, livestock grazing, and global warming in tandem affect the rodent biomass through reduction of forage availability and habitats of rodents. Alteration of habitat can also destroy burrows and increase soil compaction, which affects the reproductive cycle and survival of rodents. Loss of habitat further threatens the survival of the Ethiopian wolf by intensifying competition with the sympatric African wolf. The future survival of many endangered species including Ethiopian wolves relies in part on efforts to conserve rodent populations of the Ethiopian highlands.

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Extinction of endemic taxa as a direct consequence of global climate change

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Global climate change occurs from both natural and anthropic causes. Anthropic climate change has effects at various scales and occurs faster than the adaptation of species to these changes. Protected natural areas have been created to preserve species from the different threats facing them. Sierra La Laguna is a sky island with almost no anthropic pressure given its natural isolation; it is home to several endemic taxa, including *Peromyscus truei lagunae* and *Sorex ornatus lagunae*. This study aims to assess the possible impact of climate change on species endemic to a sky island exposed to virtually no local anthropic pressure. The Sierra La Laguna sky island, located in the southern region of the Baja California peninsula, harbors different vegetation types, including an oak-pine forest at the highest elevations and xeric vegetation at lower ones. Ecological niche models were developed under three climate change scenarios contemplating temperature rises of 1.5 °C and 4.4 °C. There are insufficient localities to make statistically robust models for mammalian species. Therefore, we used plant species typical of the oak-pine forest (*Pinus cembroides lagunae*, *Quercus brandegeei*, and *Q. devia*) and the rodents *Peromyscus eva*, that thrives in dry deciduous forests, and *Chaetodipus rudinoris* and *C. spinatus,* associated with xeric ecosystems. The models show that ecological suitability for the oak species decreases, while it is completely lost for the pine species. On the other hand, *P. eva* broadens its elevational range, while *C. rudinoris* and *C. spinatus* increase their ecological suitability in both area and elevation. The Sierra La Laguna sky island is an area with virtually no regional or local anthropic pressure. Nonetheless, the projections conducted under various climate change scenarios show a loss of up to 100 % of the area of climatic and elevational suitability for species characteristic of the oak-pine forest even with the minimum temperature rise of 1.5 °C. These results suggest that, under these conditions, endemic species such as *P. t. lagunae* and *S. o. lagunae* will become extinguished despite the absence of local anthropic pressures.

El cambio climático global existe de manera natural y el antrópico. El antrópico afecta a diferentes escalas y se produce de una manera más acelerada que la adaptación de las especies a estos cambios. Se han creado áreas naturales protegidas para preservar a las especies de las diferentes amenazas a las que están expuestas. La Sierra La Laguna es una isla del cielo, que gracias a su aislamiento natural tiene una presión antrópica casi nula; alberga varios taxa endémicos, incluyendo *Peromyscus truei lagunae* y *Sorex ornatus lagunae*. El objetivo de este estudio es evaluar la posible afectación del cambio climático a especies endémicas de una isla del cielo en la que prácticamente no existen presiones antrópicas locales. La isla del cielo de Sierra La Laguna, al sur de la península de Baja California, posee diferentes tipos de vegetación. En las elevaciones más altas está el bosque de encino-pino y con vegetaciones más xéricas al inferior. Se realizaron modelos de nicho ecológico con tres escenarios de cambio climático con incrementos de temperatura de 1.5 °C y 4.4 °C. No se cuentan con localidades suficientes para realizar modelos estadísticamente robustos de las especies de mamíferos, por lo que se usaron especies vegetales características del bosque (*Pinus cembroides lagunae*, *Quercus brandegeei* y *Q. devia*), así como a los roedores *Peromyscus eva* de la selva baja caducifolia y a *Chaetodipus rudinoris* y *C. spinatus* que están asociadas a ecosistemas xéricos. Los modelos muestran que la idoneidad ecológica para los encinos disminuye mientras que el pino la pierde por completo. *P. eva* disminuye en área pero incrementa altitudinalmente. *C. rudinoris* y *C. spinatus* aumentan en área y altitud su idoneidad ecológica. La isla del cielo Sierra La Laguna es un área con prácticamente nula presión antrópica regional y local, a pesar de esto, con las proyecciones realizadas bajo escenarios de cambio climático se muestra una pérdida hasta del 100 % del área de idoneidad climática y altitudinal aún con el incremento mínimo de temperatura de 1.5 °C para especies características del bosque de encino-pino. Los resultados sugieren que bajo estas condiciones especies endémicas como *P. t. lagunae* y *S. o. lagunae* se extinguirán a pesar de no tener presiones antrópicas locales.

Keywords: *Chaetodipus spinatus*; *Chaetodipus rudinoris*; endemic; extinction; global changes; local extinctions; local conservation strategies; *Peromyscus eva*; protection; Sierra La Laguna.

Introduction

Climate changes have occurred constantly throughout Earth's history (Zalasiewicz and Williams 2021). However, it has been recognized that anthropic climate has been the main driver of species extinctions over the past 100 years (Cahill *et al.* 2013) because ecosystems are being severely transformed and threatened, with impacts reaching the global scale. Deforestation, changes in land use, and extraction of certain species are among the factors causing the greatest impact on biodiversity loss (Ochoa-Ochoa and Ríos-Muñoz 2019). Anthropic climate change is likely to compound and exacerbate these factors.

The main effects of climate change are rising ambient temperature and changes in humidity and dryness (IPCC 2021). The global rise in temperature has unavoidable effects at global, regional, and local scales that occur at a faster rate than the capacity of species for physiological adaptation, thus affecting variations in population dynamics, behavior, and ecological interactions, leading to changes in their geographic distributions (Elith and Leathwick 20091; Ackerly *et al.* 2010; Aguado and Escalante 2015). Protecting the remaining primary forests, especially those with high carbon capture, has been suggested as a natural approach to controlling climate change and preventing biodiversity loss (Griscom *et al.* 2017).

Local stressors, mainly derived from the ever-growing human population, have led to changes in forest cover and land use. As a result, primary or secondary vegetation has been converted into extensive crop fields, pastures dedicated to intensive livestock raising, and human settlements (Mas and Flamenco 2011). Urban areas are also undergoing expansion, most often with no planning or structure. This phenomenon is causing damage to biodiversity, hydrological systems, and ecosystems due to the growing demand for services, construction of roads and airports, urban development, and water extraction for human consumption, among others (Grimm *et al.* 2008).

The term "protect" (to cover or shield from injury or destruction; to defend, guard; Merriam-Webster 1961) is frequently mentioned and has been adopted in the conservation field. In 2015, a group of world leaders agreed on an agenda for sustainable development, with the protection of the Earth included as one of the goals (CDB 2018). Aiming to meet the objective of "protection" against the different anthropic pressures, México has created a system of Protected Natural Areas (PNAs) covering 11.14 % of the country (Conanp 2019). This system harbors different ecosystems with their respective assemblages of flora and fauna. In many cases, PNAs were created to protect species endemic to the region or the country that are in some risk category (Bezaury-Creel and Gutiérrez-Carbonell 2009).

Worldwide, the vast majority of PNAs are affected by anthropic pressures at three levels (global, regional, and local), so that assessing the effects of climate change on particular species is a complex task. General and specific pressures act in synergy where the individual effect of each of the different stressors cannot be clearly identified. In Baja California Sur, Sierra La Laguna has an unique condition worldwide for being part of a sky island — an isolated area hosting different types of ecosystems along an elevational gradient (Osborne *et al.* 2019). It faces little anthropic disturbance: it has no access roads to the middle and upper parts, it is located in an area with very low human population density, there are no productive activities associated with the mountain range, and any human activities carried out in the area are minimal and low-impact. The oak-pine forest located at the highest elevations can only be reached on foot and with controlled access. The mountain range is home to several endemic taxa, such as the reptiles *Elgaria paucicarinata* and *Xantusia vigilis*; the birds *Hylocharis xantusii, Melanerpes formicivorus, Pipilo maculatus magnirostris*, *Sitta carolinensis,* and *Vireo victoriae*; and the mammals *Peromyscus truei lagunae* and *Sorex ornatus lagunae* (Álvarez-Cárdenas *et al.* 1988; Rodríguez-Estrella 1988; Cortés-Calva 2012; Segura-Trujillo *et al.* 2012). Despite these favorable features, global climate change may affect some taxa that are endemic to this PNA. The objective of this study is to assess the potential impact of climate change on taxa endemic to this sky island exposed to virtually no local anthropic pressures.

Materials and Methods

Study area. The Sierra La Laguna Biosphere Reserve is located in the southern region of the Baja California peninsula, in the state of Baja California Sur, between the municipalities of La Paz and Los Cabos. This reserve is unique in its type for being part of a sky island due to its natural isolation, with a maximum elevation of 2,080 meters (Figure 1). The low human population density in the region presents virtually no anthropic pressure, making this region an ideal model of ecosystem protection. This sky island harbors various vegetation types, including arid ecosystems such as dry deciduous forest and crassicaule shrubland at lower areas of the mountain range and oak-pine forests at higher elevations.

To assess the effects of global temperature rise at the local level, we applied ecological niche models to make projections for climate change scenarios considering different temperature rise levels. Historically, *P. t. lagunae* and *S. o. lagunae* are found in the oak-pine forest. Given their inaccessible and restricted habitat, there are very few records with unique localities (4 and 5, respectively, separated by less than one km between them); therefore, these two species were not candidates for use in ecological niche models because the models would not be statistically robust, they have to be considered a cluster of localities (Pawar *et al.* 2007). Instead, we used the tree species *Pinus cembroides lagunae*, *Quercus brandegeei*, and *Q. devia*, which are typical of the oak-pine forest in Sierra La Laguna. Also included were *Peromyscus eva*, a rodent species that inhabits lower elevations associated with the dry deciduous forest, and *Chaetodipus rudinoris* and *C. spinatus*, representative of arid

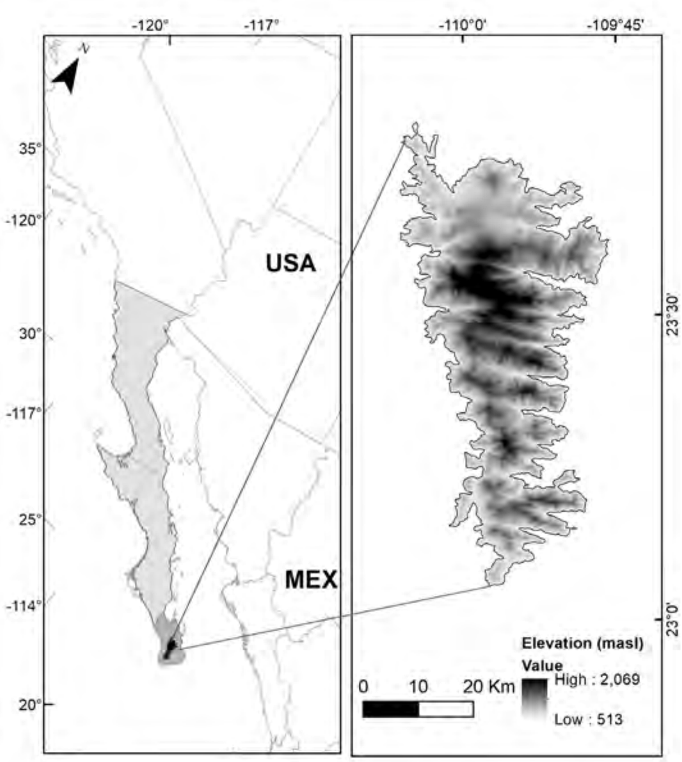

Figure 1. Geographic location of the sky island Sierra La Laguna, Baja California Sur, México. Light gray represents the Baja California peninsula. Medium gray represents the Cabo region. Dark gray represents Sierra La Laguna sky island.

ecosystems. These mammal species were used as references to examine their potential elevational displacement due to global climate change.

The ecological niche models were developed using the Maximum Entropy (MaxEnt) algorithm in R (R Development Core Team 2020) for the present time using climatic variables from the Digital Climate Atlas of Mexico on a 250-meter scale (http://uniatmos.atmosfera.unam.mx/ACDM/servmapas). We used r < 0.80 to avoid collinearity and correlation (Dormann *et al.* 2013). The best models were selected based on good performance (< 10 % omission rate; Peterson *et al.* 2011), lowest value of the Akaike's Information Criterion corrected for small sample size (AICc), and a ROC < 0.05 (Peterson *et al.* 2011). These were projected using three general circulation models: HadGEM2-ES (Jones *et al.* 2011), CCSM4 (Vertenstein *et al.* 2016), and MPI-ESM-LR (Giorgetta *et al.* 2013) considering a minimum global temperature rise of 1.5 °C and a maximum of 4.4 °C (for details of the modeling methodology, refer to Monroy-Gamboa *et al.* 2021).

Results

To assess the status of mammal species, two different analyses were conducted. The first included the associated plant species that define the oak-pine forest, *i. e., Pinus cembroides*, *Quercus brandegeei*, and *Q. devia*. The second was based on the fact that the temperature rise will lead to a forest desertification process with a shift toward xeric species.

The result of the modeling of *P. c. lagunae*, *Q. brandegeei*, and *Q. devia* showed a decrease in the area with climatic suitability under the three projected scenarios, except for *Q. devia* with the general circulation model HadGEM2-ES; with an increase of 4 °C the model showed a minimum increment (2.28 km^2) in the surface (Figure 2; Table 1). Both the optimistic and pessimistic climate-change scenarios predicted the total disappearance of climatic suitability for the endemic population of *P. c. lagunae*, a species that is characteristic of the forest at higher elevations. The models for *Peromyscus eva*, associated with the dry deciduous forest, showed a loss of between 18 % and 21 % of the climatically suitable area (Figure 2; Table 1). The models for *Chaetodipus rudinoris* and *C. spinatus,* strongly associated with the xeric habitats in the lower part of the mountain range, showed a broadening of their elevational range between 108 to 682 and 1,295 m, respectively, and an expansion of the area with climatic suitability (Figure 2; Table 1). Both results indirectly show the reduction of the forest and the mammal species associated with it, which can be considered a collapse of the forest due to desertification.

Table 1. Area, in km^2, presenting suitable climatic conditions for the species inhabiting the Sierra La Laguna sky island, currently and under three general circulation models as climatic change scenarios assuming minimum and maximum temperature rises of 1.5 ºC and 4.4 ºC, respectively.

	Current	Climate change					
		1.5° C			4.4° C		
		CCSM4	HadGEM2-ES	MPI-ESM-LR	CCSM4	HadGEM2-ES	MPI-ESM-LR
Pinus cembroides lagunae	693.25	0.00	0.00	0.00	0.00	0.00	0.00
Quercus brandegeei	1,390.78	1,306.57	1,389.51	1,187.66	1,268.23	874.52	977.51
Quercus devia	1,378.36	614.23	1,130.76	743.40	303.86	1,380.64	1,052.88
Chaetodipus rudinoris	0.00	236.76	428.70	50.62	829.87	820.41	78.85
Chaetodipus spinatus	86.61	1,302.89	1,392.54	651.03	1,392.54	1,392.54	903.14
Peromyscus eva	1,345.34	1,050.28	1,098.43	1,097.39	1,095.74	1,096.99	1,099.00
Sky island	1,392.54						
Protected area	1,124.50						

General circulation models: CCSM4 (Vertenstein *et al.* 2016), HadGEM2-ES (Jones *et al.* 2011), and MPI-ESM-LR (Giorgetta *et al.* 2013).

Discussion

In the Sierra La Laguna Biosphere Reserve, there are no vehicle roads to reach the oak-pine forest; a private road reaches up to an elevation of 1,220 meters but allows no access to the public. Public vehicular accesses are located at the foothills of the mountain range up to 620 masl. The forest can only be accessed by walking through five specific points: La Burrera, San Dionisio, La Zorra, La Victoria, and San Pedro del Frijolar, through paths running across approximately 900 meters of elevation with very steep slopes. There are three points controlled by park rangers: two in the accesses most frequently used by visitors (La Burrera and San Dionisio) and a third at the destination site, the park ranger's hut (Conanp 2015).

The only regular visitors to the reserve are park rangers and forest fire brigades; property and land owners visit the reserve occasionally to conduct monitoring and surveillance activities in the areas granted to them. In some seasons of the year, small groups of visitors register with park rangers; the activities and camping sites are restricted by PNA regulations that visitors meet. Sierra La Laguna is an area where the extraction of forest materials is prohibited, including dead wood, so there is neither tree cutting nor firewood collection. Also, there are no human settlements above ~600 masl, except for the forest station in La Laguna (for forest guards) and a hut owned by the Centro de Investigaciones Biológicas del Noroeste at Palo Extraño. Both facilities are for temporary use only and are reached by walking an average time of six and eight hours, respectively. Most of the human settlements within the reserve (around 65) are located between 400 and 600 masl and are single-family houses, with a very low percentage of permanent households. Most of these rural households are registered as inhabited (INEGI 2020).

There are no agricultural activities associated with the forest. Also, there is no goat or sheep farming, and bovine cattle farming is minimal; some feral farm animals have been recorded, which have escaped from extensive cattle raising carried out in the ranches located at lower elevations.

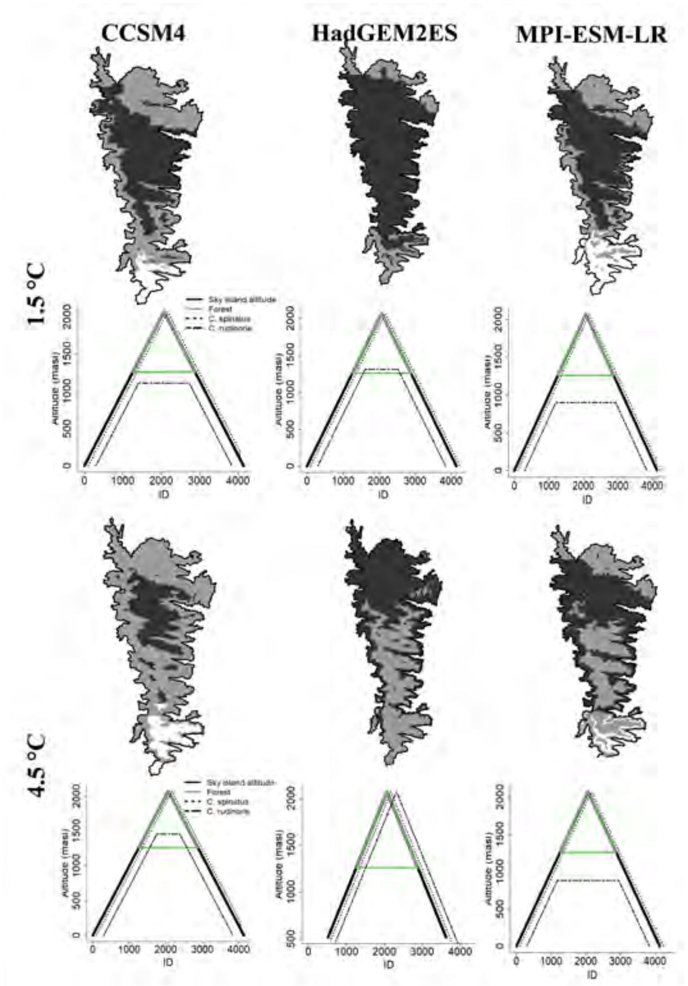

Figure 2. Area and elevations with suitable climatic conditions for characteristic species of the sky island of Sierra La Laguna under climatic change scenarios. Rows show the increments of temperature and columns the general circulation models used in each case. The area representing the sky island is shown with a black outline, where the three characteristic species of trees (*Pinus cembroides lagunae*, *Quercus brandegeei*, and *Q. devia*) are currently distributed. Gray represents the suitable climatic area with climatic change scenarios for *Q. brandegeei*. Black represents the suitable climatic area with climatic change scenarios for two species: *Q. brandegeei* and *Q. devia*. *Pinus cembroides lagunae* is missing because this species lost its climatic suitability in all the climatic change scenarios).

Results of our niche models show that the plant species typical of the oak-pine forest will face a decrease in their areas of optimal climatic conditions under temperature rises of 1.5 °C and 4.4 °C, projected from the three general circulation models. In all scenarios, *Pinus cembroides lagunae* loses the climatic suitability conditions that allow it to survive. The results of the model for *Pinus* show a reduction of its areas with optimal climatic conditions. This means that the expected recruitment of *Pinus* will be lower than its mortality rate, leading to a negative demographic trend; thus, the total number of *Pinus* individuals would decline gradually through time, leading to the increasing isolation of mature individuals until their ultimate disappearance. Although the models for *Q. devia* and *Q. brandegeei* suggest areas with climatic suitability for the different temperature-rise scenarios, the increase in global temperature will affect these species by reducing the area climatically suitable for their survival and reproduction. The results generally project that, in the short term, the vegetation will evolve from an oak-pine forest to an oak forest and then will entirely disappear. The historical records of *Peromyscus truei lagunae* and *Sorex ornatus lagunae* associate these species with sites where *P. c. lagunae* and *Q. devia* predominate (Woloszyn 1985). However, there is a high probability that these two tree species will lack the conditions of climatic suitability allowing them to survive if temperature rises as much as 1.5 °C and 4.4 °C; therefore, the species associated with them will certainly be highly affected.

It has been shown that suitable climatic conditions for xeric species will expand in area, reaching elevations where more temperate conditions currently exist (Monroy-Gamboa *et al.* 2021), so *P. eva* may populate the area where *P. t. lagunae* currently thrives.

The analysis of species associated with desert ecosystems shows an expansion of the area of distribution and elevational range, so the overall modeling suggests the replacement of forest species by species with xeric characteristics. *Chaetodipus rudinoris* and *C. spinatus*, species that are characteristic and closely associated with the desert, broaden their potential elevational range because niche models project the expansion of areas with xeric climates; this implies that these species will gradually colonize higher elevations and replace the species that inhabit current forests.

Worldwide, the five years with the highest temperatures since 1990 have been recorded from 2015, with 2020 being the year with the second-highest temperature. Indeed, temperature has increased by 1.25 °C, *i. e.,* we have nearly reached the 1.5 °C rise that was formerly projected to occur not before 2050 (Ripple *et al.* 2021); it has now been envisaged that limiting the temperature rise to even 2 °C will be an unattainable goal (IPCC 2021). These facts, combined with the virtually absent local anthropic influence on the environment and the results of boreal plant species showing a collapse and the expansion of xeric mammals, allow hypothesizing that forest mammals such as *S. o. lagunae* and *P. t. lagunae* are undergoing an apparently irreversible local extinction process directly resulting from a climate change effect that causes variations in environmental parameters. In the present case, these will not be favorable for the oak-pine forest and will likely cause its extinction in the short term.

The results obtained indicate that even for an area characterized by restricted access and with low or no anthropogenic impact, the 1.5 °C and 4.4 °C temperature-rise scenarios will directly impact the oak-pine forest. Changes in the forest as a vegetation type will have an immediate impact on the associated fauna. The results of our analyses point to the possibility of local extinctions of *P. t. lagunae* and *S. o. lagunae*, mammal populations that are endemic to this sky island associated with different historical and climatic processes in the Baja California peninsula. The changes in climate that previously occurred historically have been of lower intensity and over longer periods of time, allowing these species to survive. By contrast, the current climate change is occurring faster than the capacity of these species to adapt; seemingly, the current rise in temperature driven by anthropic causes will inevitably lead to the local extinction of these species.

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Geographic patterns of electrophoretic and morphological variation in the sagebrush least chipmunk (*Tamias minimus scrutator*)

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Variation and differentiation among populations provide a framework to decipher how populations are, or are not, changing due to gene flow, genetic drift, and selection. The sagebrush least chipmunk (*Tamias minimus scrutator*) is distributed in arid and semi-arid habitats throughout much of the Great Basin and adjacent regions. The broad distribution and variation in elevation of populations make this a good system to assess population variation and the forces shaping differentiation. Here, we use allozyme and morphological datasets to: 1) assess the relative roles of geographic locality and elevation of populations in shaping population structure; 2) examine the level of differentiation of peripheral and isolated populations; and 3) compare the genetic and morphological signals of population variation and structure. We sampled 312 individuals from 12 *T. minimus scrutator* populations and other areas of their distribution. Individuals were measured for 27 genetic and 61 morphological traits. These datasets were analyzed to determine the distribution of variation and the differentiation among populations and tested for correlations with geographic distance and elevation. Multiple approaches were used to thoroughly compare the signals from each dataset. We found 13 polymorphic electrophoretic loci with most of the variation structured among populations within regions. Eight loci exhibited elevational heterogeneity but most high-elevation populations showed no heterogeneity among populations. Thirty-two morphological characters varied among populations but with no discernable trends across regions or elevations. Populations had varying levels of asymmetric distinctness in morphological characters, but there were no significant differences among populations. Morphological and genetic distance measures were correlated and there was some evidence of a correlation of genetic and geographic distance. We also found some correlation of asymmetric distances with morphological or genetic distances at smaller scales. There was substantial variation of genetic and morphological traits among sagebrush least chipmunk populations. Each population had a unique genetic signature and significant morphological differentiation. Our results suggest that genetic drift is contributing to the structure of these populations, with some evidence of selection shaping the distribution of variation at different elevations. The peripheral populations had mixed signals of isolation among the different datasets, with an overall signature suggesting that genetic drift is also driving the variation among these populations. The different measures of population variation yielded inconsistent signals of population structure, highlighting the need for multiple approaches to assess population variation. The variation among sagebrush least chipmunk populations is impacted by a variety of factors and contemporary investigations may reveal populations responding to alterations in habitat and climate.

La variación y diferenciación entre poblaciones proporcionan un marco para descifrar cómo las poblaciones están cambiando o no debido al flujo de genes, la deriva genética y la selección. La ardilla listada (*Tamias minimus scrutator*) se distribuye en hábitats áridos y semiáridos en gran parte del Great Basin y regiones adyacentes. La amplia distribución y la variación en la elevación de las poblaciones hacen de este un buen sistema para evaluar la variación de la población y las fuerzas que dan forma a la diferenciación. Aquí, utilizamos conjuntos de datos morfológicos y aloenzimáticos para: 1) evaluar los roles relativos de la localidad geográfica y la elevación de las poblaciones en la configuración de la estructura de la población; 2) examinar el nivel de diferenciación de poblaciones periféricas y aisladas, tambien; y 3) comparar las señales genéticas y morfológicas de la variación y estructura de la población. Tomamos muestras de 312 individuos de 12 poblaciones de *T. minimus scrutator* de su distribución. Se midieron 27 rasgos genéticos y 61 morfológicos de los individuos. Estos conjuntos de datos se analizaron para determinar la distribución de la variación y la diferenciación entre poblaciones y se probaron las correlaciones con la distancia geográfica y la elevación. Encontramos 13 loci electroforéticos polimórficos con la mayor parte de la variación estructurada entre poblaciones dentro de las regiones. Ocho loci mostraron heterogeneidad de elevación, pero la mayoría de las poblaciones de gran altitud no mostraron heterogeneidad entre las poblaciones. Treinta y dos caracteres morfológicos variaron entre poblaciones pero sin tendencias discernibles entre regiones o elevaciones. Las poblaciones tenían distintos niveles de distinción asimétrica en los caracteres morfológicos, pero no hubo diferencias significativas entre las poblaciones. Las medidas de distancia morfológica y genética se correlacionaron y se encontró evidencia de una correlación de distancia genética y geográfica. También encontramos alguna correlación de distancias asimétricas con distancias morfológicas o genéticas a escalas más pequeñas. Hubo una variación sustancial de rasgos genéticos y morfológicos entre las poblaciones de la ardilla listada. Cada población tenía una firma genética única y una diferenciación morfológica significativa. Nuestros resultados sugieren que la deriva genética está contribuyendo a la estructura de estas poblaciones, con alguna evidencia de selección que da forma a la distribución de la variación en diferentes elevaciones. Las poblaciones periféricas tenían señales mixtas de aislamiento entre los diferentes conjuntos de datos, con una firma general que sugiere que la deriva genética también está impulsando la variación entre estas poblaciones. Las diferentes medidas de variación de la población arrojaron señales inconsistentes de la estructura de la población, destacando la necesidad de múltiples enfoques para evaluar la variación de la población. La variación entre las poblaciones de ardillas menos artemisas se ve afectada por una variedad de factores y las investigaciones contemporáneas pueden revelar poblaciones que responden a alteraciones en el hábitat y el clima.

Keywords: Developmental asymmetry; genetic drift; natural selection; population structure; western North America.

Introduction

Small mammals in western North America tend to have population structure influenced by historical biogeography across the highly variable topography of the landscape (Hewitt 1996; Riddle 1996; Brunsfeld *et al.* 2001). The genetic and morphological variation in these populations exhibit a range of population structure, from highly diverged populations (*e. g., Tamias amoenus*, Demboski and Sullivan 2003; *Chaetodipus intermedius*, Hoekstra *et al.* 2004) to species with relatively homogeneous populations (*e. g., Dipodomys heermanni*, Benedict *et al.* 2019), illustrating that although there are some shared biogeographic patterns (Arbogast and Kenagy 2008), small mammal species often have unique signatures of population structure that reflect species-specific ecologies. In addition to the role of historical biogeography, abiotic factors, such as elevation, may exert selective pressures that further impact population structure. Examining variation across populations that inhabit a range of habitat types can help identify the intrinsic traits and habitat characteristics that drive these differences in population variation and help develop testable hypotheses about population differentiation.

Assessments of variation across populations can differ according to different traits examined. Several studies have indicated at least some degree of independence between morphological and genetic datasets (*e. g.,* Turner 1974; Avise *et al.* 1975; King and Wilson 1975; Smith and Patton 1984; Hoekstra *et al.* 2004; Hornsby and Matocq 2014), supporting the need for a multi-pronged approach to assessing variation. One explanation for the lack of concordance between morphological and genetic data may be the strong influence of environmental and developmental factors on morphological features (Smith and Patton 1984). Many morphological characters used for systematic studies have a significant degree of sexual dimorphism and age-related variation, which must be controlled for (Kennedy and Schnell 1978). Variation in discontinuous or quasi-continuous characters that result from developmental factors coupled with environmental pressures (Waddington 1953) are thought to be due to the action of a threshold effect on underlying continuous variation (Grewal 1962). Minor deviations from normal morphological appearance can be measured by comparing differences between the right and left sides for a bilateral character and is termed asymmetry. Levels of asymmetry in these morphological traits have been related to the genetic environment (Soulé 1967; Soulé and Baker 1968; Leary *et al.* 1985). Any factor that destroys coadapted gene complexes is hypothesized to increase asymmetry.

Assessing the role of geography, elevation, and location within an organism's range in shaping morphological and genetic variation can be done with species that inhabit a variety of habitats across a broad distribution. The widely distributed least chipmunk (*Tamias minimus*) exploits a number of habitat types including forest (mesic), alpine tundra (montane), and Great Basin sagebrush (semi-arid). One subspecies, the sagebrush least chipmunk (*Tamias minimus scrutator*) is a good model for exploring intra- and inter-population variations in phenotype and population dynamics. Its geographic distribution covers substantial portions of the Great Basin (Hall and Kelson 1959) and appears coincident with the availability of arid sagebrush habitats (Johnson 1943), which it can successfully exploit due to an ability to tolerate higher heat loads than other chipmunk species (Heller and Poulson 1972). The populations found at high elevation (up to 3,200 masl) are thought to inhabit ecologically marginal habitats because otherwise suitable, but unoccupied, habitat extends to around 3,700 masl in some parts of its range. In some parts of its range, *T. m. scrutator* has been excluded from adjacent suitable habitats by competitive interactions with other chipmunk species (Heller 1971) or by habitat preference (States 1976). Within the range of this one subspecies, isolated populations, populations in ecologically marginal habitats, and populations representing a wide geographic, and hence, environmental range, can be found, including in areas with no congeneric competition. Their elevational distribution also allows us to examine the potential role of selection at different elevations in shaping genetic and morphological traits. Presently, *T. m. scrutator* is found only at higher elevations in the southern part of its range, in the mountains on both sides of the Owens Valley, but not the valley itself (Sullivan 1985). Here, we investigate populations of *T. m. scrutator* using multiple data types to determine how comparable different data types are and characterize variation across these populations.

We used genetic and morphological data to characterize the variation in sagebrush least chipmunk populations and address three questions: 1) Is population variation structured by elevation or geography? 2) Are geographically peripheral or isolated populations differentiated or distinct from other populations? 3) Do the genetic and morphological traits show consistent patterns?

The data and analyses presented here are part of a Ph.D. dissertation (Baccus 1986) conducted under the guidance of Dr. W. Z. Lidicker, Jr. Although there have been many advances in the methods for collecting and analyzing genetic and morphological data used for these types of investigations, we believe that the questions we address and the variation we found are relevant to contemporary research. Our findings are pertinent to the mammalogical community, particularly to researchers of least chipmunks, and serve as a source of baseline data and generator of new hypotheses to be tested.

Materials and Methods

Specimens examined. Specimens of *T. minimus scrutator* from the Great Basin region of western North America were collected during the spring and summer of 1979 and 1980. Twelve sampling sites (Figure 1, Supplemental Table 1) were selected in sagebrush-dominated habitats, at different elevations across the range of the sagebrush least chipmunk.

The targeted populations were first treated as 10 populations, but analyses supported splitting each of two populations (Pueblo Valley- PV and Malheur - MO in Oregon, see Results) so we analyzed 12 populations, with all but those four (PV1, PV2, MO1, MO2) designated based on sampling locality. The four sites in eastern Oregon (PV1, PV2, MO1, MO2) represent low-elevation populations (1,200 masl) in the geographic center of the subspecies range. One site in central Nevada (Gamble Basin - GB) was chosen to represent an isolated population, near the geographic center of the subspecies range, with intermediate elevation (1,800 masl). The other sites were all in east-central California and bordering Nevada. Three sites (June Lake – JL, Sand Canyon – SC, Coyote Flats – CO) were sampled from the eastern slope of the Sierra Nevada. Two were intermediate elevation (JL and SC; 2,100 to 2,500 masl), and one represented a high-elevation sample (CO; 3,000 masl). Four sites were sampled from the White Mountains, three (Queen Canyon – QC, Big Prospector Meadow – BP, Silver Peak – SP) from high elevations (2,900 to 3,200 masl) and one from an intermediate elevation (Dead Horse Meadows – DH; 2,100 masl). We calculated both direct distance and indirect distance among sites (Supplemental Table 2). Indirect geographic distances were measured following presumed paths of migration, which were the shortest distances that only went through sagebrush habitat. Indirect distances were slightly longer than direct distances, but they were highly correlated. For this reason, and because we do not know the full spatial extent of the sampled populations, we report most analyses based on direct distances.

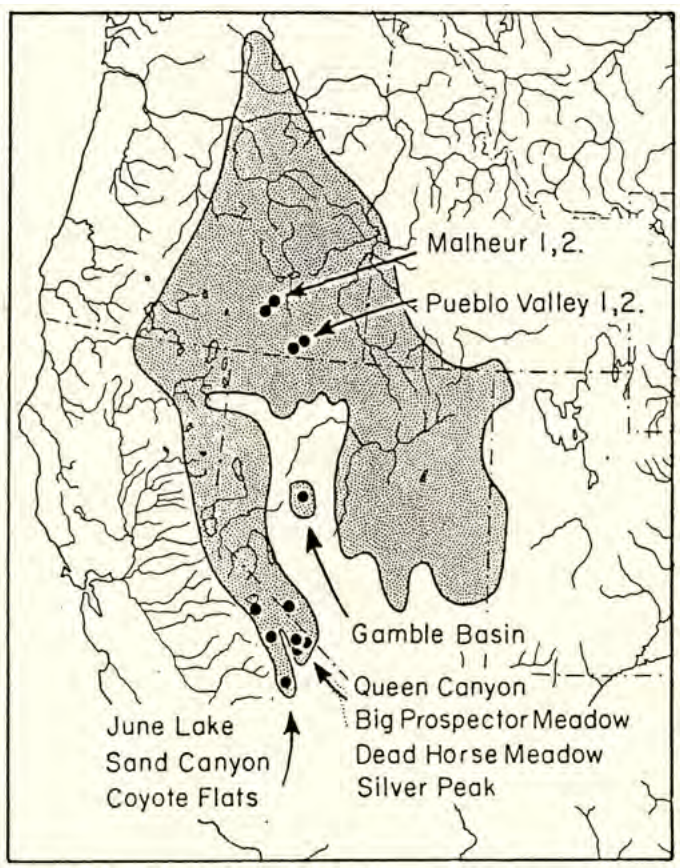

Figure 1. Map of the geographic range of the sagebrush least chipmunk, *Tamias minimus scrutator*, showing the locations of the populations sampled in Oregon, California, and Nevada.

Table 1. Estimates of genic variability at 27 presumptive allozyme loci in *Tamias minimus scrutator*. Standard errors are in parentheses for the mean heterozygosity (H) and average number of alleles (A). Percent polymorphic loci (P) is estimated for both the 0.01 and the 0.05 criteria (= frequency of the alternative allele).

Population	*n*	*H*	*A*	*P*(0.01)	*P*(0.05)
Malheur 1 (MO1)	18	8.42 (.02)	1.70 (.26)	33.33	29.63
Malheur 2 (MO2)	26	10.36 (.01)	1.89 (.26)	48.15	29.63
Pueblo Valley 1 (PV1)	23	9.16 (.01)	1.89 (.37)	37.04	22.22
Pueblo Valley 2 (PV2)	29	9.70 (.01)	1.96 (.30)	48.15	22.22
Gamble Basin (GB)	14	9.55 (.01)	1.63 (.23)	29.63	22.22
June Lake (JL)	25	9.79 (.01)	1.81 (.27)	44.45	33.33
Sand Canyon (SC)	32	10.78 (.01)	1.78 (.32)	33.33	25.93
Coyote Flats (CO)	22	9.40 (.01)	1.59 (.25)	33.33	22.22
Queen Canyon (QC)	17	9.41 (.01)	1.59 (.24)	29.63	22.22
Big Prospector Meadow (BP)	33	10.05 (.01)	1.85 (.29)	40.74	25.93
Silver Peak (SP)	18	10.00 (.02)	1.74 (.27)	37.04	29.63
Dead Horse Meadow (DH)	22	10.76 (.01)	1.56 (.21)	29.63	25.93
Mean	23.25	9.87	1.75	37.04	25.93

Data collection and management. Collection methods included Sherman livetraps (H. B. Sherman Co., Tallahassee, Florida, USA), Museum Special snap-traps, and shotgun. A total of 280 individuals were collected from the target 12 populations. An additional 32 specimens were collected within the range of *T. m. scrutator*, but only one or a few from each site so they did not constitute a population-level sample. Analyses and comparisons of populations used the 280 individuals from the 12 populations, but all 312 specimens were used for pooled analyses. Species identifications were based on morphology and geography and our analyses (see Results) confirmed all specimens were *T. minimus*. We assigned them as *T. m. scrutator* based on the geographic distribution of the subspecies. Skulls were collected from all the animals captured and post-cranial skeletons and skins were collected from some of the animals. There was variation in sample sizes among the characters measured due to damage from birdshot. Tissue samples (liver, heart and kidney, and blood) were frozen at -70°C for later processing.

Chipmunks were measured for 27 genetic (Supplemental Table 3), 50 morphological (Supplemental Table 4), and 11 lateral pairs of morphological cranial variants (to assess asymmetry; Supplemental Table 5). Sex was determined for all individuals, and they were assigned to one of seven age categories based on tooth wear and reproductive condition (Smith 1977). Sample sizes ranged from $n = 14$ (GB) to $n = 33$ (BP)

All individuals were analyzed for a standard set of 27 presumptive allozyme loci using established electrophoretic techniques (Selander *et al.* 1971) at the Museum of Vertebrate Zoology, University of California, Berkeley. Although not generally used in contemporary research, assessing allozyme alleles (the various forms of enzymes coded for by a single locus) was a useful method for characterizing genetic diversity prior to the development of genetic sequencing methods. Fifty morphological characters were measured (Supplemental Table 4). Four were external characters measured to the nearest mm. The remaining 20 skull and 26 skeletal characters were measured to the nearest 0.05 mm with dial calipers. Eleven paired sets of lateral epigenetic cranial threshold variants (hereafter lateral variants; Supplemental Table 5) were identified and tallied on 312 individuals (170 males, 142 females). These variants were scored as present (+) or absent (-).

Analyses. We assessed genetic variation within and among populations using goodness-of-fit statistics (Sokal and Rohlf 1969) and Wright's F-statistics calculated across all alleles (Wright 1978) with their significance calculated using the procedure described in Eanes and Koehn (1978). All populations were tested for Hardy-Weinberg proportions using Levene's (1949) corrections for small sample sizes in the estimation of expected genotype frequencies. Mean heterozygosity (H) by the direct count method, average number of alleles per locus (A), and percent polymorphic loci (P) were calculated for each population.

All morphological characters exhibited considerable sex-by-age interaction when combined over all populations. We attempted to diminish the influence of sexual dimorphism on the variation in characters and eliminate the potential bias due to variation in age distributions (see Baccus 1986). We calculated one-way analysis of variance (ANOVA) and t-tests for each character measured across the 12 populations and between sexes and age categories. A multiple range test using the Student-Newman-Keuls procedure was also used to assess trends in the means of the characters across populations. We calculated univariate comparisons of differences between populations for the external and skull characters and the skeletal characters using t-tests. Additionally, morphological variation was quantified for each population separately as a multivariate coefficient of variation (CV_n) following the procedure of Van Valen (1974). CV_n is independent of the number of variables used and so is numerically comparable to the univariate CV.

To compare the frequencies of the lateral variants among the 12 populations, we used a test of independence using the G-statistic. We calculated a sums-of-squares simultaneous-test-procedure (SS-STP) for characters with significant G-tests. We assessed the asymmetry measures for directional asymmetry using the Student's t-test for paired comparisons, and for antisymmetry using a chi-square test for departures from normality (Soulé 1967). Additionally, the data were analyzed using Kendall's coefficient of concordance, W, to determine if the level of fluctuating asymmetry is similar across all characters measured in the populations (Siegel 1956).

Relationships among populations within and between regions and within and between elevations were compared with geographic distances between populations. Genotype and allele frequencies were calculated for each population and for each region, each elevation, and the subspecies. Genetic distance measures were calculated using Nei's (1978) genetic identity (I) and Roger's (1972) genetic distance (S). We tested correlations between populations and elevation with a G-test of heterogeneity using allele frequencies. ANOVA was used to compare the frequency of the common alleles across populations and between regions and between elevations. We used Spearman's rank correlation to determine any north-south or east-west clinal tendencies.

To evaluate the influence of geography on morphological differences among populations, we employed two separate distance indices. The first was Mahalanobis D^2 (Reyment 1961; Gould and Johnston 1972). The mean of a character was substituted for missing values for that character in an individual. Mahalanobis D^2 is highly affected by the sign and degree of correlation between the characters used. However, a major advantage of using Mahalanobis D^2 is that it accounts for variation within populations. The significance of differences between population samples was determined by a multivariate analysis of variance using the BMDP(3D) program (BMDP Statistical Software, Inc., Los Angeles, California, USA).

The second morphological distance index we used was Lidicker's Σd (Lidicker 1962). This index uses the differences between means of the characters divided by the minimum significant difference (msd), such that only mean differences greater than the amount that might be due to chance are treated as real differences. We used the estimate of msd equivalent to $2(SE_x)_1 + 2(SE_x)_2$. This yields a conservative estimate with confidence limits usually well in excess of 95% (Lidicker 1962). The ratio of the difference between means for one character and the msd yields dimensionless numbers $d_1, d_2, ..., d_n$ for successive characters. Adding these pure numbers gives an estimate of total differentiation between a pair of samples in the characters studied (Σd). This index was modified slightly from Lidicker (1962) by including all characters, not just the ones with means greater than the msd. A given amount of differentiation between two samples in close geographic proximity has more biological significance than the same amount of differentiation between a geographically distant pair of samples. Lidicker (1962) suggested compensating for this by dividing the total differentiation by the distance between the two samples. We used indirect distances measured using presumed paths of gene flow between populations (Supplemental Table 2). This yields the Index of Differentiation (ID) representing the proportion of significant change that occurs between the two samples per kilometer. If distance is kept constant, ID will tend to increase as gene flow is reduced (Lidicker 1962).

We conducted a discriminant function analysis to visualize patterns of geographic variation across the 12 populations. We constructed phenograms from the genetic distance measures using Roger´s S and for the cranial dataset using Mahalanobis D^2 values and Lidicker's Σd values. Divergence measures of the 12 populations based on the asymmetry estimates were calculated following Grewal (1962). Correlations (Sokal and Rohlf 1969) were calculated between all the biological distance measures (Nei's I and Roger's S; Mahalanobis D^2 and Lidicker's Σd; asymmetric distinctiveness) and the geographic distance to determine the degree of concordance between the measures.

Results

Genetic variation within and among populations. The two Malheur (MO1, MO2) sites and the two Pueblo Valley sites (PV1, PV2) were first thought to be two populations (Malheur and Pueblo Valley). However, electrophoretic data at four loci (ALB-2, ADA, P-LGG, P-LA) revealed a Wahlund effect, therefore these two areas were each subdivided into two populations (MO1 and MO2, PV1 and PV2) such that each population had a sample size of at least 18 individuals captured within 0.75 miles (1.2 kilometers) of one another. The subdivided populations exhibited Hardy-Weinberg proportions. Because of the subdivisions and the spatial constraints placed on the "new" populations, 19 individuals from Malheur and nine individuals from Pueblo Valley were excluded from the population analyses but were included in analyses for the whole subspecies.

Of 27 presumptive loci, nine loci were slightly polymorphic, and four were highly polymorphic. Mean heterozygosities (H) ranged from 8.42 % at MOl to 10.78 % at SC and 9.86 % for the subspecies. The average number of alleles per locus (A) and percent polymorphic loci (P) were similar across populations (Table 1). Two criteria, 0.01 and 0.05 minimum frequency of alternate alleles, have been suggested for evaluating the polymorphism of a locus (Ayala *et al.* 1972; Nevo *et al.* 1974). Using the 0.01 criterion, virtually all rare alleles contributed to the values of P. Therefore, we used the values of P with the 0.05 criterion as it is much less affected by sample size. All values fell within two standard deviations of the mean and hence are considered to reflect a single statistical population. Across 170 comparisons of genotype, only three indicated a significant deviation from Hardy-Weinberg expectations: MO1 and SP at the ALB-2 locus and PV1 at the P-LA locus. With the large number of tests conducted, one would expect occasional (eight in this case) spurious differences to be found.

Geographic and elevational patterns in genetic variation. There was no pattern in any of the three indices (P, H, A) that could be construed as regional or elevational. However, there were no unique alleles found in populations located south of the 37° 30' N parallel, suggesting some geographic role for shaping population variation. Generally, the ability to detect unique alleles increases with sample size. However, the two trapping localities (BP and SC) with the largest sample sizes contained no unique alleles, and the trapping locality with the lowest sample size (GB) had the largest proportion of individuals exhibiting a unique allele (35.7 %, Table 2). For the other four of the southernmost populations, the number of individuals with a unique allele ranged from 3.4 to 12.0 %. Measures of genetic distance (Roger's S) and identity (Nei's I) had similar patterns (Supplemental Table 6). The CO population had the largest average genetic distance using Roger's S and the least average genetic identity using Nei's I. A phenogram constructed from the values of Roger's S between populations also showed CO as the most different (Figure 2). This phenogram also shows MO2 as being quite different from the other low-elevation populations and the other northern populations.

The patterns of genetic differentiation between populations were not consistent across loci. Regional (*i. e.*, grouping populations by mountain ranges) heterogeneity was found in two of the 13 heteroallelic loci. The White Mountains population samples (BP, SP, DH, QC) were significantly different ($P < 0.05$ and $P < 0.01$ for αGPD and SDH, respectively) from the Sierra Nevada population samples (CO, JL, SC). Spearman's Rank correlation revealed a rela-

Table 2. Distribution of unique alleles across populations and loci. Total number of alleles at each locus are in parentheses. Populations that are not listed (SC, CO, QC, BP, SP, DH) had no unique alleles.

	Sample size	# Unique alleles	Loci w/unique alleles	% Individuals w/allele	% Individuals w/ a unique allele
MO1	18	1	ALB-2 (13)	5.6	5.6
MO2	26	2	IDH-1 (4)	3.8	7.7
			CK-3 (3)	3.8	
PV1	23	1	LDH-1 (2)	4.3	4.3
PV2	29	1	ALB-1 (2)	3.4	3.4
PV*	1	1	CK-2 (3)	----	----
GB	14	3	P-LGG (4)	2.86	7.5
			MPI (3)	0.71	
			6-PGD (2)	0.71	
JL	25	3	IDH-1 (4)	0.40	12.0
			IDH-1 (4)	0.80	
			ACON1 (2)	0.40	

*from one individual removed from the detailed population analyses due to subdivision of the Pueblo Valley sample into two populations.

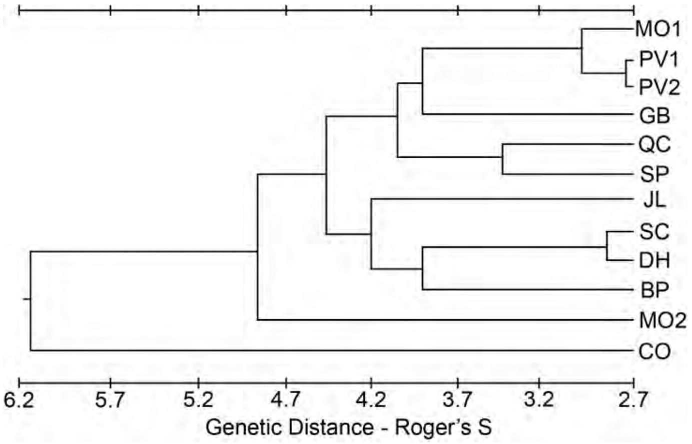

Figure 2. Phenogram from the cluster analysis using an unweighted pair-group method of the genetic distance estimated using Roger's S.

tionship between common allele frequency and longitude (P < 0.05) for SDH, supporting an east-west pattern differentiating the Sierra Nevada and White Mountains.

Wright's F_{PT} (heterogeneity among populations), F_{RT} (heterogeneity among regions), and F_{PR} (heterogeneity among populations within regions) are in Table 3. The populations were divided into four regions based on geographic proximity: Oregon (MO1, MO2, PV1, PV2), Stillwater Mountains (GB), Sierra Nevada (JL, SC, CO), and White Mountains (QC, BP, SP, DH). For 16 of the 21 loci, the values of F_{PR} exceeded those of F_{RT} indicating more variation among populations within regions than between regions. The loci that were exceptions to the pattern (SDH, 6-PGD, MPI, NP, CK-2) showed significant F_{RT} values.

Eight of the 13 polymorphic loci showed elevational heterogeneity (G-test of independence) without any geographic distance correlations or heterogeneity within elevations. The high-elevation populations exhibited no within-elevational heterogeneity with the exception of CO (also peripheral). Elevational heterogeneity (observation of a single allele in samples from similar elevations, but different from alleles at other elevations) was found for the CK-3 locus ($P < 0.001$), the PGM locus ($P < 0.05$), and the MDH-2 locus ($P < 0.05$) at mid and/or high elevations and the GOT-1 locus ($P < 0.05$) at low elevations. The mid-elevation JL, SC, and DH populations exhibited the greatest degree of polymorphism, while the low-elevation samples had the lowest degree of polymorphism for the CK-2 locus ($P < 0.001$) and the PGI locus ($P < 0.01$). A slight cline was exhibited by the IDH-1 locus ($P < 0.05$) with the high-elevation samples exhibiting the greatest degree of polymorphism and the low-elevation samples the lowest degree of polymorphism. We also found a latitudinal correlation in the IDH-1 locus (Spearman's Rank correlation, $P < 0.05$). The highly polymorphic P-LA locus exhibited only elevational heterogeneity ($P < 0.001$), even when the CO sample was removed from consideration. The CO sample contained only two of the five alleles present in all other populations plus a reversal of the dominant allele. The highly polymorphic P-LGG locus also exhibited elevational heterogeneity, but the heterogeneity between elevations was due mainly to the low elevations possessing a greater frequency of alternate alleles ($P < 0.01$). The fact that the low-elevation populations were also geographically distant complicates the pattern of elevational heterogeneity. There was a slight degree of heterogeneity ($P < 0.05$) between the mid- and high-elevation samples, but it disappears when GB, which is geographically distant, is removed from consideration. The Sierra Nevada and White Mountains samples are homogeneous with respect to this locus.

Supplemental Table 7 gives the values for F_{PE} (measures heterogeneity among populations within elevations), F_{ET} (measures heterogeneity among elevations), and F_{PT} (measure the overall degree of heterogeneity among populations) for the loci that were heteroallelic in the Sierra Nevada and White Mountains populations. Restricting the analysis to these two areas eliminated biases due to region. The Sierra Nevada and White Mountains are adjacent and parallel mountain chains containing populations that were classified as either mid- or high-elevation. These data indicated that genetic structuring did not follow an elevational pattern. Twelve of the 13 loci exhibited more variation among populations within elevations than between elevations. One locus (P-LA) had high within-elevation heterogeneity, likely due to the uniqueness of the CO population.

Table 3. Summary of F_{PT}, a measure of among population variance; F_{PR}, a measure of among population variance within regions; and F_{RT}, a measure of among region variance in allele frequency for electrophoretic loci in the sagebrush least chipmunk.

Locus	F_{PR}	F_{RT}	F_{PT}
αGPD	0.0674	0.0469***	0.1111***
ADA	0.0561	0.0358***	0.0899***
PLA	0.0521	0.0387***	0.0888***
PLGG	0.0377	0.0288**	0.0654***
ALB-2	0.0410	0.0214**	0.0615***
MPI	0.0209	0.0374***	0.0575**
SDH	0.0035	0.0522***	0.0555**
PGI	0.0367	0.0170*	0.0531**
CK-2	0.0111	0.0410***	0.0516**
IDH-1	0.0323	0.0133	0.0452*
CK-3	0.0216	0.0207*	0.0419*
GOT-1	0.0217	0.0171*	0.0384*
PGM	0.0214	0.0136	0.0347
6PGD	0.0061	0.0272**	0.0331
MDH-2	0.0245	0.0065	0.0308
NP	0.0053	0.0150*	0.0202
GDA	0.0157	0.0037	0.0193
LDH-1	0.0149	0.0040	0.0188
ACON1	0.0117	0.0053	0.0169
ALB-1	0.0216	0.0032	0.0158
IDH-2	0.0103	0.0035	0.0138
Mean	0.0249	0.0215**	0.0459*

* P<0.05, ** P<0.01, *** P<0.001

When the CO sample was removed from consideration, G-tests showed no significant heterogeneity within low- and mid-elevation samples, and the heterogeneity within high-elevation samples disappeared.

Two of the highly polymorphic loci (ALB-2, ADA) were responsible for the Wahlund effects that necessitated a division of the Pueblo Valley and Malheur samples. The high degree of populational heterogeneity in the ALB-2 samples ($P < 0.001$) confounded any elevational heterogeneity that might be present. Among the low-elevation samples, PV1 and PV2 were significantly different ($P < 0.001$) from MO1 and MO2 while, within each area, there was homogeneity. All mid- and high-elevation populations were unique at these loci.

The ADA locus showed a pattern of elevational heterogeneity overlain with a pattern of latitudinal heterogeneity (Spearman's Coefficient of Rank Correlation, $P < 0.05$). There was homogeneity among the low-elevation samples; however, they were significantly different from both the mid-elevation samples ($P < 0.001$) and the high-elevation samples ($P < 0.001$). There appears to be a break in continuity around the 37° 30′ N parallel among the mid-elevation samples, causing JL and GB to be grouped and SC and DH to be grouped even though these populations are not geographically close. Among the high-elevation populations, the break in continuity may occur around the 37° 20′ N parallel which would group the three White Mountains populations (QC, SP, BP) together leaving the CO population (in the Sierra Nevada) unique. Whether the latitudinal break is valid for the high-elevation populations or the populations are exhibiting regional heterogeneity could not be determined from this dataset.

Geographic and elevational patterns in morphological variation. Twenty-two of the 24 skin and skull characters (Table 4) and 12 of the 26 postcranial skeleton characters showed significant interpopulation variation (Supplemental Table 8). A sums of squares-simultaneous test procedure (SS-STP) across means of the characters in the cranial dataset with significant interpopulation variation showed no discernable trends across regions or elevation. However, the CO samples had the greatest mean value for 10 of the 24 characters; only 1.2 cases would be expected by chance alone. The BP sample had the greatest mean value for three characters. MO1, MO2, PV1, and PV2 (all low-elevation samples) were grouped together or separated by only SC, JL, or GB in eight characters. The four southernmost populations (BP, SP, DH, CO) were grouped together for 10 characters. For 19 characters, there were same-elevation, same-geographic area clusters (MOI-MO2, PVI-PV2, JL-SC, QC-BP, BP-SP).

For the cranial dataset, the MO1, CO, and BP samples had the highest multivariate CV_n and the SP and PV1 samples had the lowest values. Overall, the postcranial skeletal characters had higher CV_n than the skin and skull characters. The CV_n had no discernable geographic trends.

The morphological distance indices, Mahalanobis D^2 along with F-values and a modification of Lidicker's Σd along with an Index of Differentiation, recovered similar distances among populations, with some notable exceptions (Supplemental Table 9). SC was significantly different from all other populations and CO was significantly different from all but two (SP and DH, the other southernmost populations). JL exhibited significant differences from five other populations, with no apparent pattern to the distribution of differences. This population, centrally located (both geographically and elevationally), had one of the smallest values for both Mahalanobis D^2 and Lidicker's Σd. GB, the most geographically isolated population, had the highest Mahalanobis D^2 value but one of the smallest for Lidicker's Σd. GB also had the smallest average Lidicker's ID value, which is not unexpected given that GB is geographically distant from the other sampled populations. Overall, a comparison of Lidicker's ID against geographic distance between the populations yielded a significant negative correlation ($r = -0.44$, $P < 0.001$), indicating that within the subspecies, differentiation among populations did not consistently increase with the distance between them. For the cranial dataset, there was no correlation between Lidicker's Σd and geographic distance ($r = 0.15$) nor between Mahalanobis D^2 and geographic distance ($r = 0.02$).

A phenogram constructed from the Mahalanobis D^2 values for the cranial dataset (Figure 3) indicated GB was the most different and CO and SP clustered closely together. DH was grouped with PV1 and PV2, and the rest of the populations formed a fourth cluster. The phenogram constructed from the modified Lidicker's Σd values for the cranial dataset (Figure 4) showed a clustering of the southernmost populations (CO, SP, DH, BP), but with JL and QC associating with the northern populations; SC was intermediate.

Geographic and elevational patterns in asymmetry. Divergence of the 12 populations was calculated based on the frequencies of asymmetry (Supplemental Table 10). None of the populations was significantly different from any other population. Asymmetry between the right and left sides of the cranium was recorded for 11 bilateral variants (22 total, 11 characters on each side). The JL, SC, and DH samples had the highest level of asymmetry and CO had the lowest level

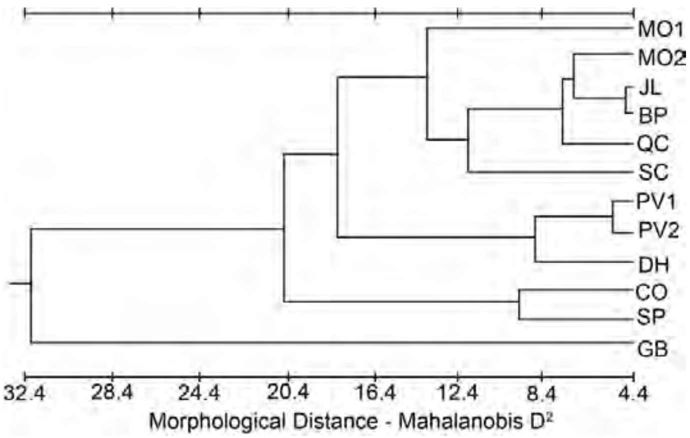

Figure 3. Phenogram from the cluster analysis using the unweighted pair-group method for population distances based on Mahalanobis D^2 from the cranial dataset.

Table 4. Multiple range tests (Student Newman-Keuls procedure) for means of the external and cranial morphological characters (22 of 24) exhibiting significant interpopulation variance after adjustments for sex and age variation for the 12 populations of *Tamias minimus scrutator*. Interpopulation F-values (ANOVA) and significance are below character abbreviations.

1. BDL	MO1	MO2	QC	GB	BP	SP	SC	JL	PV1	DH	CO	PV2
4.9***	|----	----	----	----	----	----	----	----|				
		|----	----	----	----	----	----	----	----|			
			|----	----	----	----	----	----	----	----	----|	
						|----	----	----	----	----	----	----|
2. TAL	SP	DH	GB	BP	QC	CO	MO1	JL	SC	PV2	MO2	PV1
2.2*	|----	----	----	----	----	----	----	----	----|			
		|----	----	----	----	----	----	----	----	----	----	----|
3. HFL	SP	SC	DH	PV2	JL	GB	PV1	BP	MO1	MO2	QC	CO
3.7***	|----	----	----	----	----	----	----	----	----|			
		|----	----	----	----	----	----	----	----	----	----|	
						|----	----	----	----	----	----	----|
4. EAR	BP	MO1	SP	JL	PV2	GB	CO	PV1	MO2	DH	QC	SC
4.2***	|----	----	----	----	----	----	----	----	----	----	----|	
											|----	----|
5. LNA	QC	MO2	JL	MO1	GB	CO	SC	PV2	PV1	SP	BP	DH
3.0***	|----	----	----	----	----	----	----	----	----	----	----	----|
7. GSL	MO2	MO1	QC	JL	PV1	SP	DH	SC	PV2	GB	BP	COI
3.2***	|----	----	----	----	----	----	----	----	----	----|		
		|----	----	----	----	----	----	----	----	----	----	----|
8. BSL	MO2	SC	MO1	DH	QC	JL	PV1	SP	PV2	CO	BP	GB
3.0***	|----	----	----	----	----	----	----|					
		|----	----	----	----	----	----	----	----	----	----	----|
9. TRL	QC	MO2	JL	GB	SC	SP	BP	PV1	MO1	CO	DH	PV2
2.5**	|----	----	----	----	----	----	----	----	----	----	----|	
				|----	----	----	----	----	----	----	----	----|
1.9*	|----	----	----	----	----	----	----	----	----	----	----|	
			|----	----	----	----	----	----	----	----	----	----|
13. MAL	QC	MO2	MO1	SC	JL	GB	PV1	PV2	DH	BP	SP	CO
2.8**	|----	----	----	----	----	----	----	----	----	----	----|	
			|----	----	----	----	----	----	----	----	----	----|
14. MAD	SC	QC	JL	PV2	MO2	MO1	PV1	DH	SP	GB	BP	CO
3.8***	|----	----	----	----	----	----	----	----	----	----|		
		|----	----	----	----	----	----	----	----	----	----	----|

15. APW	SC	MO2	MO1	PV2	DH	PV1	JL	CO	QC	SP	GB	BP
4.6***	|----	----	----	----|								
		|----	----	----	----	----	----	----	----	----	----|	
			|----	----	----	----	----	----	----	----	----	----|
16. ROD	MO2	MO1	QC	SC	PV1	PV2	GB	JL	DH	SP	CO	BP
5.8***	|----	----	----	----	----|							
		|----	----	----	----	----	----	----	----|			
						|----	----	----	----	----	----	----|
17. CRD	MO1	GB	JL	BP	PV1	MO2	SP	QC	PV2	SC	CO	DH
3.2***	|----	----	----	----	----	----	----	----	----|			
		|----	----	----	----	----	----	----	----	----	----	----|
18.SKD	QC	GB	PV1	JL	MO1	MO2	PV2	SP	BP	CO	SC	DH
4.0***	|----	----	----	----	----	----	----	----	----	----	----|	
											|----	----|
19. ILW	MO2	SC	PV1	PV2	MO1	JL	QC	GB	SP	DH	CO	BP
4.5***	|----	----	----	----	----	----	----	----	----|			
		|----	----	----	----	----	----	----	----	----|		
			|----	----	----	----	----	----	----	----	----|	
							|----	----	----	----	----	----|
20. LOW	SC	SP	MO2	JL	PV2	GB	QC	BP	MO1	PV1	DH	CO
2.8**	|----	----	----	----	----	----	----	----	----	----	----|	
					|----	----	----	----	----	----	----	----|
22. IMW	QC	MO1	JL	PV2	MO2	GB	SP	BP	DH	SC	PV1	CO
3.9***	|----	----	----	----	----	----	----	----	----	----|		
		|----	----	----	----	----	----	----	----	----	----|	
									|----	----	----	----|
23. BOW	JL	SC	GB	MO2	MO1	PV1	PV2	QC	DH	BP	SP	CO
2.4**	|----	----	----	----	----	----	----	----	----	----	----|	
			|----	----	----	----	----	----	----	----	----	----|
24. CWO	QC	MO1	JL	MO2	PV1	PV2	SC	SP	DH	BP	GB	CO
2.8**	|----	----	----	----	----	----	----	----	----	----	----|	
			|----	----	----	----	----	----	----	----	----	----|

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

1. BDL = Body length; 2. TAL = Tail length; 3. HFL- = Hind Foot length; 4. EAR = Ear length; 5. LNA = length of Nasals; 7. GSL = Greater Skull length; 8. BS = Basal Skull length; 9. TRL = Tooth Row length; 10. IFL = Incisive Foramen length; 13. MAL = Mandible length; 14. MAD = Mandible Depth; 15. APW = Angular Process width; 16. ROD = Rostral Depth; 17. CRD = Cranial Depth; 18. SKD = Skull Depth; 19. ILW = Interlacrimal width; 20. LOW = Least Orbital width; 21. GZW = Greatest Zygomatic width; 22. IMW = Intermaxillary width; 23. BOW = Basioccipital width; 24. CWO = Cranial width Obliquely

of asymmetry when averaged over all pairs of lateral variants. Two pairs of lateral variants (FOD and OFD) exhibited significant interpopulation heterogeneity (G = 22.004, $P < 0.05$; and G = 24.256, $P < 0.05$; respectively). For the FOD lateral variants, the interpopulation heterogeneity resulted from a large frequency of asymmetry in JL. Grouping populations by elevation indicated significant (G = 13.530, $P < 0.01$) between-elevation heterogeneity and no significant within-elevation heterogeneity. For the OFD lateral variants, the heterogeneity can be assigned to the White Mountains populations where the high-elevation populations (QC, BP, SP) were significantly different (G = 9.671, $P < 0.05$) from the mid-elevation DH population. The White Mountains high-elevation populations were also significantly different (G = 12.469, $P < 0.01$) from the other high-elevation population (CO). None of the other asymmetry estimates had interpopulation variation, sexual dimorphism, or heterogeneity between age categories. Tests of antisymmetry indicated that no characters we measured had a probability that the variant would be seen more often on one side than the other. All other asymmetries (except for a slight directional asymmetry in the JL population) are assumed to be fluctuating asymmetry, which are the minor departures from complete bilateral symmetry which have no known adaptive advantage. Testing the lateral variants for similarities within populations using Kendall's test for concordance yielded a non-significant value (W = 0.105, $P > 0.50$) indicating the characters form a normal distribution around a mean, supporting the conclusion that they show fluctuating asymmetry. A phenogram based on asymmetric divergences yielded no clear geographic patterns (Figure 5).

Comparisons of genetic, morphological, and geographic patterns. The two morphological distances (Mahalanobis D^2 and Lidicker's Σd) were correlated with the two genetic distance measures (Roger's S and Nei's I; Table 5). Lidicker's Σd was positively correlated with Roger's S and negatively correlated with Nei's I. Mahalanobis D^2 was negatively correlated with Roger's S and positively correlated with Nei's I (though not significantly). Roger's S was the only biological distance measure positively and significantly correlated with geographic distance. Assuming that longer geographic distances tend to distort the accuracy of the biological distance measures, we calculated correlations using only samples located less than 112 km from one another, as measured on a map. Roger's S and geographic distance were no longer correlated in the reduced dataset. Lidicker's Σd and Mahalanobis D^2 were no longer correlated with either Roger's S or Nei's I. Further restriction of the dataset to just the White Mountains and Sierra Nevada populations yielded a significant correlation between Mahalanobis D^2 and the asymmetry divergence measures. Roger's S and Nei's I were still negatively correlated, but the other correlations were no longer significant.

Discussion

Our assessment of variation in sagebrush least chipmunk populations demonstrated substantial differentiation among populations across genetic and morphological traits. The most conspicuous observation from the electrophoretic dataset is that all populations were unique and the unique factors varied among populations. As with the electrophoretic data, the morphological measures for the 12 populations exhibited a considerable degree of interpopulation differentiation. Asymmetries of lateral variants also had attributes of population-level interest. Overall, we found a lack of correlation between geographic distance and differentiation (as measured by the biological distances), supporting *T. m. scrutator* as a single subspecies.

If random genetic drift is the overriding influence in the differentiation of populations, then we expect to find a random pattern of variation between populations. Our findings for the fixation indices for the four major regions (a measure of genetic drift) indicated more differentiation within regions and elevations than between regions or elevations. For example, the two Malheur (MO1, MO2) and the two Pueblo Valley (PV1, PV2) populations exhibited a Wahlund effect in the heterozygosity measures. A random pattern of variation was also seen for six morphological characters. Taken together, these results suggest a considerable role for genetic drift in driving population structure for *T. m. scrutator*.

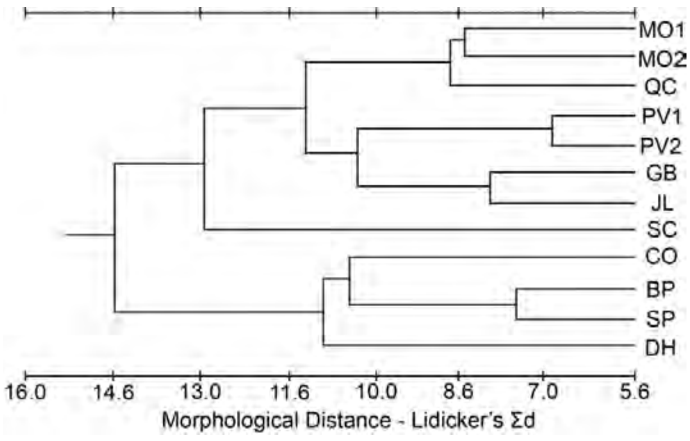

Figure 4. Phenogram from the cluster analysis using the unweighted pair-group method for population distances based on Lidicker's Σd from the cranial dataset.

Population structure. We found that geographic distance and genetic drift are the most likely explanations for how variation is structured across populations but cannot rule out contributions from selection associated with elevation in some populations. Most population differences in the genetic dataset can parsimoniously be attributed to random genetic drift. The fixation indices (Table 3) are essentially measures of genetic drift, probably due to differences in the founding populations (Wright 1978). Reduced levels of gene flow would enhance any population differences originating by genetic drift or selection, and would also tend to maintain differences between the populations.

Population variation potentially resulting from selection at different elevations was suggested by variation at seven genetic loci and one morphological character. We also found an elevational trend for population variation in asymmetry. Elevation was chosen for detecting selection as it has been shown to generate differences in other species, probably due to climatic characteristics (Dunmire 1960; Asdell 1964; States 1976; Baccus *et al.* 1980). Assessment of elevational patterns was complicated by the fact that the populations grouped within the same elevation also tended to be within the same geographic region. However, focusing on just two regions (White Mountains and Sierra Nevada) and two elevations revealed elevational heterogeneity with no regional heterogeneity in four loci. This illustrates that selection may be playing a role in the genetic structuring at these particular loci or at loci linked to them. The case is particularly strong for the CK-2 locus as it exhibited little heterogeneity within elevations. Sagebrush least chipmunks would serve as a good model to compare to the elevational adaptations found in other mammals, such as deer mice (*Peromyscus maniculatus*; Storz *et al.* 2019).

The most prevalent pattern emerging from the morphological dataset is a separation of populations based on latitude irrespective of elevation. Fully half of the 20 characters with a significant F-ratio had little variation within populations grouped according to latitude (Table 4). Populations below the 37° 30′ parallel (CO, BP, SP, DH) formed a subset for 10 characters as did populations located between 37° 30′ and 41° latitude (JL, QC, GB) and the populations above the 41° parallel (MOl, MO2, PV1, PV2). If another division is added at the 43° parallel (separating MOl and MO2 from PVl and PV2), five more characters (for a total of 75 % of the characters with significant F-ratios) conform to this pattern. The remaining 25 % of the morphological characters with

Table 5. Matrix of inter-correlations of biological and geographic distances. The first row of each measurement is correlation coefficients using the complete dataset (*n* = 66); second row is correlation coefficients using only comparisons between populations less than 1° latitude (<112 km) apart (*n* = 27); third row is correlation coefficients using only comparisons between population in the White Mountains and Sierra Nevada (*n* = 21).

	Nei's I	Roger's S	MAH D^2	LID Σd	ASYM	DIRECT GEO
Roger's S	-0.804***					
	-0.922***					
	-0.937***					
Mahalanobis D^2	0.194	-0.260*				
	0.071	-0.157				
	0.047	-0.108				
Lidicker's Σd	-0.329**	0.320**	0.037			
	-0.309	0.321	0.309			
	-0.210	0.168	0.341			
Asymmetry	-0.040	0.060	0.093	-0.218		
	-0.226	0.243	0.325	0.036		
	-0.108	0.093	0.445*	-0.044		
Direct Geographic	-0.098	0.304*	0.028	0.155	-0.202	
	-0.047	0.043	0.196	0.286	-0.066	
	-0.14	0.191	-0.052	0.272	0.071	
Indirect Geographic	-0.127	0.333**	0.084	0.149	-0.183	0.925***
	-0.396*	0.354	0.020	0.287	-0.074	0.422*
	-0.368	0.318	-0.100	0.142	-0.183	0.347*

* P<0.05; ** P<0.01; *** P<0.001

significant interpopulation variation, as well as the occurrence of sexual dimorphism across populations in some of the characters, exhibited a random pattern of variation. This would be expected under the influence of genetic drift, which is further supported by our finding of no unique allozyme alleles south of the 37° 30' parallel.

Peripheral populations. The peripheral populations (CO, BP, DH, SP) had mixed signals of population differentiation, with some traits supporting isolation (Figures 3, 4), but other approaches (Figures 2, 5) suggesting that periphery of the subspecies range is not a major factor partitioning variation among these populations. As there are no direct dispersal routes through sagebrush habitat between the CO (Sierra Nevada) population and the White Mountains populations (BP, DH, SP), if these peripheral populations were morphologically similar due to gene flow, they should also be similar to the other two Sierra Nevada populations (SC, JL) and the other White Mountains population (QC). This was not the case, as those other populations grouped with northern populations more than 350 km away (Figures 3 and 4). This pattern that cannot be explained by differentiation due to distance suggests genetic drift as a significant factor shaping the populations.

The paucity of rare alleles in the southern populations could be an indication of the marginality of these populations (although it may reflect historical biogeography). Central areas are thought to be more tolerant of alternate forms and also exhibit more genetic inertia while marginal areas maintain more intense selection limiting the number of phenotypes that are able to survive and reproduce. Chipmunks are adapted to utilize areas with harsh winters by hibernating intermittently, *i. e.*, they make use of mild days to supplement winter stores. Marginality in a geographic sense may have a greater effect on allele frequencies. For example, the occurrence of only two of the five alleles of the P-LA locus, and the reversal of the common allele for both the P-LA and ADA loci were noted in peripheral populations. Our data also indicated isolated populations are more genetically distinct, supporting isolation having a greater impact on population structure than periphery. The GB population is by far the most distinct in regard to individuals sporting a unique allele, as well as in average morphological (Mahalanobis D^2) divergence measures, and it appears to be the most geographically isolated of our samples. GB is a peninsular population (it can only receive migrants from one direction) due to incompatible habitats almost completely surrounding the Stillwater Mountains where it occurs.

Variation in population structure across markers. Genetic, morphological, and lateral variant traits did not have consistent signals. The morphological data even indicated different signals depending on how the data were analyzed. The large discrepancies between biological distance measures indicate that each may be measuring different characteristics of the phenome. For example, Mahalanobis distance and asymmetry divergences measure levels

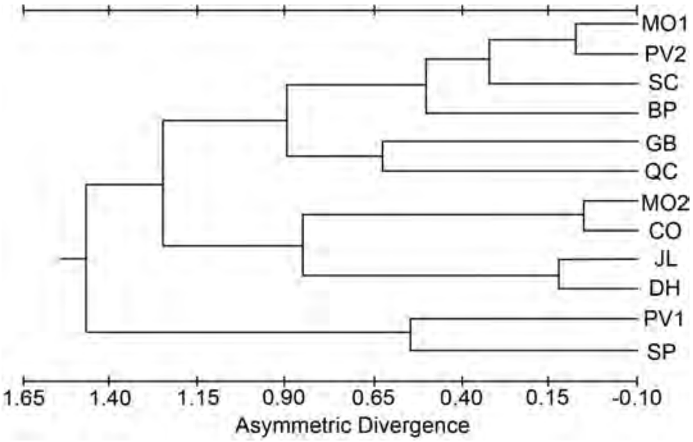

Figure 5. Phenogram from the cluster analysis using the unweighted pair-group method for population distances based on asymmetry divergence taken from the cranial dataset.

of variation among the populations accurately only over short geographic distances, whereas Lidicker's distance measure along with the genetic distance measures (Roger's and Nei's) reflect larger-scale genetic affinities among the populations.

Additional considerations. Historically, the geographic range of sagebrush least chipmunks probably extended southward into what is presently the Mojave Desert and likely included the valley floor of what is present-day Owens Valley in California (however, see Grayson 1982). As the area became increasingly arid, the least chipmunk and its associated community retreated northward and to higher elevations, leaving the valley floors to more arid-adapted species. In extreme cases, populations became relatively isolated on islands or peninsulas connected by narrow straits of suitable habitat (Spaulding 1980).

Based on the assumption that isolated and/or peripheral populations with little gene flow should have lower levels of asymmetry than populations in central areas, the JL and DH populations, with the highest average level of asymmetry, should be the least isolated and, the CO population with the lowest average level of asymmetry should be the most isolated. Our electrophoretic data were consistent with the CO population as a peripheral isolate. The JL sample, as well as the DH and SC samples, are all mid-elevation samples located well within the species' range and adjacent to areas of both higher and lower elevations. Hence, they may experience an influx of genes not well adapted to the mid-elevation environment. A higher level of asymmetry was expected for the non-peripheral ecologically marginal populations (QC, BP, SP), as they may experience maladaptive gene influx. However, these populations only grouped together in one of the lateral variant asymmetries (OFD), yielding lower asymmetry values for the grouping QC-BP-SP when compared to either their regional mate (DH) or their elevational mate (CO). There were no trends in the overall or average levels of asymmetry that corresponded to any of the regional (gene flow) or latitudinal (historical divergence time) trends, but there was an elevational (selective regime) trend. Removing the populations with a relatively high degree of isolation (GB, CO) leaves the mid-elevation samples with the highest levels of asymmetry as predicted, and the high-elevation samples with a median level. The low-elevation samples had the lowest levels of average asymmetry.

It is unlikely that the differences between the two Malheur populations and between the two Pueblo Valley populations can be attributed to selection. They are at similar elevations (implying similar climatic conditions) and in the same habitat type with similar terrains. Instead of selection, these chipmunks may have sufficiently low vagility that gene flow is incapable of overcoming stochastic differences among local populations. Limitation of gene flow would enhance the effects of any differential selection or drift (Wright 1948; Dobzhansky 1968). Examining the electrophoretic data as a complete unit, the populations show a similarity higher than would be expected for local populations of rodents (Avise 1976). So, even though there are real and striking differences between the populations, the overall similarities are high.

These data and results provide a valuable baseline for investigations of how population structure may have changed, or to investigate the impact of climate change on sagebrush least chipmunks. There is ample evidence that many mammal species, including chipmunks, are shifting distributions (Moritz *et al.* 2008) and are experiencing altered population dynamics and diversity (Rubidge *et al.* 2008) in response to climate change. Some isolated chipmunk populations in the Great Basin are genetically distinct and potentially threatened by habitat loss (Bell *et al.* 2021). Contemporary investigation of *T. m. scrutator* populations could gauge changes in population fragmentation and diversity, particularly in the peripheral and isolated populations that may warrant recognition as distinct population segments or may have experienced increased isolation and associated genetic drift. Additionally, genomic approaches could be used to test for variation in selection at different elevations, an important consideration for species that are anticipated to shift their elevational distributions in response to changing climate conditions.

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Ahead of his time: Joseph Grinnell, natural history, and inclusion and equity in STEM

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Joseph Grinnell designed the Natural History of the Vertebrates (NHV) course at the Museum of Vertebrate Zoology, University of California at Berkeley, over 100 years ago and the course has changed little over these years. In this essay, I connect modern pedagogical and cognitive understandings of what we know leads to success among students to the course. This analysis reveals that the course continues to be successful because it has all the elements of a student-centered, active-learning class that leads to better cognitive gains, better retention, and importantly, proportionately better gains for students from underserved populations. This study will be important for advocates of teaching natural history in biology curriculum.

Joseph Grinnell diseñó el curso de Historia Natural de los Vertebrados (NHV) en el Museum of Vertebrate Zoology, Universidad de California en Berkeley, hace más de 100 años y el curso ha cambiado poco durante estos años. En este ensayo, conecto la comprensión pedagógica y cognitiva moderna de lo que sabemos que conduce al éxito entre los estudiantes del curso. Este análisis revela que el curso continúa siendo exitoso porque tiene todos los elementos de una clase de aprendizaje activo centrada en el estudiante que conduce a mejores ganancias cognitivas, mejor retención y, lo que es más importante, proporcionalmente mejores ganancias para los estudiantes de poblaciones desatendidas. Este estudio será importante para los defensores de la enseñanza de la historia natural en el plan de estudios de biología.

Keywords: Natural history; teaching; active learning; inclusion.

Introduction

In 2017, the Museum of Vertebrate Zoology (MVZ) at the University of California hosted a symposium to celebrate over 100 years of the offering of the "Natural History of the Vertebrates" (NHV) course. The symposium had two foci: 1) to gather people that had taught or taken the course and celebrate its impact on our lives; and 2) highlight the value of natural history education more generally. As a teaching assistant for NHV during my days as a graduate student working under William (Bill) Lidicker, I was delighted to attend and reflect on the NHV course. In particular, I was eager to review the course in light of the *Vision and Change* report (AAAS 2011) that calls for biology educators "to rethink what and how we teach to ensure that the biology we teach engages all students and reflects the biology we practice in the laboratory and in the field." As a counselor for the Council of Undergraduate Research (cur.org) and a Fellow for the Partnerships for Undergraduate Life Science Education (pulse-community.org), I have become an advocate in promoting transformation in STEM education at the undergraduate level and was interested in stepping back and examining the NHV course more carefully. In particular, the structure of NHV has not changed significantly in over 100 years since its founding by Joseph Grinnell and I wanted to overlay modern pedagogical and cognitive understandings of what we know leads to success among students to NHV. What I discovered and reveal in this essay is a course that was successful because it has all the elements of a student-centered, active-learning class that leads to better cognitive gains, better retention, and importantly, proportionately better gains for students from underserved populations. In other words, the course is structured in a way to improve inclusion and equity in the sciences, a topic of great concern to science (see Sarma and Bagiati 2020). This topic is also highly relevant here because Bill was not only a long-time contributor to the NHV course, but he is an academic descendent of Joseph Grinnell through Bill's Ph.D. mentor D. F. Hoffmeister, who is a descendant of E. Raymond Hall, a student of Joseph Grinnell (Jones 1991).

I will organize this essay by first summarizing some of the motivation and recommendations of *Vision and Change* as it relates to biology curriculum and natural history courses specifically, and then describe briefly what student-centered, active learning entails. I will then describe some of the background and details of the NHV course, including Joseph Grinnell's contributions. I will then overlay the course on active-learning expectations to reveal just how impactful this course is for students. Lastly, I will end with a discussion of what this can mean for the future of natural history coursework in biology education and promoting equity and inclusion.

Student-centered, active learning in biology: vision and change. *Vision and Change*: A Call to Action (V&C; AAAS 2011) resulted from the convergence of many factors including recognition of the need for a biology curriculum that reflects the current practice of biology, the need to provide a framework for biological literacy in undergraduate biology education, and the need to focus on student-centered (rather than instructor-centered) life science education. After years of workshops and discussions, the V&C contributing authors identified five core concepts as foundations of a biology education that include evolution; structure and function; information flow, exchange, and storage; pathways and transformations of energy and matter; and systems. Additionally, V&C identified several core competencies that are critical for any practicing biologist including the abilities to apply the process of science, to use quantitative reasoning, to use modeling and simulation, to tap into the interdisciplinary nature of science, to communicate and collaborate with other disciplines, and to understand the relationship between science and society.

The VNH course designed by Grinnell, although designed over 100 years ago, includes many of these core concepts and competencies. In 1914, Grinnell intended students to "conduct comparative studies of the conditions in the same areas at different successive times" in order to "bring important generalizations in the field of evolution" (Sunderland 2013). The course was developed before the modern synthesis, so genetics was not emphasized, but evolution, structure and function, and physiology were and remain an important focus of VNH. Grinnell urged his students to record their observations in their notes at the moment of observation so that the memory was not lost. The VNH course was based around the "Grinnellian" method of research that involves a standardized method of note-taking (see below) that is then connected to museum specimens in a highly organized fashion to facilitate access to data associated with each specimen. The methodical fashion in which data were curated led to the MVZ leading modern efforts to digitize natural history records (Sunderland 2013). The VNH course has trained (and continues to do so) students to understand the process of science, how to use quantitative reasoning, and the interdisciplinary nature of science.

Arguably, the most important section of V&C is chapter 3, titled "Student-centered Undergraduate Biology Education." The authors call for undergraduate biology courses that are student-centered and relevant, and that provide authentic research experiences as part of the education. Ideally the courses should be embedded with authentic and frequent assessment procedures that mimic how we approach science, also aptly known as the scientific teaching approach (Handelsman *et al.* 2007). Natural History of the Vertebrates has provided such an active-learning environment where the content is learned in context (Allen and Tanner 2003; Michael 2006) since its inception. To understand this connection, more description of the VNH course is needed.

Natural History of the Vertebrates according to Grinnell. The relevance and importance of this course for the teaching and research of natural history cannot be overstated. As revealed by the thorough analysis of Sunderland (2013), the NHV course was a gateway to Grinnellian natural history, it was the trajectory for the research of the MVZ, and it was and remains the glue for the MVZ community. The last course description of the course before Grinnell's death was the following:

The birds, mammals, reptiles, and amphibians, chiefly of California; identification of species; observational methods in study of behavior and habitat relations; systematics, distribution, speciation. Field work emphasized. (1937-38 General Catalog, University of California, Berkeley)

In modern pedagogical terms, the learning outcomes of such a course are perhaps a bit opaque from this description. A careful examination of his goals for the course, the assignments, and how the course was organized provide a clearer understanding of the learning outcomes. In student-centered learning (also referred to as "Backwards Design," Wood 2009), the course begins with the formulation of broad learning goals and the formulation of specific learning outcomes. Grinnell designed the NHV course as the gateway course to 'Grinnellian' natural history so that students would be able to apply standardized practices to understand adaptations of California vertebrates (Sunderland 2013). The Grinnellian practice includes the following methods:

A field notebook to directly record observations as they are happening.

A field journal of fully written entries on observations and information, transcribed from the notes.

A species account of the detailed observations on chosen species.

A catalog or record of where and when specimens were collected.

While students of VNH rarely collected specimens, the other three elements were relevant as students were led on weekly field trips to surrounding natural areas to observe vertebrate fauna. Often the species encountered in the field were discussed in the lecture portion of the class and encountered in the laboratory, reinforcing the learning. Students also learn basics about fieldwork, using common tools of the trade (field guides, binoculars, live-traps for small mammals). This is important for students whose access to nature is limited and gives them relevant experience for pursuing research apprenticeships or field tech jobs. Teaching students to observe, write, and maintain accurate records of their observations has been maintained as a central focus of this course since its inception. Students' notes are evaluated almost weekly by teaching assistants to ensure that students are acquiring the skills to make meaningful observations (Sunderland 2013).

In active learning, frequent formative assessments are critical to understand if the student is learning. The iterative process of the field notes is an excellent way to see if students are "getting it", and it provides helpful feedback on how to improve. It is remarkable that the instructions for the field notes remain the same as when Grinnell started the course, and it is interesting to note that Grinnell apparently did not follow his own rules in writing his notes (Sunderland 2013). This may suggest that Grinnell was motivated to do this for grading ease and data extraction (Perrine and Patton 2011), but maybe he also understood the cognitive benefits of the iterative process of note-taking that is such an important element of the NHV course.

The final element of the NHV course is the independent project. Using their acquired scientific observation skills, students design field projects to answer a question based on their field observations over a span of a few weeks. On a personal note, this was always my favorite part of the class, to see how students would struggle to come up with a meaningful question they could approach. I was also impressed because regardless of student's background they could go into the field, be it a park, their backyard, or the Berkeley campus and conduct science. I remember one student who lived in San Francisco and would rise before sunrise to record what species of birds were singing first in Golden Gate Park before showing up at his family's restaurant to work the morning shift. Designing one's own independent project can lead to better confidence and a sense of accomplishment (Lopatto 2010), and such experiences are particularly important for students from underserved populations.

To summarize the connections between the VNH course and active, student-centered learning, the NHV course combines all of the elements of a successful student-centered science course including clear learning, measurable learning outcomes, meaningful formative assessments through iterative field note writing, and an authentic research experience. The course also includes traditional lectures, and summative assessments (lecture and practical exams) that are of course rather traditional.

Why this matters for science education. Numerous biologists have documented and written about the demise of natural history at their institutions including Wilcove and Esner (2000), Wilson (2000), and Schmidly (2005). It is interesting to note that the MVZ has been able to maintain its strong natural history-based research program, due in part to the foundation that the VNH course laid for students and faculty alike (Sunderland 2013). Schmidly (2005) made a strong academic argument for the continuation of natural history in the academy based on its prevalent importance to ecology and evolution, and to the public in general.

While I think these arguments are all relevant, what I discovered in examining the history of the NHV course is a student-centered course that incorporates pedagogies that have been proven to improve retention and graduation rates, particularly among students that are underrepresented in the field of science (Theobald *et al.* 2020). Does not the future of natural history, science, and frankly a functioning society depend on the success of these students? Courses such as NHV that employ active-learning and independent research experiences have a disproportionate benefit for capable students that have suffered though racial inequities in our education system. Such courses also help students from historically marginalized identities in science to see themselves as scientists (*e. g.,* Avraamidou 2020). Administrators may view these courses as expensive and boutique, but can we afford to not fund these courses that are known to improve persistence and success of all students? As Haak *et al.* (2011) demonstrated in a compelling meta-analysis, "a highly structured course design, based on daily and weekly practice with problem solving, data analysis, and other higher-order cognitive skills, improved the performance of all students in a college-level introductory biology class and reduced the achievement gap between disadvantaged and non-disadvantaged students—without increased expenditures." Grinnell may not have fully understood the relevance of his course to equity and inclusion in science and he was certainly a product of the Victorian times (Stein 2001), but we do understand the relevance today and discontinuing such classes is inexcusable and short-sighted. Grinnell must have understood the genius of engaging students in science in meaningful ways, including accepting that science is as much about the unknown as it is about the known (Anderson 2017). So many VNH classes in my experience began with a buzz among students about a new species observation, a new behavior, or an unusual coloration of a common species. I have had the privilege of teaching many types of college science classes in my career, and none compare with the excitement about science when students discover things on their own. The relevance of these types of classes has never been more important.

In honor of William Lidicker and this volume, I want to end by recognizing and celebrating Bill's participation and support of this class for his many years at the MVZ. I recall fondly numerous field trips with him surveying *Microtus* runways to estimate the density of voles, or trapping rodents in Tilden Park. As an academic descendant of Joseph Grinnell, I think it appropriate to commemorate the NHV course and the hundreds of students that Bill taught through this course. It is a lasting and meaningful legacy.

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I thank all of the organizers from the Museum of Vertebrate Zoology that hosted the symposium to celebrate the Natural History of Vertebrates course and their invitation to speak that ultimately lead to this paper. I am thankful for the encouragement I received from numerous symposium participants, especially Harry Greene, to put my analysis together in this paper. And thanks to Ed Heske and two anonymous reviewers for insightful and helpful comments. Finally, I will always be grateful for the opportunity to teach with and learn from the professors and fellow graduate students involved with the NHV course. Besides Bill, who also served as my Ph.D. advisor, I thank James Patton, Harry Greene, Ned Johnson, Beth Braker, Eldridge Adams, Pam Johnson, and Claudia Luke. Given the inclusion and equity

focus of this essay, I am compelled to acknowledge that there is at least one historical figure associated with the study and teaching of natural history, E. Raymond Hall, that was a proponent of eugenics and published on this topic.

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A new species of the genus *Microcavia* (Rodentia, Caviidae)

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Based on qualitative and quantitative morphological evidence, we describe a new species of *Microcavia* (Rodentia, Caviidae). The new species is characterized by a unique combination of morphological traits, that distinguished it from all others within the genus (*i. e.,* upper incisors moderately proodont; palatal crest low, narrow anteriorly and expanded posteriorly; paraorbital process of the jugal small; sphenopalatine vacuities small, with their anterior border located behind the anterior half of the mesopterygoid fossa). The new species seems to be endemic from northwestern Argentina, where it occurs in open shrublands and grasslands >3,100 masl. With the description of this taxon, there are already four species of *Microcavia* that are distributed in the central Andes.

Sobre la base de evidencias morfológicas cualitativas y cuantitativas, describimos una nueva especie de *Microcavia* (Rodentia, Caviidae). La nueva especie se caracteriza por una combinación única de rasgos morfológicos, que la distinguen de todas las otras dentro del género (*i. e.,* incisivos superiores moderadamente proodontes; cresta palatal baja, angosta anteriormente y expandida hacia atrás; proceso paraorbitario del yugal pequeño; vacuidades esfenopalatinas pequeñas, con el borde anterior ubicado por detrás de la mitad anterior de la fosa mesopterigoidea). La nueva especie parece ser endémica del noroeste de Argentina, donde ocupa matorrales abiertos y pastizales > 3.100 msnm. Con la descripción de este taxón, ya son cuatro las especies de *Microcavia* que se distribuyen en los Andes Centrales.

Keywords: Caviomorpha; Cavioidea; Central Andes; highlands; Hystricognathi; Puna; taxonomy.

Introducción

El género *Microcavia* H. Gervais y Ameghino, 1880 incluye cinco especies vivientes de roedores Caviidae de hábitos semifosoriales, diurnos y dieta mayormente herbívora (Dunnum 2015; Teta *et al.* 2017). Dos formas nominales, *M. niata* (Thomas 1898) y *M. shiptoni* (Thomas 1925), se encuentran mayormente restringidas a los Altos Andes (>3.000 msnm) del noroeste de Argentina, oeste de Bolivia, norte de Chile y extremo sur de Perú (Dunnum 2015; Zeballos *et al.* 2018). Los otros tres taxones se distribuyen ampliamente en las tierras bajas y elevaciones medias al este de los Andes (< 2.500 msnm), desde el noroeste de Argentina hasta el extremo austral de Argentina y Chile, y hasta hace poco tiempo eran consideradas como parte de una misma entidad específica, referida como *M. australis* (I. Geoffroy y d'Orbigny 1833).

La taxonomía de *M. australis* fue revisada por Teta *et al.* (2017) a través de una aproximación morfológica, sobre la base de rasgos craneanos cualitativos y cuantitativos. Según estos autores, *M. australis* incluye tres grupos morfológicamente cohesivos, con distribuciones aparentemente parapátricas, que pueden ser considerados como especies distintas, para los cuales usaron los nombres *M. australis*, *M. maenas* (Thomas 1898) y *M. jayat* (Teta *et al.* 2017). Estudios posteriores, centrados en *M. australis* y *M. maenas*, mostraron que ambas especies presentan variaciones clinales en su morfología craneana, las cuales se vinculan con las características ambientales de los entornos que ocupan (d'Hiriart *et al.* 2021).

Durante una revisión de materiales pertenecientes a las especies de Caviidae en la Colección de Mamíferos de la Facultad de Ciencias Naturales e Instituto Miguel Lillo, identificamos un ejemplar (CML 66) colectado en la localidad de Chorrillos (5.000 m), provincia de Salta (Argentina), que presenta una combinatoria única de características morfológicas, que no se corresponde con los de ninguna de las especies conocidas para este género. Aunque por algunos de sus rasgos (*e. g.,* morfología de los molares) este ejemplar se acerca a las especies del grupo de tierras bajas (*i. e., M. australis*, *M. jayat* y *M. maenas*), su distribución queda notoriamente por encima del límite altitudinal superior documentado para esos taxones. Recientemente, Sánchez (2020) refirió el primer registro de *M. niata pallidior* (Thomas 1902) para la Argentina, sobre la base de tres especímenes colectados en áreas de altura (3,100 msnm) de la provincia de La Rioja. Sin embargo, tal como fuese explicado por Teta *et al.* (2021), al menos el ejemplar ilustrado por esa autora (CML 13052) no presenta los caracteres diagnósticos propios de *M. niata* (incluyendo *M. n. pallidior*), ni -como se demuestra más abajo- de ninguna de las otras especies conocidas para el género; en efecto, tanto su descripción como las ilustraciones disponibles (piel y cráneo) permiten vincular los especímenes estudiados por Sánchez (2020) con el individuo CML 66, previamente mencionado.

En este trabajo se presenta un estudio morfológico detallado del ejemplar CML 66 y una revisión crítica de los datos aportados por Sánchez (2020). Teniendo en cuenta la morfología de estos individuos y sus notorias discontinuidades con las otras especies del género, tanto cualitativas como cuantitativas, hipotetizamos que el ejemplar CML 66 y aquellos reportados por Sánchez (2020) corresponden a una forma innominada del género *Microcavia*, la cual se describe en esta contribución.

Materiales y Métodos

Definición de especies. En esta contribución, las especies fueron definidas y delimitadas como grupos de organismos diagnosticables en función de discontinuidades cualitativas y cuantitativas en su morfología. Este enfoque se basa en los siguientes supuestos: i) por lo general, hay menos variabilidad morfológica entre muestras de una misma especie que entre muestras de especies distintas; ii) las discontinuidades morfológicas y morfométricas son usualmente el resultado del aislamiento reproductivo entre poblaciones; y iii) desde el momento en que las discontinuidades morfológicas están (al menos parcialmente) genéticamente codificadas, su existencia implica distintos conjuntos de genes y por lo tanto de linajes (*cf.* Prado y Percequillo 2017). Más en general, para muchos de los distintos conceptos de especie discutidos en la literatura, incluido el filogenético, la posibilidad de poder diagnosticar morfológicamente a un taxón determinado es central para su reconocimiento (*e. g.,* Nelson y Platnick 1981; Cracraft 1983, 1989; Nixon y Wheeler 1990).

Especímenes. Se estudiaron 107 especímenes de seis especies del género *Microcavia*, incluyendo pieles y cráneos, depositados en las siguientes colecciones biológicas: AMNH, American Museum of Natural History (Nueva York, Estados Unidos); CMI, Colección de Mamíferos del Instituto Argentino de Investigaciones de las Zonas Áridas (Mendoza, Argentina); CML, Colección de Mamíferos de la Facultad de Ciencias Naturales e Instituto Miguel Lillo (San Miguel de Tucumán, Argentina); FMNH, Field Museum of Natural History (Chicago, Estados Unidos); MACN-Ma, Colección Nacional de Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires, Argentina; véase el Material Suplementario 1 y Figura 1).

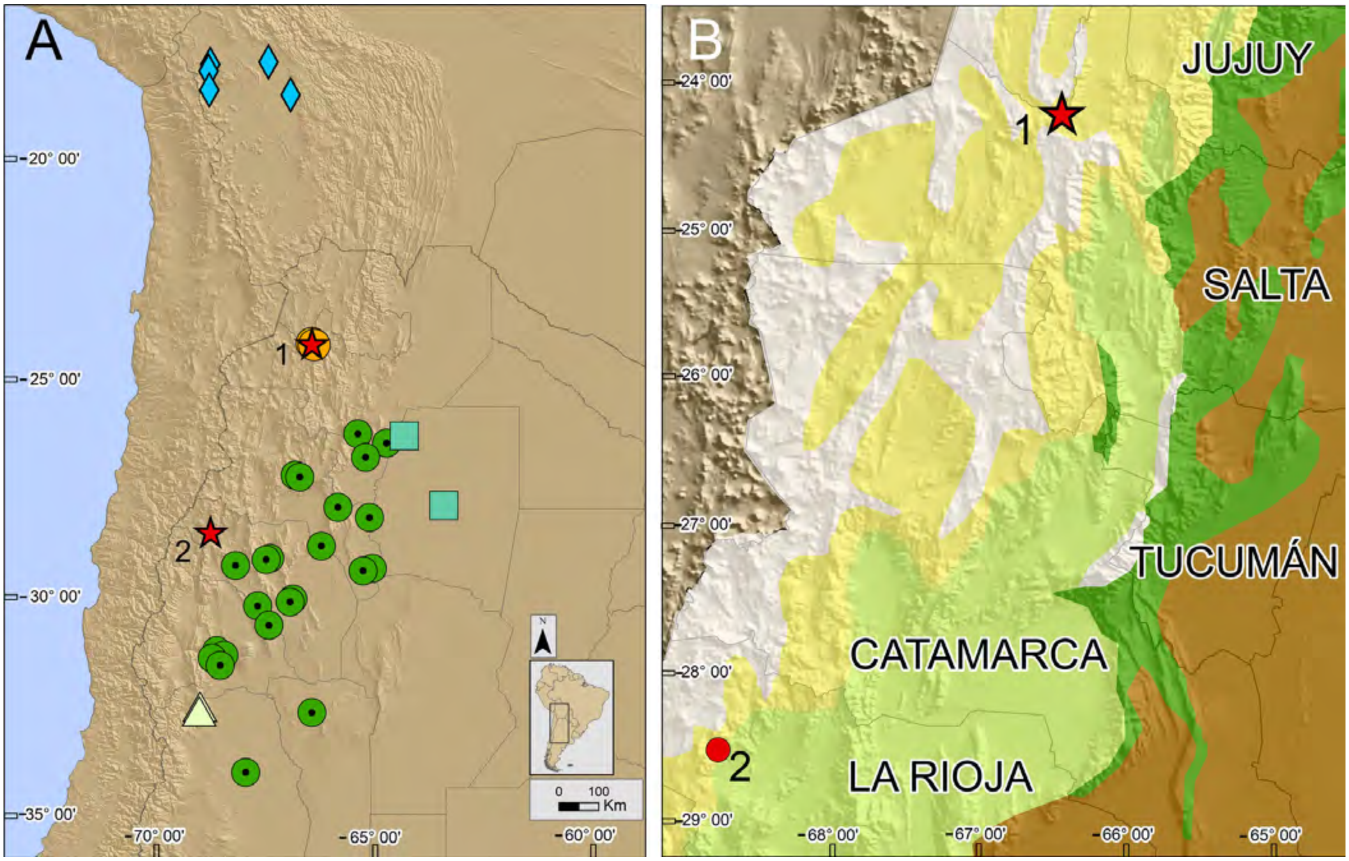

Figura 1. A. Mapa del noroeste de Argentina con las localidades de registro para los individuos revisados de seis especies del género *Microcavia*: *M. australis* (triángulos verde oliva), *M. jayat* (cuadrados verde claro), *M. maenas* (círculos verde oscuro), *M. niata* (rombos celestes), *M. shiptoni* (círculos naranja) y *M.* sp. n. (estrellas rojas). B. Localidades de registro para *M.* sp. n. y ecorregiones (la estrella indica la localidad tipo); referencias para los números: (1) Salta, La Calera, Chorrilos. 5,000 msnm; (2) La Rioja, Quebrada de Santo Domingo, 30 km al SO de Jagüé. Los colores para las ecorregiones son como sigue: verde oscuro, Yungas; verde claro, Monte de Sierras y Bolsones; marrón, Chaco Seco; amarillo, Puna Andina Central; blanco: Altos Andes.

Anatomía craneana y medidas. La terminología anatómica corresponde a la utilizada por Quintana (1996) y Cherem y Ferigolo (2012). Las diferencias cualitativas fueron ponderadas en el contexto de otras revisiones recientes, basadas en evidencias morfológicas cualitativas y cuantitativas (*e. g.*, Teta *et al.* 2017). Para cada ejemplar adulto (clases tres a cinco, sensu Bezerra 2008) se tomaron las siguientes medidas cráneo-dentarias (con calibre digital, precisión de 0,01 mm): LTC = longitud total del cráneo; LCI = longitud cóndilo-incisiva; CIO = constricción interorbitaria; AZ = ancho cigomático; ACC = ancho de la caja craneana; LN = longitud del nasal; AN = ancho del nasal; LD = longitud de la diastema superior; LFI = longitud de los forámenes incisivos; SMS = longitud de la serie molar superior (alveolar); LP = longitud palatal; APM3 = ancho del paladar a la altura del tercer molar superior; LBT = longitud de las bullas timpánicas. Las medidas para el ejemplar CML 13052 fueron tomadas de la literatura (Sánchez 2020). Aunque esta autora ofrece las medidas para un segundo ejemplar, por los valores anotados queda claro que se trata de un individuo juvenil, por debajo de la edad tres (por lo tanto, no fue incluido en nuestros análisis).

Análisis estadísticos. Primeramente, y a modo exploratorio, se aplicó un análisis de componentes principales para evaluar los patrones de variación en el conjunto de datos y ordenarlos por importancia. Los componentes principales fueron extraídos de una matriz de covarianza; antes de ser incluidas en los análisis, todas las medidas fueron transformadas a logaritmo (base 10). Seguidamente, se empleó un análisis discriminante para evaluar de qué forma las distintas variables contribuyeron a la diferenciación entre especies (Strauss 2010). Todos los procedimientos estadísticos fueron realizados mediante el software PAST v. 2.17 (Hammer *et al.* 2001).

Este trabajo y el acto nomenclatural incluido en el mismo han sido registrados en ZooBank. El LSID para esta publicación es: http://zoobank.org/urn:lsid:zoobank.org:pub:628ADFE4-4FCC-45F4-A123-0AC65AAD1EFA. La versión en línea de este trabajo estará archivada y disponible en Zenodo.

Resultados

Morfología cualitativa . El ejemplar CML 66 presenta una combinatoria única de rasgos morfológicos que lo separan de todas las otras especies del género *Microcavia*, incluyendo un tamaño general pequeño (longitud cabeza-cuerpo = 195 mm; LTC = 43.99 mm); incisivos superiores moderadamente proodontes; cresta palatal baja, angosta anteriormente y expandida hacia atrás, que no sobrepasa el borde posterior del paladar; borde posterior del paladar en forma de "V" abierta y con el vértice redondeado; presencia de un pequeño proceso paraorbitario sobre el yugal; y bulas timpánicas grandes y globosas (Figura 2). Todas estas características se verifican también en el ejemplar CML 13052, ilustrado por Sánchez (2020; Figura 122). En este último, además, se observa que las vacuidades esfenopalatinas son pequeñas, con el borde anterior ubicado por detrás de la mitad anterior de la fosa mesopterigoidea. Una comparación detallada con otras especies del género se anota más abajo y en la Tabla 1.

Morfología cuantitativa. Las medidas estadísticas descriptivas (N, media, desvío estándar [DE] y rango [Mín. - Máx.]) se sintetizan en la Tabla 2. El análisis de componentes principales (Figura 3A, B; Tabla 3) permitió definir tres conjuntos mayores sobre el espacio multivariado determinado por los primeros dos componentes principales (63.94 % y 14.97 % del total de la varianza, respectivamente). Dos de estos conjuntos corresponden a *M. niata* y *M. shiptoni*, mientras que en el tercero se solapan moderadamente *M. australis*, *M. jayat*, *M. maenas* y los ejemplares CML 66 y CML 13052 (Figura 3A). Sin embargo, estos dos últimos individuos se separan de *M. maenas* a lo largo del primer componente principal y de *M. australis* y *M. jayat* sobre el tercero (7.43 % del total de la varianza; Figura 3B). Las variables que más contribuyeron en la separación entre especímenes fueron DS y LFI (ambas con carga positiva) sobre el primer componente principal, AN (hacia valores positivos) y LFI (hacia valores negativos) sobre el segundo y LFI (hacia valores negativos) y LP (hacia valores positivos) sobre el tercero. Con el análisis discriminante (Figura 3C, D; Tabla 3) se obtuvieron resultados parcialmente similares a los alcanza-

Tabla 1. Comparaciones morfológicas entre cuatro especies de *Microcavia*.

Carácter	*M. australis*	*M. jayat*	*M. maenas*	*M. sorojchi* sp. n.
Incisivos superiores	Moderadamente proodontes	Moderadamente proodontes	Ortodontes	Moderadamente proodontes
Cresta palatal	En forma de triángulo o corazón; no sobrepasa el borde posterior del paladar	En forma de corazón, sobrepasa el borde posterior del paladar	Usualmente larga y angosta o larga y ensanchada romboidalmente hacia su mitad posterior	Baja, angosta anteriormente y expandida hacia atrás; no sobrepasa el borde posterior del paladar
Borde posterior del paladar	En forma de "V" de bordes abiertos	Trapezoidal	En forma de "V" de bordes abiertos	En forma de "V" de bordes abiertos
Proceso medial del paladar	Ausente	Ausente	Usualmente presente	Ausente
Proceso paraorbitario del yugal	Ausente	Presente, mediano	Ausente	Presente, pequeño
Extremo posterior del yugal	No sobrepasa el borde posterior de la cavidad glenoidea	Sobrepasa el borde posterior de la cavidad glenoidea	Sobrepasa el borde posterior de la cavidad glenoidea	Sobrepasa el borde posterior de la cavidad glenoidea
Vacuidades esfenopalatinas	Grandes, con el borde anterior ubicado en la mitad anterior de la fosa mesopterigoidea	Pequeñas, con el borde anterior ubicado por detrás de la mitad anterior de la fosa mesopterigoidea	Pequeñas, con el borde anterior ubicado por detrás de la mitad anterior de la fosa mesopterigoidea	Pequeñas, con el borde anterior ubicado por detrás de la mitad anterior de la fosa mesopterigoidea

dos con el análisis de componentes principales; nuevamente, sobre el espacio definido por los primeros dos ejes (47.63 % y 33.25 % del total de la varianza, respectivamente; Figura 3C) se identificaron los mismos tres conjuntos de especies; los ejemplares CML 66 y CML 13052 se separaron notoriamente de *M. australis*, *M. jayat* y *M. maenas* sobre el tercer eje (13.25 % del total de la varianza; Figura 3D). Las medidas cráneo-dentarias que más contribuyeron en la separación entre individuos fueron DS y LFI (ambas con cargas positivas) sobre el primer eje, LFI y LN (ambas con carga negativa) sobre el segundo y LBT (hacia valores positivos) y LN (hacia valores negativos) sobre el tercero.

Taxonomía. Los resultados de los análisis cualitativos y cuantitativos sugieren que el espécimen CML 66 (y el CML 13052) no puede ser referido a ninguna de las especies conocidas del género *Microcavia*. En efecto, este taxón posee una combinatoria única de rasgos morfológicos que permiten diagnosticarlo como una nueva especie, según se describe a continuación:

Microcavia sorojchi sp. n.

Microcavia niata pallidior: Sánchez 2020:82 (no Thomas 1902)

Figuras 2, 4-8

Localidad tipo. Argentina: provincia de Salta, departamento Los Andes, Chorrillos. 5,000 msnm (*ca.* -24.22°, -66.45°).

Holotipo. CML 66, hembra adulta, preservada como piel y cráneo, coleccionada en febrero de 1930 por Emilio Budin.

Tabla 2. Estadística descriptiva (media, desvío estándar [DE] y rango [Mín.-Máx.]) para 13 medidas cráneo-dentarias en las seis especies de *Microcavia*. Véase "Materiales y métodos" para una explicación de las abreviaturas.

	M. australis					***M. jayat***					***M. maenas***				
	n	**Media**	**DE**	**Mín.**	**Máx.**	***n***	**Media**	**DE**	**Mín.**	**Máx.**	***n***	**Media**	**DE**	**Mín.**	**Máx.**
LTC	9	44.02	2.11	41.32	46.63	6	43.98	1.38	41.56	45.22	64	48.56	1.94	44.5	52.96
LCI	9	40.11	2.28	36.8	42.83	6	39.56	1.23	37.41	41.04	64	43.98	2.04	39.17	48.66
CIO	9	9.87	0.61	9.09	10.75	6	10.04	0.83	8.85	11.04	64	10.99	0.75	9.48	12.96
AZ	9	27.30	1.04	25.57	29.14	6	26.36	0.97	24.73	27.54	64	28.65	1.32	25.90	30.83
ACC	9	21.70	1.24	20.09	23.63	6	20.48	0.76	19.30	21.61	64	21.99	0.82	20.30	23.77
LN	9	14.35	1.26	12.66	15.99	6	14.37	0.73	13.47	15.21	64	17.13	1.06	14.50	19.73
AN	9	6.75	0.40	6.19	7.47	6	6.80	0.51	6.27	7.59	64	7.44	0.55	6.38	9.16
DS	9	10.47	0.86	9.52	11.51	6	10.93	0.86	9.83	11.91	64	11.65	0.85	10.00	14.17
LFI	9	6.15	0.65	5.20	7.11	6	6.02	0.20	5.89	6.42	64	7.40	0.83	5.76	9.24
SMS	9	10.46	0.73	9.46	11.33	6	10.70	0.46	9.95	11.17	64	11.66	0.65	9.75	12.94
LP	9	17.94	1.20	16.38	19.73	6	18.29	0.89	16.78	19.22	64	20.23	1.67	11.07	23.27
APM3	9	11.60	0.35	10.87	12.02	6	10.63	0.44	10.16	11.22	64	11.88	0.69	10.00	13.16
LBT	9	11.94	0.70	11.00	12.89	6	10.98	0.72	9.55	11.43	64	11.89	0.63	10.64	13.63

Tabla 2 (continuación). Estadística descriptiva (media, desvío estándar [DE] y rango [Mín.-Máx.]) para 13 medidas cráneo-dentarias en las seis especies de *Microcavia*. Véase "Materiales y métodos" para una explicación de las abreviaturas.

	***M. sorojchi* sp. n.**					***M. niata***					***M. shiptoni***				
	n	**Media**	**DE**	**Mín.**	**Máx.**	***n***	**Media**	**DE**	**Mín.**	**Máx.**	***n***	**Media**	**DE**	**Mín.**	**Máx.**
LTC	2	44.39	-	43.99	44.79	18	44.3	1.86	40.33	46.67	7	42.78	3.12	38.07	47.34
LCI	2	40.01	-	39.98	40.03	18	38.76	1.77	35.42	41.13	7	37.87	3.28	32.17	42.31
CIO	2	9.25	-	9.08	9.42	18	10.80	0.56	9.59	11.79	7	8.57	0.69	7.54	9.76
AZ	2	27.16	-	26.79	27.53	18	28.57	1.28	26.32	30.63	7	26.13	1.48	23.62	28.23
ACC	2	22.29	-	22.26	22.32	18	21.01	0.57	20.23	21.88	7	19.59	0.62	18.63	20.65
LN	2	13.59	-	13.53	13.64	18	14.69	1.21	12.62	16.40	7	13.54	1.66	10.54	15.77
AN	2	6.14	-	5.47	6.82	18	8.27	0.50	7.36	9.42	7	5.63	0.35	5.25	6.15
DS	2	10.52	-	10.14	10.89	18	9.20	0.74	7.93	10.47	7	9.67	1.15	8.18	11.60
LFI	2	5.33	-	5.29	5.38	18	5.12	0.56	3.51	6.11	7	5.04	0.49	4.43	5.76
SMS	2	10.86	-	10.55	11.17	18	10.23	0.55	9.18	11.37	7	10.52	0.73	9.50	11.56
LP	2	18.74	-	18.70	18.77	18	17.88	1.08	16.09	20.12	7	17.67	1.96	14.58	20.44
APM3	2	11.31	-	11.03	11.60	18	11.27	0.49	10.33	12.17	7	10.46	1.03	9.14	12.25
LBT	2	13.64	-	13.46	13.81	18	11.94	0.49	10.80	12.9	7	8.87	0.45	8.05	9.55

Medidas del holotipo (en mm). Longitud cabeza-cuerpo, 195; longitud de la pata posterior (con uña), 32; longitud de la oreja, 18; longitud total del cráneo, 43.99; longitud cóndilo-incisiva, 39.98; constricción interorbitaria, 9.08; ancho cigomático, 27.53; ancho de la caja craneana, 22.32; longitud del nasal, 13.53; ancho del nasal, 6.82; longitud de la diastema superior, 10.01; longitud de los forámenes incisivos, 5.38; longitud de la serie molar superior (alveolar), 11.17; longitud palatal, 18.77; ancho del paladar a la altura del tercer molar superior, 11.60; longitud de las bullas timpánicas, 13.81.

Diagnosis morfológica. Una especie pequeña de *Microcavia* (longitud cabeza cuerpo, 190 a 195 mm; longitud cóndilo-incisiva, 39.98 a 40.03 mm), que se diferencia de las otras incluidas en el género por una combinatoria única de rasgos morfológicos: coloración dorsal marrón, salpicada de amarillento; vientre color crema; cráneo pequeño pero robusto, con el perfil dorsal abovedado sobre la mitad posterior; rostro corto, ancho en la base y estrecho hacia adelante; yugal (en vista lateral) ancho anteriormente y estrecho hacia atrás, extendiéndose posteriormente (en vista ventral) más allá del borde posterior de la cavidad glenoidea; cresta del paladar baja, angosta anteriormente y expandida hacia atrás, que no sobrepasa el borde posterior del paladar; vacuidades esfenopalatinas pequeñas, con el borde anterior ubicado por detrás de la mitad anterior de la fosa mesopterigoidea; bullas timpánicas grandes e infladas; incisivos superiores moderadamente proodontes; M3 con una prolongación posterior alargada y robusta.

Otros ejemplares referidos a la especie. Al menos uno de los especímenes citados por Sánchez (2020) como pertenecientes a *M. niata pallidior* (CML 13052) puede ser considerado como perteneciente a *Microcavia sorojchi* sp. n. (Figura 122 de Sánchez 2020).

Distribución. Conocido únicamente para la localidad tipo en la provincia de Salta, y para la localidad de Quebrada de Santo Domingo, 30 km al SO de Jagüé, en la provincia de La Rioja (Sánchez 2020).

Declaración nomenclatorial: se obtuvo un número identificador de ciencias de la vida para la nueva especie descrita en este trabajo: urn:lsid:zoobank.org:act:E93DCEE1-DA63-428C-A596-9C14D59915F3.

Descripción. La piel del ejemplar CML 66, taxidermizada en posición de vida, está deteriorada y parcialmente decolorada. La coloración dorsal es marrón-amarillenta, más pálida hacia los flancos, con los pelos individuales de base marrón (3/4) y punta amarillenta (1/4). El vientre es color crema, con los pelos individuales de base marrón grisácea y la punta blanco-amarillenta. La cabeza es del mismo color que el dorso; el anillo periocular es amarillento y está bien marcado. Las orejas están cubiertas por pelos finos de color marrón. Las manos y las patas están cubiertos por pelos marrón claro a plateados, con las plantas desnudas y oscuras. En el ejemplar CML 13052 la coloración es similar, pero

Figura 2. Vistas dorsales (A-F) y ventrales (G-L) de los cráneos en las seis especies de *Microcavia*: *M. australis* (A, G; MACN-Ma 14.543), *M. jayat* (B, H; MACN-Ma 17333), *M. maenas* (C, I; MACN-Ma 34.116), *M.* sp. n. (D, J: CML 66), *M. niata* (E, K: AMNH 244252) y *M. shiptoni* (F, L; MACN-Ma 28155). Escala = 5 mm.

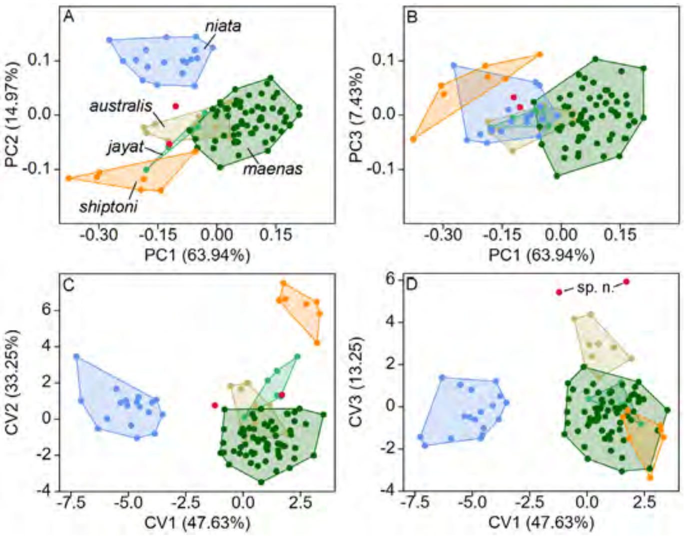

Figura 3. Polígonos y puntuaciones (= "scores") individuales de individuos adultos (edad 3-5) de *Microcavia* (*n* = 107) para: (A) componentes principales 1 y 2; (B) componentes principales 1 y 3; (C) variables canónicas 1 y 2 y (D) variables canónicas 1 y 3, extraídas de una función discriminante del análisis de seis taxones. Referencias: círculos verde oliva, *M. australis*; círculos verde claro, *M. jayat*; círculos verde oscuro, *M. maenas*; círculos celestes, *M. niata*; círculos naranja, *M. shiptoni*; círculos rojos, *M.* sp. n.

Tabla 3. Resultados del análisis de componentes principales (columnas 1 a 3) y del análisis discriminante (columnas 4 a 6) realizados sobre individuos adultos (*n* = 107) de cinco especies del género *Microcavia*. Véase "Materiales y métodos" para una explicación de las abreviaturas.

	PC 1	PC 2	PC 3	CV1	CV2	CV3
LTC	0.2097	0.0262	0.15637	0.00368	-0.0094	-0.0053
LCI	0.2523	-0.0157	0.16955	0.0057	-0.0111	-0.0039
CIO	0.2136	0.3654	-0.19623	-0.0032	-0.0144	-0.0066
AZ	0.1273	0.1872	0.13207	-0.0017	-0.0059	-0.0029
ACC	0.1243	0.0822	0.025986	0.0011	-0.0070	0.0028
LN	0.3633	0.0689	0.25034	0.0058	-0.0175	-0.0118
AN	0.1704	0.6842	-0.12716	-0.0121	-0.0142	-0.0080
DS	0.3646	-0.1957	0.30252	0.0131	-0.0140	-0.0023
LFI	0.5791	-0.4077	-0.65781	0.0184	-0.0276	-0.0082
SMS	0.2297	-0.0753	0.20883	0.0068	-0.0087	-0.0055
LP	0.2802	-0.0254	0.41597	0.00556	-0.0103	-0.0055
APM3	0.1777	0.1338	0.11069	0.0011	-0.0085	0.0006
LBT	0.1514	0.3495	-0.24127	-0.0047	-0.0147	0.0115

algo más brillante (cf. Sánchez 2020: Figura 121).

El cráneo (Figura 4) es pequeño, pero robusto y abovedado hacia la mitad posterior; el rostro es corto, ancho hacia la base y afinado anteriormente; los nasales están ligeramente abovedados en su porción anterior y sus márgenes exteriores son apenas divergentes hacia atrás; la sutura naso-frontal forma un ángulo obtuso, casi recto; la constricción interorbitaria es ancha, plana y recuerda a un reloj de arena; los márgenes supraorbitarios son finos y tienen forma de repisa; la sutura frontoparietal es recta; en vista lateral, las órbitas son grandes y de contorno subcuadrangular; los arcos cigomáticos son robustos y tienen un proceso paraorbitario pequeño (Figura 6D); el yugal es ancho anteriormente y se estrecha hacia atrás, extendiéndose posteriormente más allá del borde posterior de la cavidad glenoidea; los lagrimales son grandes y están parcialmente interpuestos entre el maxilar y el premaxilar; el margen posterior del diastema superior es casi vertical; los agujeros incisivos tienen forma lanceolada; el paladar está profundamente excavado; el margen posterior del paladar tiene forma de "V" muy abierta, con el vértice redondeado (Figura 7D); la cresta palatal es baja, angosta anteriormente y expandida hacia atrás y no sobrepasa el borde posterior del paladar; las vacuidades esfenopalatinas son pequeñas, con el borde anterior ubicado por detrás de la mitad anterior de la fosa mesopterigoidea; las bullas timpánicas son grandes e infladas; el meato auditivo es ancho y moderadamente largo, dirigido tanto hacia atrás como hacia afuera y hacia arriba; los procesos paraoccipitales prácticamente no se proyectan por debajo de las ampollas timpánicas.

La mandíbula (Figura 4) es baja y delgada; en vista labial, la cresta lateral se extiende entre el m1 y la base del proceso condilar, encerrando una fosa dorsal profunda; el proceso coronoides es muy pequeño y triangular; el pro-

Figura 4. Cráneo en vista lateral (arriba), dorsal (abajo, izquierda) y ventral (abajo, derecha) y mandíbula en vista labial (al medio) de *Microcavia sorojchi* sp. n. (CML 66; holotipo). Escala = 10 mm.

ceso condilar es ancho y se ubica por encima del proceso coronoides.

Los incisivos superiores son moderadamente proodontes y están cubiertos anteriormente por esmalte de color blanco; las series molariformes superiores son convergentes anteriormente, con los P4 casi en contacto por su lado medial; el P4 y el M1-M2 están cada uno formados por dos prismas lanceolados de dentina rodeados por una pared continua de esmalte; los lóbulos aumentan gradualmente de tamaño desde el P4 al M3; el hipoflexo en el M1-3 es estrecho y penetrante, mientras que el flexo externo es amplio y casi semicircular; el M3 tiene una ampliación posterior larga, que se estrecha hacia la base y se adjunta al segundo prisma (Figura 5); el p4 es menor que el m1-m3; el lóbulo anterior de p4 tiene forma de triángulo isósceles, mientras que el lóbulo posterior se parece a una gota; los lóbulos anteriores en m1-m3 son lanceolados y más anchos que los posteriores; el hipofléxido en el m1-3 es penetrante y estrecho y se orienta ligeramente hacia adelante; los fléxidos internos primarios son anchos y se orientan hacia atrás (Figura 5).

Comparaciones morfológicas. Microcavia sorojchi sp. n. presenta sus mayores afinidades morfológicas con el grupo de especies de tierras bajas que antes se refería como *M. australis* (*i. e.*, *M. australis*, *M. jayat* y *M. maenas*), tal como se deduce también de los análisis estadísticos multivariados. Los dos individuos referidos a la nueva especie se separaron de *M. maenas* sobre el primer componente principal, y de *M. australis* y *M. jayat* sobre el tercero, y de todas esas especies sobre el tercer eje del análisis discriminante (Figura 3). Además, como muestran las comparaciones detalladas con esos taxones en la Tabla 1, *M. sorojchi* sp. n. se diferencia claramente sobre la base de una combinación única de caracteres cualitativos, incluyendo el grado de proodoncia de los incisivos, la forma y longitud de la cresta palatal, la forma del borde posterior del paladar, la presencia (o ausencia) de los procesos medial del paladar y paraorbitario del yugal, la extensión posterior del yugal, y el desarrollo y posición de las vacuidades esfenopalatinas (Figs. 6A-D, 7). En todas las especies de este grupo, los M1-3 se caracterizan por tener flexos externos penetrantes y redondeados, y el M3 con una prolongación posterior alargada y con el flexo adicional (sensu Quintana 1996) penetrante (8A-C); en *M. jayat*, además, los bordes de los prismas en todos los molariformes son más rectos que en los otros taxones (donde tienden a ser más convexos) y el ápice lingual del segundo prisma en el M1-3 tiene cierto aspecto truncado (Figura 8A-C).

Figura 5. Vista oclusal de la serie molariforme superior derecha (A) e inferior izquierda (B) de *Microcavia sorojchi* sp. n. (CML 66; holotipo). Escala = 2 mm.

Microcavia sorojchi sp. n. se distingue de *M. niata* (incluyendo *M. n. niata* y *M. n. pallidior*, que se diferencian entre sí por rasgos sutiles de la coloración externa; véase Thomas 1902) por el perfil menos abovedado del cráneo, y el rostro proporcionalmente más angosto (Figura 2). Además, en *M. sorojchi* sp. n. el perfil superior del arco cigomático en vista lateral es recto, con un proceso paraorbitario pequeño sobre el yugal, mientras que en *M. niata* el borde es acusadamente cóncavo y el proceso paraorbitario grande y ancho (Figura 6D, E). Los molares superiores de *M. sorojchi* sp. n. presentan los flexos externos profundos y redondeados, mientras que en *M. niata* son superficiales y poco penetrantes. Finalmente, la ampliación posterior del M3 es larga y con el flexo adicional penetrante en *M. sorojchi* sp. n. (Figura 8C), y corta y con el flexo adicional superficial en *M. niata* (Figura 2).

Microcavia sorojchi sp. n. se diferencia de *M. shiptoni* por el perfil más abovedado del cráneo, y el rostro más corto y acuminado (proporcionalmente más largo y angosto en *M. shiptoni*). Los ejemplares de la nueva especie no se superponen con los de *M. shiptoni* en ninguno de los análisis morfométricos multivariados realizados (Figura 3). Adicionalmente, *M. sorojchi* sp. n. tiene las bullas timpánicas mucho más grandes e infladas, tanto en términos relativos como absolutos (13.46-13.81 vs. 8.05-9.55 mm) (Figura 2). Los molares superiores de *M. sorojchi* sp. n. presentan los flexos externos penetrantes y redondeados, mientras que en *M. shiptoni* son superficiales, con prismas de aspecto general más globoso. Finalmente, la ampliación posterior del M3 es larga y con el flexo adicional penetrante en *M.*

sorojchi sp. n. y corta y con el flexo adicional superficial *M. shiptoni* (Figura 8C, D).

Microcavia sorojchi sp. n. se distingue de las especies fósiles del género (*i. e., M. chapadmalensis*, *M. criolloensis*, *M. reigi* y *M. robusta*) por su tamaño mucho menor (serie molar superior < 11.9 mm, vs. 12–18 mm en las formas fósiles; cf. Ubilla *et al.* 1999; véase también Quintana 1996) y su cráneo menos robusto.

Historia natural. No hay datos sobre la historia natural de esta especie. La localidad de Chorrillos se ubica en la Puna Andina Central y su fisonomía corresponde a la de un pastizal y arbustal de altura. Otros micromamíferos registrados en esta localidad (entre 4,500 y 5,000 msnm), actualmente depositados en la colección MACN-Ma, fueron *Abrocoma cinerea*, *Abrothrix andina*, *Ctenomys* sp., *Galea comes*, *Eligmodontia* sp., *Microcavia shiptoni*, *Octodontomys gliroides* y *Phyllotis* sp. En La Rioja, Sánchez (2020) reportó la captura de tres hembras, una juvenil y dos adultas, en un ambiente de Puna, en relación con pequeñas quebradas y un lecho de río. Uno de los ejemplares presentaba la vagina abierta en el mes de marzo, mientras que otro tenía ectoparásitos (pulgas) de la especie *Delostichus talis* (Familia Rhopalopsyllidae, Subfamilia

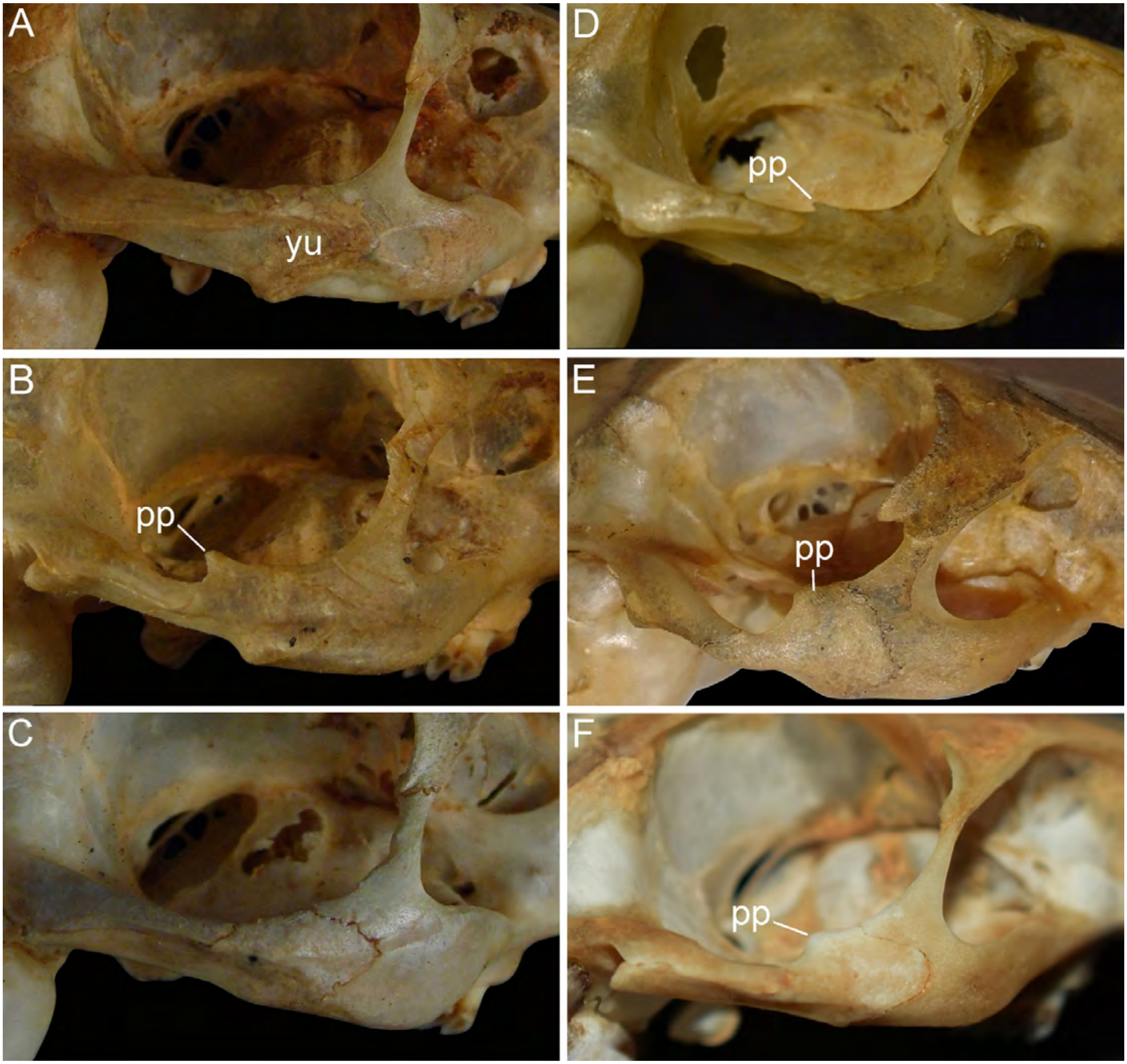

Figura 6. Vistas laterales de los arcos cigomáticos derechos en las seis especies de *Microcavia*: *M. australis* (A, MACN-Ma 14.543), *M. jayat* (B, MACN-Ma 17333), *M. maenas* (C, MACN-Ma 34.116), *M. sorojchi* sp. n. (D, CML 66; rotado), *M. niata* (E, AMNH 244252) y *M. shiptoni* (F, MACN-Ma 28155 [rotado]). Abreviaturas: pp, proceso paraorbitario; yu, yugal. Las figuras no están en escala para facilitar las comparaciones.

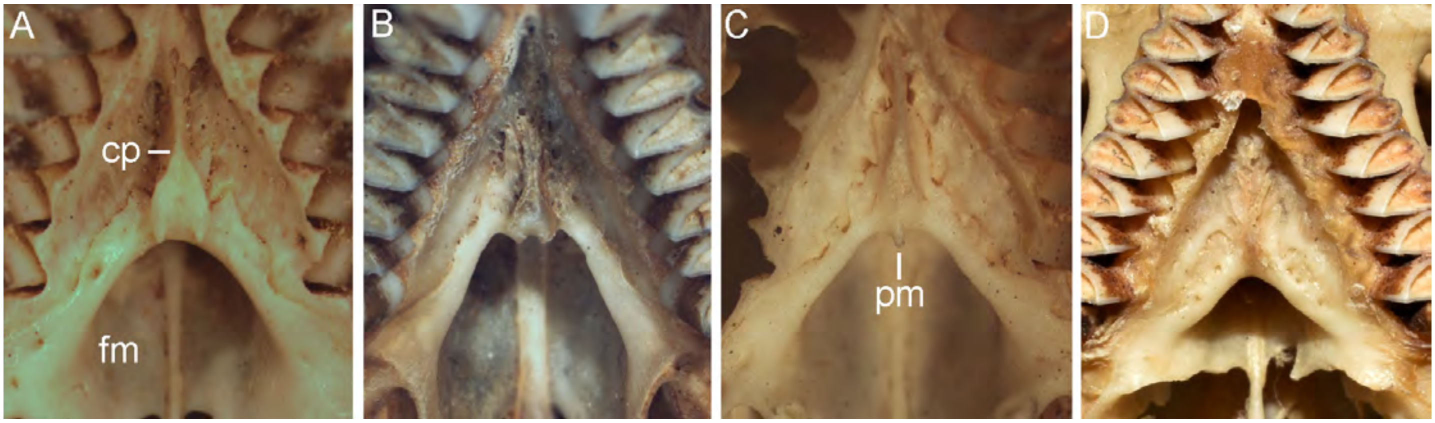

Figura 7. Vistas ventrales de los paladares en cuatro especies de *Microcavia*: *M. australis* (A, MACN-Ma 16379), *M. jayat* (B, MACN-Ma 17331), *M. maenas* (C, MACN-Ma 36.72) y *M. sorojchi* sp. n. (D, CML 66). Abreviaturas: cp, cresta del paladar; fm, fosa mesopterigoidea; pm, proceso medio del paladar. Las figuras no están en escala para facilitar las comparaciones.

Parapsyllinaela). Otros roedores registrados en esta localidad fueron *Abrothrix andina* y *Phyllotis vaccarum* (Sánchez 2020).

Conservación. Dado que se trata de una especie conocida de sólo dos localidades, en áreas que están siendo actualmente afectadas por actividades antrópicas, su estatus de conservación podría estar comprometido. Sin embargo, sin mayores datos que los actualmente disponibles, lo más acertado parece ser considerarla como Datos Deficientes. Si bien el uso de esta categoría no es del todo deseable (*e. g*., Teta *et al.* en prensa), por el momento es la que mejor se ajusta con las evidencias en mano. En el futuro, sería auspicioso que la especie sea adecuadamente evaluada por la Unión Internacional para la Conservación de la Naturaleza.

Etimología. "sorojchi" o "soroche" es una palabra utilizada por los pueblos andinos originarios para referirse al "mal de altura" o "apunamiento", una sensación de malestar corporal generalizado (dolor de cabeza, fatiga, náuseas, taquicardia, trastornos digestivos, etc.) ocasionada por la falta de oxígeno en las zonas de altura de la Puna y los Altos Andes. Elegimos esta palabra en alusión a los dos registros de distribución conocidos para la especie, ambos por encima de los 3,000 msnm, y a la sensación que seguramente experimentará todo aquel que viaje a esas regiones para estudiar la especie.

Discusión

A pesar del reducido tamaño de la muestra, en donde sólo uno de los dos especímenes referidos a la nueva especie pudo ser revisado directamente, la homogeneidad morfológica que exhiben los individuos CML 66 y CML 13052 (figurado por Sánchez 2020) nos permite hipotetizar que ambos corresponden a un mismo taxón, caracterizado por una combinatoria única de rasgos cráneo-dentarios. La constancia de ciertas características, especialmente aquellas vinculadas con la constitución general del arco cigomático y paladar, sumada a su distinción morfométrica, nos permiten separar a esos dos individuos de otros taxones reconocidos dentro del género. Notablemente, a pesar de su registro en dos localidades alejadas entre sí (*ca.* 540 km), los individuos CML 66 y CML 13052 resultan métricamente muy similares (Figura 2). Recientemente, Teta *et al.* (2017) reconocieron una nueva especie de *Microcavia* (*i. e*., *M. jayat*) y revalidaron otra (*M. maenas*) sobre la base de un razonamiento similar, demostrando la existencia de discontinuidades morfológicas cualitativas y cuantitativas claras entre poblaciones que por ese entonces eran ampliamente referidas a *M. australis*.

La descripción de taxones sobre la base de pocos ejemplares puede no ser el escenario ideal, desde el momento en que se tiene poco control sobre la variabilidad intraespecífica. Aun así, se trata de una práctica relativamente frecuente en ciertos grupos de mamíferos, incluso en la actualidad (*e. g*., Eulipotyphla; véase Quiroga-Carmona 2013; Quiroga-Carmona y Molinari 2012; Quiroga-Carmona y Woodman 2015; Andino-Madrid *et al.* 2020). En todo caso, es también una situación esperable para regiones ampliamente inexploradas en cuanto a sus especies de pequeños mamíferos, como es el caso de los Altos Andes del noroeste de Argentina. Más en general, incluyendo el caso de algunas especies de roedores, este accionar está justificado si el ejemplar (o los ejemplares) en cuestión es (son) lo suficientemente distintivo(s). Por ejemplo, *M. shiptoni* fue descripto a partir de sólo dos individuos (Thomas 1925; véanse otros ejemplos en Patterson 1992; Gippoliti y Amori 2011; Fernández de Córdova *et al.* 2020). En última instancia, y tal como ha sido documentado previamente, la hipótesis propuesta en este trabajo es la que mejor se ajusta con nuestro actual conocimiento de la variabilidad morfológica en este grupo de roedores. En efecto, muchos de los caracteres considerados diagnósticos de la nueva especie (*e. g*., la forma y longitud de la cresta palatal, la forma del borde posterior del paladar, la presencia o ausencia de los procesos medial del paladar y paraorbitario del yugal, la extensión posterior del yugal y el desarrollo y posición de las vacuidades esfenopalatinas) han demostrado ser muy constantes en otras especies del género (cf. Teta *et al.* 2017).

Microcavia sorojchi sp. n. se distingue claramente de *M. niata* y *M. shiptoni*, tanto cuantitativamente (Figura 3) como cualitativamente (Figuras 2, 6 y 8). Entre otras diferencias en la anatomía cráneo-dentaria (*e. g.*, tamaño de las bullas timpánicas), se destacan algunos rasgos notables de la arquitectura de los molares, como por ejemplo la forma y profundidad de los flexos externos y la prolongación posterior del M3. Si bien existe cierta variabilidad en la morfología dentaria en *Microcavia* (cf. Contreras 1964), este rasgo del M3 es relativamente constante y ha sido usado previamente como carácter taxonómico informativo (*e. g.*, Thomas 1925; Quintana 1996).

Por el contrario, *M. sorojchi* sp. n. presenta sus mayores afinidades morfológicas con *M. australis*, *M. jayat* y *M. maenas*, tal como lo destacan los análisis morfométricos y las comparaciones de rasgos cualitativos. La moderada superposición entre *M. sorojchi* sp. n., *M. australis* y *M. jayat* en el espacio multivariado de los análisis de componentes principales y discriminantes no es del todo inesperada, sobre todo si se tiene en cuenta que entre otros Cavioidea se dan situaciones similares o incluso superposiciones entre especies mucho más amplias (*e. g.*, Campo *et al.* 2020; Teta 2019; Teta *et al.* 2019). Aun así, *M. sorojchi* sp. n. puede ser claramente diferenciada de *M. australis*, *M. jayat* y *M. maenas* por una combinatoria única de rasgos cualitativos y cuantitativos (Tabla 1, Figuras 2, 6, 7 y 8). De hecho, las diferencias registradas entre *Microcavia sorojchi* sp. n. y esos taxones son comparables o más importantes que las reconocidas para otras especies entre sí (*e. g.*, entre *M. australis* y *M. maenas*, véase Teta *et al.* 2017). Por último, la nueva especie se conoce para dos localidades por encima de los 3,100 m y en ambientes de Puna, mientras que *M. australis*, *M. jayat* y *M. maenas* se registran mayormente por debajo de los 2,500 m y en otro tipo de ambientes (*e. g.*, Chaco Seco, Monte de Sierras y Bolsones, Monte de Llanuras y Mesetas, Estepa Patagónica).

Con el nuevo taxón descrito en esta contribución, el número de especies de *Microcavia* asciende a seis, y el de especies registradas para el noroeste de Argentina, a cuatro. Para el sector de altura que corresponde a la Puna entre Catamarca y Jujuy, por encima de los 3,000 m, las distribuciones de estos animales permanecen muy pobremente conocidas, en consistencia con las escasas colectas de pequeños mamíferos realizadas en ese sector. Un ejemplo paradigmático de esta aseveración es el caso de *M. shiptoni*, una especie documentada para sólo dos localidades, separadas por más de 270 km, en las provincias de Catamarca y Salta (Dunnum 2015). Por debajo de los 2,500 metros se registra una tercera especie, referida por Teta *et al.* (2017) como *M. maenas*; si bien este taxón resulta mucho mejor conocido en distintos aspectos de su historia natural que otras especies del género (véase Tognelli *et al.* 2001), el límite norte de su distribución tampoco está del todo claro (Teta *et al.* obs. pers.). La cuarta especie es *M. jayat* (Teta *et al.* 2017), recientemente descripta y conocida hasta el momento para unas pocas localidades en tierras bajas de las provincias de La Rioja y Santiago del Estero. Adicionalmente, Sánchez (2020) reconoció a *M. salinia* (Thomas 1921) como una especie válida y distinta de *M. australis*, pero nuestra inspección de muchos de los mismos especímenes revisados por esta autora indica que no pueden diferenciarse de *M. maenas*, tanto en términos cualitativos como cuantitativos (véase también Teta *et al.* 2017, d'Hiriart *et al.* 2021). Muchos de los rasgos diagnósticos referidos por Sánchez para *M. salinia* (*e. g.*, forma de los nasales, convexidad del parietal, contorno de la muesca lunar de la mandíbula) son variables entre individuos y se diluyen cuando se consideran series extensas de ejemplares.

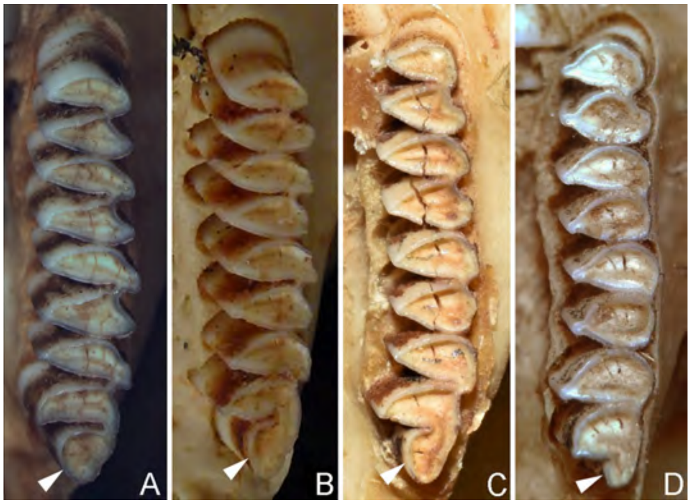

Figura 8. Vistas oclusales de las series molariformes superiores en cuatro especies de *Microcavia*: *M. jayat* (A, MACN-Ma 17333), *M. maenas* (B, MACN-Ma 34.116), *M. sorojchi* sp. n. (C, CML 66 [rotado]) y *M. shiptoni* (D, CML 7237). La flecha señala la prolongación posterior del M3. Las figuras no están en escala para facilitar las comparaciones.

En menos de cinco años, la diversidad reconocida para el género *Microcavia* aumentó de tres a seis especies, indicando con elocuencia lo pobre de nuestro conocimiento de este grupo de roedores, para el que las revisiones más recientes previamente publicadas tenían más de medio siglo (*e. g.*, Cabrera 1953). Si se tiene en cuenta que estas modificaciones taxonómicas han sido realizadas utilizando solamente evidencias morfológicas (cualitativas y cuantitativas), no sería inesperado que todavía existan algunas especies crípticas, reconocibles a través de otras aproximaciones (*e. g.*, análisis de ADN), esperando ser descubiertas. En este sentido, es destacable que más de la mitad de las especies incluidas en este género no cuentan todavía con secuencias disponibles de ADN, tal es el caso de *M. australis* (las referidas para esta especie en GenBank corresponden a *M. maenas*), *M. jayat*, *M. shiptoni* y *M. sorojchi* sp. n. Esta situación limita las posibilidades de realizar un trabajo verdaderamente integrativo y de contrastar la hipótesis aquí presentada con otras líneas de evidencia. Sería deseable que esta situación sea subsanada en el futuro, mediante la colecta de nuevos especímenes en el campo o a través de la extracción de ADN antiguo a partir de los numerosos ejemplares disponibles en colecciones.

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Morphological and ecological data confirm *Reithrodontomys cherrii* as a distinct species from *Reithrodontomys mexicanus*

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The integrative taxonomy approach has recently been widely suggested in systematic studies. Lines of evidence such as the geometric morphometrics and ecological analyses have been useful for discriminating between genetically well-differentiated species. Within the genus *Reithrodontomys*, *R. mexicanus* is one of the more taxonomically complex species, being considered a cryptic species complex. *R. cherrii* was considered a subspecies of *R. mexicanus*, until molecular evidence raised it to the species-level. Herein, we evaluate these two forms using morphological and ecological data based on the premise that they constitute genetically differentiated species. We carried out geometric morphometric analyses on dorsal and ventral views of the skull. Landmark and semi-landmark configurations for both views of the skull were selected based on previous studies of cricetid rodents. We tested the presence of sexual dimorphism, and the skull shape and size differences between species on both cranial views. Additionally, we characterized the environmental space of each species habitat using bioclimatic variables, elevation, and the Normalized Difference Vegetation Index (NDVI). Females and males of *R. mexicanus* and *R. cherrii* did not show sexual dimorphism in shape or size of both skull views. We found significant differences between the two species in both shape and size of the skull. Cranial structures of the ventral view were more useful to differentiate both species. *R. mexicanus* exhibited a broader environmental space than *R. cherrii*, with relatively similar values of temperature and elevation, but not of precipitation. The pairwise comparison showed significant differences in the majority of the environmental variables analyzed. Although for each view, we found statistical differences in the skull shape of *R. cherrii* and *R. mexicanus*, the ventral side showed major resolutive power differentiating both species. Our findings suggest that *R. cherrii* tends to have a larger skull than *R. mexicanus*. However, the morphological and pelage coloration similarity between these species reported in the past, could explain the previous inclusion of *R. cherrii* as a subspecies of *R. mexicanus*. *R. mexicanus* occurs in a variety of vegetation-types coinciding with the broader environmental space that it occupies compared to that of *R. cherrii*. The natural areas where both species are distributed were associated with high NDVI values. Our results complement the molecular evidence and, under an integrative taxonomy approach, support *R. cherrii* as a different species from *R. mexicanus*.

Recientemente, el enfoque de taxonomía integrativa ha sido ampliamente sugerido en estudios sistemáticos. Líneas de evidencia como la morfometría geométrica y los análisis ecológicos han sido útiles para discriminar entre especies genéticamente bien diferenciadas. Dentro del género *Reithrodontomys*, *R. mexicanus* es una de las especies más complejas taxonómicamente, siendo considerada un complejo de especies crípticas. *R. cherrii* se consideró una subespecie de *R. mexicanus*, hasta que la evidencia molecular la elevó al nivel de especie. En este estudio, evaluamos las diferencias entre estas dos formas utilizando datos morfológicos y ecológicos, basados en la premisa de que constituyen especies genéticamente diferenciadas. Se realizaron análisis de morfometría geométrica para las vistas dorsal y ventral del cráneo. Las configuraciones de marcas y semimarcas para ambas vistas fueron seleccionadas utilizando estudios previos en roedores cricétidos. La presencia de dimorfismo sexual y las diferencias en la forma y tamaño del cráneo entre las especies se evaluaron en ambas vistas del cráneo. Asimismo, se caracterizó y comparó el espacio ambiental que cada especie ocupa utilizando variables bioclimáticas, la elevación y el Índice de Vegetación de Diferencia Normalizada (NDVI). Hembras y machos de *R. mexicanus* y *R. cherrii* no mostraron dimorfismo sexual para la forma y el tamaño en ambas vistas del cráneo. Se encontraron diferencias significativas entre las especies para la forma y tamaño del cráneo. Las estructuras craneales de la vista ventral resultaron más útiles para diferenciar ambas especies. *R. mexicanus* exhibió un espacio ambiental más amplio que *R. cherrii*, con valores relativamente similares de temperatura y elevación, pero no de precipitación. La comparación por pares mostró diferencias significativas en la mayoría de las variables ambientales. Aunque para cada vista, encontramos diferencias estadísticas en la forma del cráneo de *R. cherrii* y *R. mexicanus*, el lado ventral mostró mayor poder resolutivo diferenciando ambas especies. Nuestros resultados sugieren que *R. cherrii* tiende a tener el cráneo de mayor tamaño que *R. mexicanus*. No obstante, la gran similitud morfológica y de coloración del pelaje reportada entre estas especies en el pasado, pudiera explicar la previa inclusión de *R. cherrii* como una subespecie de *R. mexicanus*. *R. mexicanus* ocurre en distintos tipos de vegetación, coincidiendo con el espacio ambiental más amplio que ocupa en comparación con el de *R. cherrii*. Las áreas naturales donde se distribuyen ambas especies mostraron asociación con altos valores de NDVI. Nuestros resultados complementan la evidencia molecular y, con un enfoque de taxonomía integrativa, confirman a *R. cherrii* como una especie diferente de *R. mexicanus*.

Keywords: Cricetidae; cryptic species; environmental space; harvest mice; integrative taxonomy; skull morphometry.

Introduction

The morphological species concept has been used historically to describe new taxa (Mayden 1997; Mayr 2000). In fact, the majority of species that we know today were delimited and/or assigned to different taxonomic categories based on their morphological characteristics (Seifert 2014). However, establishing species boundaries in some instances is problematic (Mayr 2000). For example, for cryptic species, which are genetically different entities that do not show distinctive morphological characteristics (Struck *et al.* 2018). In these cases, species concepts with different criteria have been proposed, most of them based on the use of a single operational criterion to describe new species (Sites and Marshall 2003, 2004). In contrast, the General Lineage concept (de Queiroz 1998, 2007) employs multiple lines of evidence (genetic, morphological, ecological, ethological, etc.) to propose species as a separately evolving metapopulation lineage. This approach implements the use of an integrative taxonomy, which has been widely suggested in systematic studies (Dayrat 2005; Alström *et al.* 2008; Sangster 2018).

Recently, Leaché *et al.* (2009) argued that the use of morphological and ecological data, in addition to molecular data, allows better discrimination among species. Geometric morphometric analysis is a robust tool to highlight interspecific variation in zoological groups, such as mammals, corroborating the phylogenetic relationships within them (*e. g.*, Bogdanowicz *et al.* 2005; Camul and Polly 2005; Pavan and Marroig 2016). In addition, ecological niche studies are being increasingly used for these same purposes (*e. g.*, Rissler and Apodaca 2007; Rivera *et al.* 2018; Zhao *et al.* 2019), and for making inferences related to evolutionary questions of both historical distributions and speciation processes (Graham *et al.* 2004).

The genus *Reithrodontomys* (Cricetidae, Rodentia) constitutes a taxon in which species were originally described based on pelage coloration (Allen 1895), and morphological characteristics of the skull and dentition (Merriam 1901; Hooper 1952). However, variation in these characters overlap among populations of different species (Hooper 1952), making taxonomic recognition difficult and leading to misidentifications in many cases.

Reithrodontomys mexicanus (Saussure, 1860) is one of the most taxonomically complex species within the genus, nowadays considered as a complex of cryptic species (Arellano *et al.* 2003, 2005; Miller and Engstrom 2008). Hooper (1952, 1959) recognized 13 subspecies, but currently only 10 are remain valid (Bradley 2017). One of the species that has been subject to taxonomic changes is *R. cherrii* (Allen, 1891), restricted to some highland localities in central Costa Rica (Hooper 1952; Hall 1981). Howell (1914) relegated *R. cherrii* as a subspecies of *R. mexicanus*, without a clear justification for this nomenclatural change. Almost a century later, Arellano *et al.* (2005) raised *R. cherrii* back to the species level based on a molecular phylogenetic analysis of the mitochondrial cytochrome b gene. Specimens of *R. cherrii* were grouped into a genetically well-differentiated clade from *R. mexicanus* (recognized herein as *R. mexicanus* "classic" clade), with a genetic distance value (using the K2P evolutionary model) greater than 12 % (Arellano *et al.* 2006). Also, the species status of *R. cherrii* was recognized by Gardner and Carleton (2009) using traditional morphometrics and pelage coloration. However, it is desirable to complement the taxonomic distinction between *R. cherrii* and *R. mexicanus* with a larger sampling and under an integrative taxonomy approach employing alternative data sources such as geometric morphometrics and ecological attributes. Therefore, the goal of this study is to compare both species using cranial features and environmental characteristics of their habitats, based on the premise that they constitute genetically well-differentiated species.

Materials and methods

Geometric morphometrics data. We examined 47 skulls of adult individuals (M3 erupted, age classes following Arellano *et al.* 2012) from different museum collections (Appendix 1), and each specimen was photographed in the dorsal and ventral views of the skull. We based the selection of specimens; *R. mexicanus* (*n* = 28) and *R. cherrii* (*n* = 19); and their localities (Figure 1; Appendix 1), on the *R. mexicanus* "classic" and *R. cherrii* clades obtained in the phylogeny reported by Arellano *et al.* (2005). The specimens used in Arellano *et al.* (2005), but not available for morphometric analysis, were replaced by individuals from the same localities or within a radius less than 60 km. Digital images of skulls were taken using an Olympus DP73 Digital Camera coupled to an optical microscope, and to the computer through the CellSens program. The skulls were positioned on a black background, always keeping the same distance from the camera lens, and using a millimeter rule as a scale bar.

Landmark and semi-landmark configurations for both views were selected based on previous studies of cricetid rodents (*e. g.*, Martínez and Di Cola 2011). Configurations were digitized assuming positional homology among individuals (Zelditch *et al.* 2004), with the TPSdig 2.31 program (Rohlf 2015). We used 17 landmarks, 13 semi-landmarks for the ventral view and 12 landmarks, 23 semi-landmarks for the dorsal view (Figure 2; Appendix 2). We aligned, rotated, and scaled all landmarks and semi-landmarks configurations using a Generalized Procrustes analysis (GPA; Rohlf and Slice 1990) implemented in the package geomorph 3.3.1 (Adams and Otárola-Castillo 2013) from R library (R Core Team 2018). During this processing, semi-landmarks position on the curved structures were allowed to slide along their tangent vectors until reaching the minimum point of bending energy (Bookstein 1997; Zelditch *et al.* 2004). Shape variables (Procrustes distances and Procrustes coordinates) and centroid size (CZ) were obtained from the GPA. The CZ is related to skull size and computed as the square root of the sum of the squared distances between each landmark and the configuration centroid (Bookstein 1991).

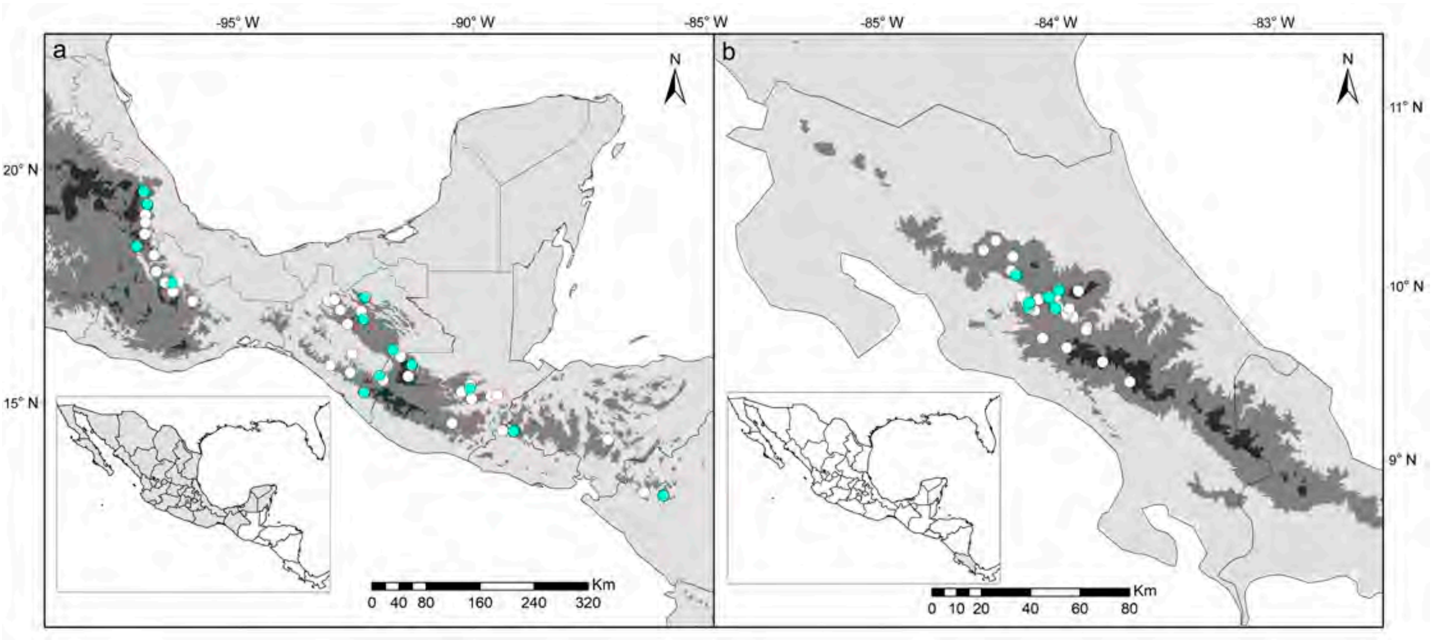

Figure 1. Map showing localities of the specimens used in this study. (a) *Reithrodontomys mexicanus* from Mexico and Central America and (b) *R. cherrii* from Costa Rica. Localities for geometric morphometric analysis are highlight in blue dots. Gray tones depict elevation gradient: light gray < 1,000 m, gray 1,000 to 2,500 m; and dark gray > 2,500 m.

Sexual dimorphism and allometry. We evaluated the sexual dimorphism in shape and size of the skull within species for each view. A Procrustes ANOVA (Goodall 1991; Anderson 2001) was performed for skull shape using the function ProcD.lm, and a factorial design with shape as the dependent variable, sex as the main factor, and CZ as a covariate. Significant differences ($P \leq 0.05$) in skull size between sex were tested using the function lm.rrpp in the R package RRPP (Collyer and Adams 2018). The allometric component (possible effect of the skull size on the shape variation) was analyzed using a Procrustes ANOVA and the same factorial design previously declared. Analyses of sexual dimorphism (shape) and allometry were carried out in geomorph 3.3.1.

Skull shape and size differences. Principal component analysis (PCA) on the Procrustes coordinates were performed for each view of the skull in geomorph 3.3.1. Then, we used the first two components to visualize the ordering of the data according to the skull morphometric variation, and the extreme variation (minimum and maximum) of the shape along component 1 were represented using deformation grids.

We determined shape differences between species for each skull view using a Procrustes ANOVA in geomorph 3.3.1. A factorial design was used with shape as the dependent variable, species as the main factor, and CZ as a covariate. The mean skull shape differences between species were quantified (Procrustes distances) and tested for its statistical significance ($P \leq 0.05$; resampling = 1000), using a pairwise permutation test (function permudist) in the R package Morpho 2.4 (Schlager 2016).

We employed a similar approach to compare skull shape between species for skull size. This analysis was developed for each view with the function lm.rrpp of the RRPP package. The factorial design consisted of CZ as the dependent variable, species as the main factor, and shape as a covariate. We visualized the results of these analyses using the shiny application Extended Boxplot Graphics (Ramirez-Arrieta *et al.* 2020).

Ecological niche data. For the ecological analysis, we included the occurrences localities for the specimens used in the morphometric analysis. Additional localities were incorporated to represent the largest number of sites reported for both species (Figure 1; Appendix 3). Occurrence records were obtained from museums databases or downloaded from the VertNet database (http://portal.vertnet.org). Geographic coordinates were rectified against the known distribution of *R. cherrii* and *R. mexicanus* (Hooper 1952; Hall 1981), to reduce georeferencing errors.

We characterize the species ecological niche using six bioclimatic variables from Wordclim 2.0 (Fick and Hijmans 2017; http://www.worldclim.org): BIO1 = Annual Mean Temperature, BIO5 = Max Temperature of Warmest Month, BIO6 = Min Temperature of Coldest Month, BIO12 = Annual Precipitation, BIO13 = Precipitation of Wettest Month, and BIO14 = Precipitation of Driest Month, with a spatial resolution of ~1 km^2. The selection of variables was based on previous studies that highlight their importance for small mammals ecological analyses (Santos *et al.* 2017; Guevara *et al.* 2018; Stanchak and Santana 2018). Because the distribution of small mammals may also depend on elevation gradient and vegetation quality (Patterson *et al.* 1989; McCain 2005; Umetsu and Pardini 2007), we also used elevation as a topographic variable derived from a digital elevation model (data available at http://www.worldclim.org), and the Normalized Vegetation Difference Index (NDVI; Pettorelli *et al.* 2005). The NDVI layer was obtained from the

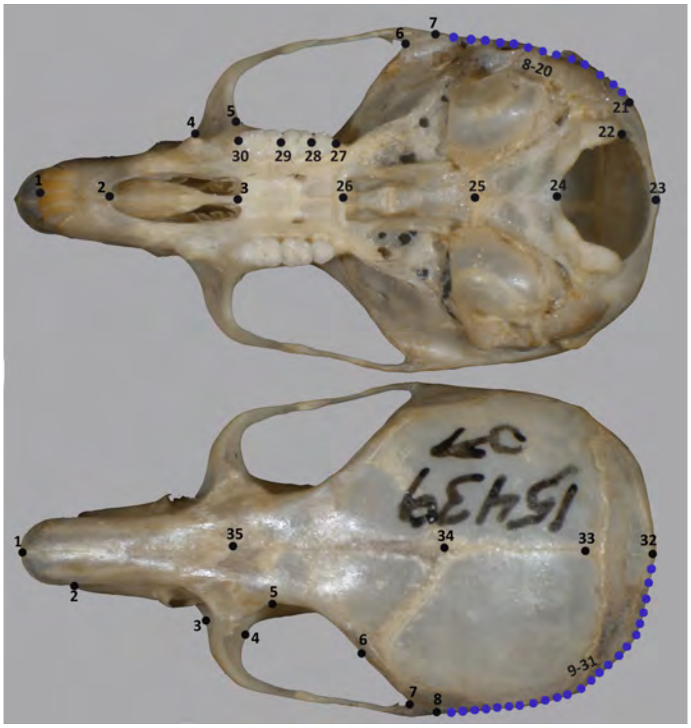

Figure 2. Landmarks (black dots) and semi-landmarks (blue dots) digitized in ventral and dorsal views of the skull. Anatomical positions of landmarks described in Appendix 2. The specimen voucher (BYU 15439) is a male of *Reithrodontomys mexicanus*.

Climate Engine Platform available at http://ClimateEngine.org (Huntington *et al.* 2017), which represents the average conditions of this index in the last five years.

Ecological niche differences. Ecological niche characteristics of *R. cherrii* and *R. mexicanus* were summarized using the predictor variables described above (bioclimatic, elevation, and NDVI). To determinate the environmental ranges of each species, we calculated descriptive statistics (Mean, Standard Error, Maximum and Minimum values, Confidence Intervals constructed from the percentile method, Standard Deviation, and Coefficient of Variation) using information extracted from the occurrence records.

With the predictor variables, we generated an environmental background using ArcGIS 10.8 (ESRI 2020), which included the information extracted from 10,000 random points within a buffer of 100 km^2, around each occurrence record. This buffer selection allows to consider regions with suitable environmental conditions for the species and to minimize the inclusion of areas where they would not be found due to the presence of physical barriers or biotic interactions (Kubiak *et al.* 2017).

The environmental background and the occurrence data were used to visualize the species ecological niche in a three-dimensional space constructed from the first three principal components (which explained over 95 % of the variance in the data). For this, the minimum-volume ellipsoid (Van Aelst and Rousseeuw 2009) and convex polyhedron (Soberón and Nakamura 2009) were displayed as a representation of the fundamental and realized niche (Qiao *et al.* 2016) for each species, respectively. Analyses were performed using NicheA (Qiao *et al.* 2016), a software for exploring and analyzing the environmental and geographic spaces of virtual and real species. Niche similarity between species was quantified in NicheA, based on Jaccard index (Jaccard 1912), and using the minimum-volume ellipsoid calculation method. This index based on the superposition of ellipsoids in the environmental space, captures the fundamental niche rather than the realized.

Additionally, we performed PCA on the environmental data of the occurrence records, to determine whether the ecological niches were significantly different ($P \leq 0.05$) between species, using the first two principal components (which explained 99.7 % of the total variance). Finally, we performed a Mann-Whitney U test for each variable in the program Statistica 8.0 (STATSOFT 2007), to know which of them contributed to the environmental niche differentiation between *R. mexicanus* and *R. cherrii*.

Results

Sexual dimorphism and allometry. Females and males of *R. mexicanus* and *R. cherrii* did not show sexual dimorphism in shape or size of the skull for both ventral and dorsal views (Table 1). Consequently, we did not distinguish between sexes to perform the morphometric analyses. Likewise, none of the species demonstrated significant allometry between shape or size of any skull view, therefore, we used the Procrustes distances matrix in our analyses of interspecific comparison.

Table 1. Results of sexual dimorphism and allometry analyses in *Reithrodontomys mexicanus* and *R. cherrii*, using shape and size (centroid size) of the skull from ventral and dorsal views.

	SS	*MS*	R^2	*F*	*Z*	*P*
A. *Reithrodontomys mexicanus*						
Ventral view						
Shape~Sex	0.002	0.002	0.051	1.416	0.870	0.208
Centroide size~Sex	2.856	2.856	0.028	0.764	0.400	0.404
Shape~Centroide size	0.002	0.002	0.048	1.319	0.809	0.207
Dorsal view						
Shape~Sex	0.002	0.002	0.054	1.554	0.985	0.162
Centroide size~Sex	8.509	8.509	0.064	1.779	0.805	0.207
Shape~Centroide size	0.003	0.003	0.079	2.272	1.556	0.078
B. *Reithrodontomys cherrii*						
Ventral view						
Shape~Sex	0.002	0.002	0.091	2.017	1.569	0.067
Centroide size~Sex	0.165	0.165	0.012	0.210	0.168	0.651
Shape~Centroide size	0.002	0.002	0.092	2.029	1.448	0.084
Dorsal view						
Shape~Sex	0.003	0.003	0.103	1.949	1.288	0.106
Centroide size~Sex	2.310	2.310	0.133	2.612	0.924	0.157
Shape~Centroide size	0.002	0.002	0.063	1.196	0.531	0.283

SS = sum of squares; *MS* = means squares; *Z* and *P* values based on 1000 permutations

Skull shape and size differences. For the ventral view of the skull, the first principal component (PC1) separated *R. cherrii* from *R. mexicanus* almost completely, which together with the second component (PC2) explained 63.12 % of shape variation (Figure 3a). For the dorsal view, the first two principal components overlapped in the skull shape for both species (Figure 3b). The PC1 segregated the two species better than the PC2, explaining 49.67 % and 11.05 % of the skull shape variation, respectively.

Procrustes ANOVA analyses revealed differences between *R. mexicanus* and *R. cherrii* for the ventral ($F_{1.46} = 6.42$; $P \leq 0.01$) and dorsal ($F_{1.46} = 3.19$; $P \leq 0.01$) views of the skull shape. Differences between mean shape for the ventral view were found mainly in the posterior region of the cranium (Figure 4). *R. mexicanus* displayed an expansion of the landmarks of the foramen magnum, and a relatively broader braincase than *R. cherrii*. In the dorsal view, the most notable differences were located on the anterior and middle region of the cranium (Figure 4). *R. cherrii* exhibited a relatively longer nasal bones, a broader configuration between the 3-4-5 landmarks that described the zygomatic plate and the interorbital region, and a relatively broader parietal bone. Skull size differences between species (Figure 5) were highly significant for the ventral view ($F_{1.46} = 17.01$; $P \leq 0.01$), and significant for the dorsal view ($F_{1.46} = 4.50$; $P \leq 0.05$).

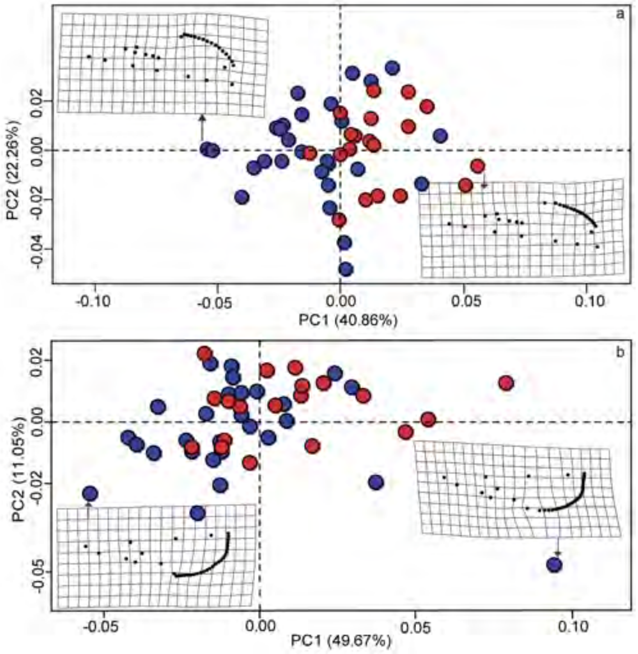

Figure 3. Principal component analysis of ventral (a) and dorsal (b) views of the skull. Red dots = *Reithrodontomys mexicanus* and blue dots = *R. cherrii*. Deformation grids represent the minimum and maximum variation in skull shape along the first component.

Ecological niche differences. Most variables that characterized the ecological niche of each species were relatively distinct in mean and ranges (Table 2). The environmental space of *R. mexicanus* had ranges with higher values of temperature for the warmest and coldest months, although the mean annual temperature was similar for both species. With respect to precipitation, the environmental space of both species showed similar means for the driest month, but not for the wettest month. Annual precipitation values were notably different, the environmental niche of *R. cherrii* exhibited a higher mean value than that reported for the geographic region where *R. mexicanus* is distributed. The

Table 2. Descriptive statistics used to summarize the ecological niche characteristics of *Reithrodontomys mexicanus* and *R. cherrii* based on the environmental information from occurrence records.

	Environmental Variables	***Mean ± SE***	***Min - Max***	***CI***	***SD***	***CV***
R. mexicanus	Annual Mean Temperature	17.87 ± 0.53	10.44 - 25.43	12.36 - 21.57	3.61	20.26
	Max Temperature of Warmest Month	25.94 ± 0.62	18.80 - 36.00	19.50 - 31.30	4.21	16.25
	Min Temperature of Coldest Month	9.58 ± 0.50	1 - 18.90	5.50 - 13.20	3.42	35.68
	Annual Precipitation	1906.39 ± 128.08	482 - 4875	1145 - 2943	868.68	45.57
	Precipitation of Wettest Month	346.09 ± 22.38	103 - 886	223 - 546	151.82	43.87
	Precipitation of Driest Month	34.80 ± 4.45	2 - 144	6 - 68	30.16	86.85
	Elevation	1696.91 ± 82.87	438 - 3083	997 - 2434	562.09	33.12
	NDVI	0.77 ± 0.02	0.34 - 0.90	0.58 - 0.87	0.12	15.90
R. cherrii	Annual Mean Temperature	17.88 ± 0.56	8.41 - 22.03	12.51 - 20.42	3.28	18.36
	Max Temperature of Warmest Month	24.35 ± 0.62	14.1 - 29	18.10 - 27.20	3.61	14.85
	Min Temperature of Coldest Month	11.92 ± 0.56	2.3 - 16.3	6.70 - 14.60	3.28	27.55
	Annual Precipitation	2721.65 ± 90.67	1961 - 4052	2197 - 3562	528.75	19.43
	Precipitation of Wettest Month	426.48 ± 11.73	317 - 592	340 - 520	68.42	16.04
	Precipitation of Driest Month	46.29 ± 5.50	10 - 131	10 - 100	32.07	69.29
	Elevation	1629.76 ± 96.25	900 - 3297	1170 - 2573	561.28	34.43
	NDVI	0.67 ± 0.03	0.23 - 0.87	0.38 - 0.83	0.17	25.87

SE = Standard Error, *Min* = Minimum, *Max* = Maximum, *CI* = Confidence Intervals (Percentile method), *SE* = Standard Deviation, *CV* = Coefficient of Variation elevation gradient occupied by *R. cherrii* ranged from 900 to almost 3,300 masl, whereas in *R. mexicanus* it ranged from over 400 to around 3,000 masl. Distribution areas of *R. mexicanus* presented NDVI ranges slightly higher than those of *R. cherrii*, although in both species the NDVI means were above 0.6.

The ecological niche visualization using the first three components showed that *R. mexicanus* occurs in a broader environmental space than *R. cherrii* (Figure 6a). The minimum-volume ellipsoids displayed a partial overlap of the environmental conditions of each species, with a low niche similarity of Jaccard index (0.08). The statistical comparison of the principal component scores showed significant differences ($U = 313$; $P = 0.02$) between the environmental niche of each species for the first component, while no differences were found ($U = 458$; $P = 0.25$) for the second component (Figure 6b, 6c). In the pairwise comparisons, all variables were statistically different, except for BIO1, BIO14, and elevation (Figure 7).

Discussion

Geometric morphometrics has shown great applicability in mammal taxonomic studies, mainly for anatomical structures such as the cranium, dentition, or mandibles (*e. g.*, Cordeiro-Estrela *et al.* 2008; Barčiová 2009; Kryštufek *et al.* 2021). As part of an integrative taxonomy, this morphological tool has allowed researchers to corroborate hypotheses derived from phylogenetic studies and to establish species boundaries (Camul and Polly 2005; Pavan and Marroig 2016). This taxonomic approach also includes other lines of evidence, such as ecological data (Dayrat 2005). In particular, the environmental niche characteristics can be useful to delimit cryptic species or phylogenetically related groups, especially when their relationships are known, something that has been confirmed in several rodent species (Martínez-Gordillo *et al.* 2010). This could be the case of the harvest mice *R. mexicanus* and *R. cherrii*, for which genetic differences are well established, but lack modern morphometrics and ecological data. In this study, we tested the premise that differences in the skull and the environmental characteristics would be consistent with the genetic divergence documented between these species (Arellano *et al.* 2003, 2005, 2006).

Our findings of sexual non-dimorphism in both species coincide with that previously described for *Reithrodontomys* (Hooper 1952). In *R. mexicanus*, the absence of sexual dimorphism was reported by Arellano *et al.* (2012) analyzing the morphometric variation in a population from Sierra Juárez, Oaxaca. Whereas for *R. cherrii,* here we report for the first time sexual non-dimorphism for cranial characteristics.

The PCA revealed some overlap in the skull shape for both ventral and dorsal views. However, the cranial structures on the ventral view were more useful to differentiate *R. cherrii* from *R. mexicanus*. The greater discriminative power of the ventral side versus the dorsal of the skull has been noted for other cricetid rodents (Martínez and Di Cola 2011). Particularly for *Reithrodontomys*, Mayares (2012) evaluated the morphometric variation in the skull ventral view among *R. sumichrasti* populations distributed on both sides of the Isthmus of Tehuantepec in Mexico and correctly differentiated populations grouped according to genetic clades suggested as different species by Hardy *et al.* (2013).

Despite the overlap in skull shape, we found statistically significant differences between *R. cherrii* and *R. mexicanus* for ventral and dorsal views. Gardner and Carleton (2009) used craniodental measurements to compare different *Reithrodontomys* taxa distributed in Costa Rica and Panama, including *R. cherrii*, *R. m. garichensis*, and *R. m. potrerograndei*. The skull of *R. cherrii* was differentiated by "its overall robust size and evenly arched dorsal profile, especially over the braincase and occiput; it is notably broad across the braincase and zygomata but has a proportionally shorter rostrum" (Gardner and Carleton 2009:167). These characteristics partially differ from our results, since *R. cherrii* has a narrower foramen magnum region and braincase than *R. mexicanus*, while the nasal bone was relatively longer. Hooper (1952) compared specimens of *R. cherrii* from central Costa Rica to *R. m. lucifrons* central Honduras. Hooper (1952) described *R. m. lucifrons* as possessing a rostrum and incisive foramen that were slightly smaller than that of *R. cherrii*, consistent with the differences we documented for the ventral view of the skull.

The differences in size (CS) for both views of the skull showed that *R. cherrii* tends to have a larger cranium than *R. mexicanus*. These results are consistent with the linear measurements given by Hooper (1952) and traditional morphometric analyses carried out by Gardner and Carleton (2009). Hooper (1952) highlighted *R. cherrii* as one of the largest subspecies within *R. mexicanus*, comparing it in body size and skull length with *Peromyscus maniculatus*.

Although our morphometric analyses statistically differentiate *R. cherrii* from *R. mexicanus*, both species showed overlap in shape and size of the skull. The degree of morphological overlap among species of *Reithrodontomys* has

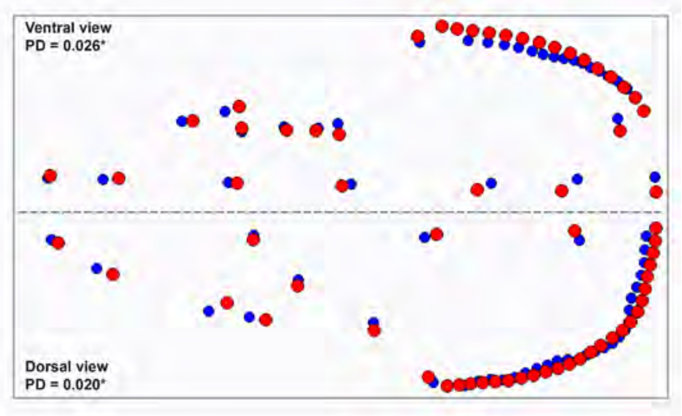

Figure 4. Differences in mean shapes of ventral and dorsal views of the skull, using the Procrustes distances. Red dots = *Reithrodontomys mexicanus* and blue dots = *R. cherrii*, PD = Procrustes distances, asterisks = significant differences based on pairwise permutation test ($P < 0.05$).

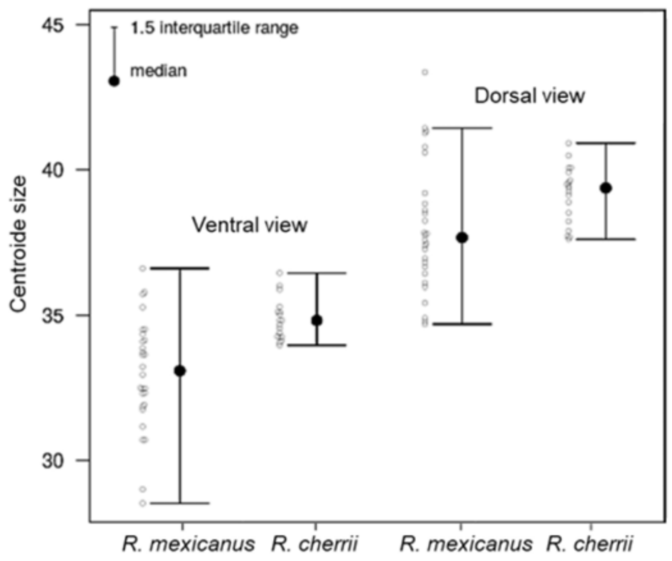

Figure 5. Skull size differences (based on centroid size variable) between *Reithrodontomys mexicanus* and *R. cherrii* for ventral and dorsal views. Statistical significance considered with $P \leq 0.05$.

been evident since the earliest monographs of the genus (Howell 1914; Hooper 1952). This may be why the taxonomic identification of *Reithrodontomys* species is difficult, leading to an underestimation of the actual number of species within this genus. For *R. mexicanus*, Hooper (1952) reported cranial and body measurements very similar or with very wide ranges among all its subspecies, including the former *R. m. cherrii*. The strong similarity of morphological (cranial and body measurements) and pelage coloration among these subspecies explains the inclusion of *R. cherrii* within *R. mexicanus* (Howell 1914), even though it was originally described as a species (Allen 1891).

Reithrodontomys mexicanus has one of the widest distributions within the subgenus *Aporodon* (Arellano 2015), whereas *R. cherrii* is restricted to the highlands of central Costa Rica and the Cordillera de Talamanca (Gardner and Carleton 2009; Villalobos-Chaves *et al.* 2016). Throughout its distribution, *R. mexicanus* is associated with a variety of vegetation-types such as humid oak forests, cloud forests, deciduous arid forests, and deciduous lowland forests (Hooper 1952), which coincides with its broader environmental space here reported compared to that of *R. cherrii*. *R. mexicanus* also occupies areas with high mean values of temperature and low values of precipitation compared to those for the distribution area of *R. cherrii*. The overlap of the minimum-volume ellipsoids in a small region, as well as the low Jaccard similarity index value, may be due to shared environmental characteristics between cloud forests and montane pluvial forests, the main plant formations where *R. mexicanus* and *R. cherrii* occurs, respectively.

The bioclimatic variables used in this study have been previously used in mammal ecological studies (Santos *et al.* 2017; Guevara *et al.* 2018; Stanchak and Santana 2018). BIO5, BIO6, BIO14, and BIO15 are variables that may be limiting the distribution of cloud forest species (Guevara *et al.*

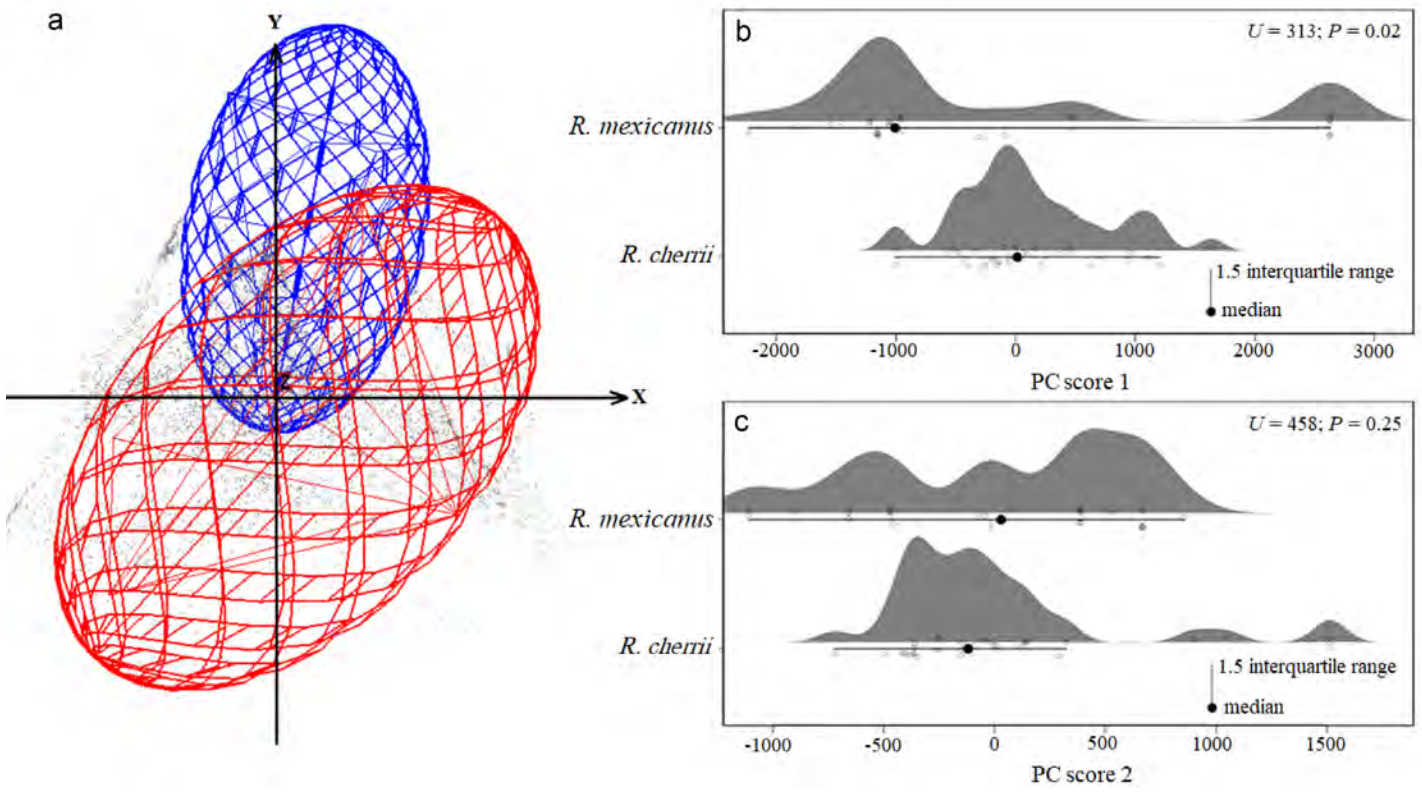

Figure 6. Environmental niche of *Reithrodontomys mexicanus* (red ellipsoid) and *R. cherrii* (blue ellipsoid) displayed in a three-dimensional space and based on the occurrence records and a background data (a). On the right (b and c) show the statistical comparisons using the scores of the first two principal components derived from the environmental variables. Statistical significance considered with $P \leq 0.05$.

2018). Of these four variables, only BIO14 (Precipitation of the driest month) was not significantly different, while the annual precipitation values were the most divergent among regions occupied by these species. These values were higher than 2,000 mm per year for *R. cherrii*, coinciding with the physical-geographical characteristics of the Central Valley (Gómez 1986), which is the climatic region where it is distributed in Costa Rica.

Additionally, we used elevation and NDVI variables to characterize the environmental space of each species. Although the minimum and maximum elevation values were higher for *R. cherrii*, the mean was similar between species. The altitudinal gradient of *Aporodon* species is variable, but most of them inhabit above 1,000 masl (Hooper 1952; Hall 1981). This could explain the lack of statistical differences when comparing this variable between the two species. Elevation has been widely used in studies focused on small rodents (McCain 2005), and it is useful to characterize the habitat in this group. However, this variable should be treated with caution when carrying out ecological analyses, such as niche modeling, due to the high association to temperature and precipitation, especially for small mammals distributed at high elevations (Rubidge *et al.* 2011; Santos *et al.* 2017; Guevara *et al.* 2018).

The NDVI is related to different vegetation parameters (Pettorelli 2013), with values ranging between 0.2 and 0.8, where higher numbers are indicators of photosynthetic activity linked to vegetation types such as temperate forest, rain forest, among others (Meneses-Tovar 2011). Beyond the statistical differences found for this index between *R. mexicanus* and *R. cherrii*, it is important to highlight that the natural areas where these two species are distributed could be considered high quality ecosystems following Pettorelli et al. (2007), considering that the mean values were greater than 0.6. However, quantitative and qualitative indicators are needed to assess integrative ecosystem health (Lu *et al.* 2015). The NDVI application in animal ecology appears to be helpful, especially since it can be linked to animal distribution and abundance (Pettorelli *et al.* 2005). Its use in carnivorous and omnivorous mammal species has been well explored but little is known for small mammals (Pettorelli *et al.* 2011). Our results confirm the utility of this index in habitat characterization and encourages their inclusion in ecological studies for small rodents.

Howell (1914) included *R. cherrii* within *R. mexicanus* as one of its largest and brightest subspecies (Hooper 1952). In mammals, environment can include changes in structures such as skull and jaw, leading to ecophenotypic variations (Camul and Polly 2005). This phenotypic change due to habitat could justify *R. cherrii* misclassification at the subspecific level. However, the high genetic divergence reported between this former subspecies and *R. mexicanus*, translates into different evolutionary histories that vindicates it at the species-level, now as a member of the *R. tenuirostris* species group (Arellano *et al.* 2003, 2005). We found these two species to be different based on the skull morphometry and environmental. Thus, complementing the previous molecular evidence as a whole integrative taxonomy approach that supports *R. cherrii* as a different species from *R. mexicanus*.

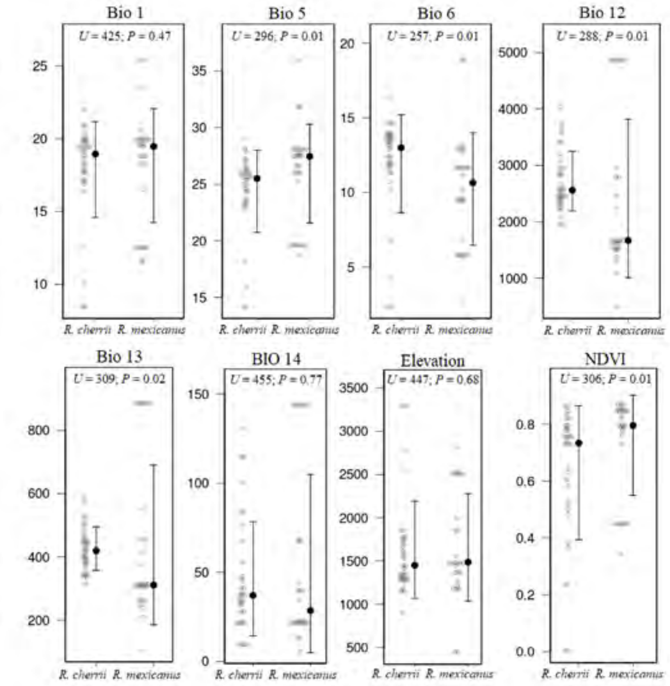

Figure 7. Pairwise comparisons of variables used to characterize the environmental space between *Reithrodontomys mexicanus* and *R. cherrii*. Variable names are in the methods section. Statistical significance considered with $P \leq 0.05$.

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Appendix 1

List of *Reithrodontomys mexicanus* and *R. cherrii* voucher specimens and their associated collecting localities used in the geometric morphometric analyses. Abbreviations before catalogue number represent the mammal collection housing the specimens: AMNH = American Museum of Natural History; BYU = Brigham Young University; CMC = Colección de Mamíferos del Centro de Investigación en Biodiversidad y Conservación; ECOSUR = Colección Mastozoológica de El Colegio de la Frontera Sur, Unidad San Cristóbal; UMMZ = Museum of Zoology, University of Michigan.

Voucher	Species	Locality
UMMZ-109894	*R. mexicanus*	Los Esesmiles, Chalatenango, El Salvador
UMMZ-109897	*R. mexicanus*	Los Esesmiles, Chalatenango, El Salvador
UMMZ-109900	*R. mexicanus*	Los Esesmiles, Chalatenango, El Salvador
UMMZ-109903	*R. mexicanus*	Los Esesmiles, Chalatenango, El Salvador
UMMZ-109905	*R. mexicanus*	Los Esesmiles, Chalatenango, El Salvador
UMMZ-116882-116884	*R. mexicanus*	Santa María de Ostuma, 9 km N of Matagalpa, Nicaragua, 1,400 m
UMMZ-118145-118146	*R. mexicanus*	Municipio La Libertad, Hacienda El Injerto, río Aguacate, Huehuetenango, Guatemala, 1600 m.
UMMZ-118147-118150	*R. mexicanus*	Barillas, Hacienda Santa Gregoria, Huehuetenango, Guatemala
UMMZ-118152-118153	*R. mexicanus*	Barillas, Hacienda Santa Gregoria, Huehuetenango, Guatemala
UMMZ-118154-118155	*R. mexicanus*	Finca Concepción, Tucurú, Alta Verapaz, Guatemala
AMNH-142460	*R. mexicanus*	Coto Brus, Cañas Gordas, Puntarenas, Costa Rica
AMNH-142462-142463	*R. mexicanus*	Coto Brus, Cañas Gordas, Puntarenas, Costa Rica
AMNH-142465	*R. mexicanus*	Coto Brus, Cañas Gordas, Puntarenas, Costa Rica
AMNH-142468-142472	*R. mexicanus*	Coto Brus, Cañas Gordas, Puntarenas, Costa Rica
BYU-15426	*R. mexicanus*	Municipio Santiago Comaltepec, 11 km SW (by road.) La Esperanza, Oaxaca, México
BYU-15436	*R. mexicanus*	Municipio Teotitlán de Flores Magón, 1.5 km S Puerto de la Soledad, Oaxaca, MX
BYU-15439	*R. mexicanus*	Municipio Ixhuacán, 18 km NW Teocelo, Veracruz, México
BYU-20781	*R. mexicanus*	Rancho La Providencia, Chiapas, México, 1775 m
CMC-872	*R. mexicanus*	Municipio Huatusco, 1.9 km N Las Cañadas (Eco reserva), Veracruz, México
CMC-874	*R. mexicanus*	Municipio Huatusco, 1.9 km N Las Cañadas (Eco reserva), Veracruz, México
CMC-877	*R. mexicanus*	Municipio Huatusco, 1.9 km N Las Cañadas (Eco reserva), Veracruz, México
ECOSUR -2842	*R. mexicanus*	Santo Tomás Oxchuc, Mercado Indígena, Chiapas, México
ECOSUR-3000	*R. mexicanus*	Ejido Sombra Chica, 1 km NW Tumbalá, Chiapas, México
ECOSUR-931	*R. mexicanus*	Las Grutas. PN Lagos de Montebello, 3.45 Km N El Vivero, Chiapas, México
AMNH-7905	*R. cherrii*	Cerro La Carpintera, Cartago, Costa Rica
AMNH-123503	*R. cherrii*	Cerro La Carpintera, Cartago, Costa Rica
AMNH-7902-7904	*R. cherrii*	Cerro La Carpintera, Cartago, Costa Rica
AMNH-7908	*R. cherrii*	Cerro La Carpintera, Cartago, Costa Rica
AMNH-131739	*R. cherrii*	Escazú, San José, Costa Rica
AMNH-135258	*R. cherrii*	Vázquez de Coronado, Nubes, San José, Costa Rica
AMNH-135924	*R. cherrii*	Alajuela, Sabanilla, Costa Rica
AMNH-138088	*R. cherrii*	Escazú, Los Higuerones, San José, Costa Rica
AMNH-139284	*R. cherrii*	Montes de Oca, Sabanilla, San José, Costa Rica
AMNH-139289	*R. cherrii*	Montes de Oca, Sabanilla, San José, Costa Rica
AMNH-141878	*R. cherrii*	Alajuelita, Santa Teresa, Peralta, Costa Rica
AMNH-141880-141881	*R. cherrii*	Alajuelita, Santa Teresa, Peralta, Costa Rica
AMNH-141883	*R. cherrii*	Alajuelita, Santa Teresa, Peralta, Costa Rica
AMNH-19187-19188	*R. cherrii*	Montes de Oca, San Pedro, San José, Costa Rica
AMNH-19192	*R. cherrii*	Montes de Oca, San Pedro, San José, Costa Rica

Appendix 2

Anatomical and numerical position (see Figure 2) of landmarks and semi-landmarks used in the geometric morphometric analyses for ventral and dorsal views of the skull.

	Ventral		Dorsal
1	Rostralmost point of the upper incisor tooth next to the midline	1	Rostralmost point of the nasal bone
2	Anteriormost point of the incisive foramen	2	Anteriormost point of suture between nasal bone and nasal process of the incisive
3	Posteriormost point of the incisive foramen	3	Rostral end of zygomatic plate in a dorsal projection
4	Rostral end of zygomatic plate in a ventral projection	4	Anteriormost point of the orbit in a dorsal projection
5	Anteriormost point of the orbit in a ventral projection	5	Narrowest point of the interorbital region
6	Caudalmost point of the orbit in a ventral projection	6	Rostralmost point of the parietal bone
7	Posterior end of zygomatic bar in a ventral projection	7	Caudalmost point of the orbit in a dorsal projection
8-20	Semi-landmarks	8	Posterior end of zygomatic bar in a dorsal projection
21	Lateral margin of the basioccipital	9-31	Semi-landmarks
22	Lateral margin of the foramen magnum	32	Caudal end of the curvature of the occipital bone
23	Posteriormost point of the occipital foramen in the midline	33	Intersection of the sagittal and parietal-interparietal sutures
24	Anteriormost point of the occipital foramen in the midline	34	Intersection of the coronal and sagittal sutures
25	Midpoint of suture between basisphenoid and basioccipital	35	Intersection of the naso-frontal suture in the midline
26	Posteriormost extent of palate at the midline		
27	Posteriormost point of the third molar		
28	Contact point between second and third molars		
29	Contact point between first and second molars		
30	Anteriormost point of the first molar		

Appendix 3

Geographical coordinates (Datum WGS-84) of localities used in the ecological analysis for *Reithrodontomys mexicanus* and *R. cherrii*.

Species	Longitude	Latitude	Species	Longitude	Latitude
R. mexicanus	-89.133	14.383	*R. mexicanus*	-92.016	15.566
R. mexicanus	-85.925	13.005	*R. mexicanus*	-90.066	15.300
R. mexicanus	-91.315	15.803	*R. mexicanus*	-96.447	17.555
R. mexicanus	-97.220	18.356	*R. mexicanus*	-92.340	15.216
R. mexicanus	-97.064	19.525	*R. mexicanus*	-91.720	16.130
R. mexicanus	-96.984	19.258	*R. cherrii*	-83.984	9.881
R. mexicanus	-92.346	16.794	*R. cherrii*	-84.216	10.076
R. mexicanus	-92.315	17.270	*R. cherrii*	-84.144	9.894
R. mexicanus	-87.106	14.208	*R. cherrii*	-84.136	9.913
R. mexicanus	-96.305	17.599	*R. cherrii*	-84.029	9.947
R. mexicanus	-96.016	17.176	*R. cherrii*	-84.021	9.944
R. mexicanus	-92.340	15.216	*R. cherrii*	-83.962	9.987
R. mexicanus	-93.120	17.190	*R. cherrii*	-84.083	9.933
R. mexicanus	-91.700	16.100	*R. cherrii*	-83.849	9.979
R. mexicanus	-92.640	15.650	*R. cherrii*	-83.798	9.768
R. mexicanus	-93.070	15.800	*R. cherrii*	-83.981	9.896
R. mexicanus	-92.692	16.684	*R. cherrii*	-84.153	9.913
R. mexicanus	-92.400	16.963	*R. cherrii*	-84.406	10.221
R. mexicanus	-90.031	15.089	*R. cherrii*	-84.059	9.705
R. mexicanus	-92.851	16.990	*R. cherrii*	-83.850	9.983
R. mexicanus	-92.975	17.208	*R. cherrii*	-83.902	9.833
R. mexicanus	-91.932	15.485	*R. cherrii*	-83.916	9.839
R. mexicanus	-86.339	13.080	*R. cherrii*	-84.244	10.102
R. mexicanus	-89.366	14.400	*R. cherrii*	-83.982	9.950
R. mexicanus	-90.455	14.558	*R. cherrii*	-84.107	9.868
R. mexicanus	-89.623	15.136	*R. cherrii*	-84.183	9.950
R. mexicanus	-96.605	17.579	*R. cherrii*	-83.548	9.450
R. mexicanus	-96.842	18.168	*R. cherrii*	-83.877	9.823
R. mexicanus	-97.040	18.618	*R. cherrii*	-83.916	9.650
R. mexicanus	-97.028	19.037	*R. cherrii*	-83.881	9.833
R. mexicanus	-96.798	17.811	*R. cherrii*	-83.903	9.879
R. mexicanus	-90.062	15.385	*R. cherrii*	-83.983	9.890
R. mexicanus	-97.024	18.869	*R. cherrii*	-83.803	9.753
R. mexicanus	-91.394	15.571	*R. cherrii*	-84.139	9.883
R. mexicanus	-89.481	15.166	*R. cherrii*	-84.333	10.277
R. mexicanus	-91.560	15.984	*R. cherrii*	-83.707	9.566
R. mexicanus	-90.251	15.236	*R. cherrii*	-83.968	9.888
R. mexicanus	-96.436	17.386	*R. cherrii*	-84.233	10.183
R. mexicanus	-92.591	16.051	*R. cherrii*	-84.465	9.920