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Academics, academia, and intellectual fulfilment: lessons from the career of an eminent mammalogist

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Dr. William (Bill) Lidicker, Jr., was a classically trained mammal biologist who played an important role in pushing the field of mammalogy from largely descriptive beginnings into conceptual arenas soundly rooted in theory and principles. Whereas many readers will know Bill primarily as the architect of a "multifactorial approach" to understanding population cyclicity in arvicoline rodents, less well-known is how Bill's thematic focus shifted over the years. In an career that often prioritizes high-level productivity, I argue that Bill's willingness to pursue novel themes provides an compelling model of how to live a rich and fulfilling life in academia.

Dr. William (Bill) Lidicker, Jr., fue un biólogo de mamíferos de formación clásica que desempeñó un papel importante en impulsar el campo de la mastozoólogo desde comienzos en gran parte descriptivos hasta arenas conceptuales sólidamente arraigadas en la teoría y los principios. Mientras que muchos lectores conocerán a Bill principalmente como el arquitecto de un "enfoque multifactorial" para comprender la ciclicidad de poblaciones en roedores de arvicolina, menos conocido es cómo el enfoque temático de Bill cambió a lo largo de los años. En una carrera que a menudo prioriza la productividad de alto nivel, propongo que la voluntad de Bill de perseguir temas novedosos proporciona un modelo convincente de cómo vivir una vida rica y satisfactoria en la academia.

Keywords: Academic diversity; conservation biology; landscape ecology; mammalogy; population ecology; systematics; thematic diversity; William Z. Lidicker, Jr.

Dr. William (Bill) Zander Lidicker, Jr. (1932-2022) was perhaps best known as a population ecologist, with an emphasis on arvicoline rodents. However, I share the view espoused by Heske *et al.* (2023), that Bill was a systems biologist, albeit one focused clearly on mammals, and throughout his career he moved across at least four thematic arenas, which I believe reflects his unbridled intellectual curiosity and his endless desire to expand his own limits. As such, I believe that Bill's career highlights the joys of following one's intellectual passions wherever they may take one. Perhaps more fundamentally, it underscores the benefits that accrue when we avoid feeling canalized by our own experiences.

Reflecting his stature, colleagues at the UC Berkeley Museum of Vertebrate Zoology, where Bill spent his career, organized a symposium to reflect on Bill's legacy and impact (Figure 1). I was invited to speak to Bill's influence on the field of mammalogy, but as I prepared my presentation, I found that a larger message gradually emerged. Heske *et al.* (2023) had already penned an outstanding obituary, and this journal hosted a special issue (Vol. 13(1)) in honor of Bill's career and legacy. Rather than repeat what these authors have so capably highlighted, I wish to emphasize what I think may be a different message from Bill's career, and one that may carry some weight in the current academic marketplace.

Bill started out as a classically trained mammalogist, although it wasn't long before his publications turned to population biology, and he later extended this to the spatial realm of landscape ecology and ecological corridors (Figure 2). Perhaps not surprisingly in a world facing significant anthropogenic threats to biodiversity, Bill added conservation biology to his retinue in later years.

If the data from Figure 2 are adjusted to show the *proportion* of Bill's publications in four themes, a pattern of gradual transition becomes more clear (Figure 3). In particular, Bill's early publications emphasized systematics and taxonomy, and (mostly upon arrival at Berkeley) population ecology. Overall, population ecology was a dominant theme throughout his career, but this was gradually complemented with papers at broader spatial scales, and finally in the arena of conservation.

Word clouds can provide visual depictions of the differential dominance of key words among a series of items. A word cloud based on the titles of Bill's research publications (Figure 4) highlights his career in California and with a focus on populations (and the role of dispersal) and factors regulating these, and in particular with the California Vole (*Microtus californicus*). However, his early work in New Guinea and Australia also stand out, as does his interest in landscapes, conservation, and corridors. These latter two figures set a stage for viewing Bill Lidicker's career, and in turn highlight the value of never limiting the potential avenues for pursuit, a message that I think may be particularly important for younger investigators in a competitive academic marketplace.

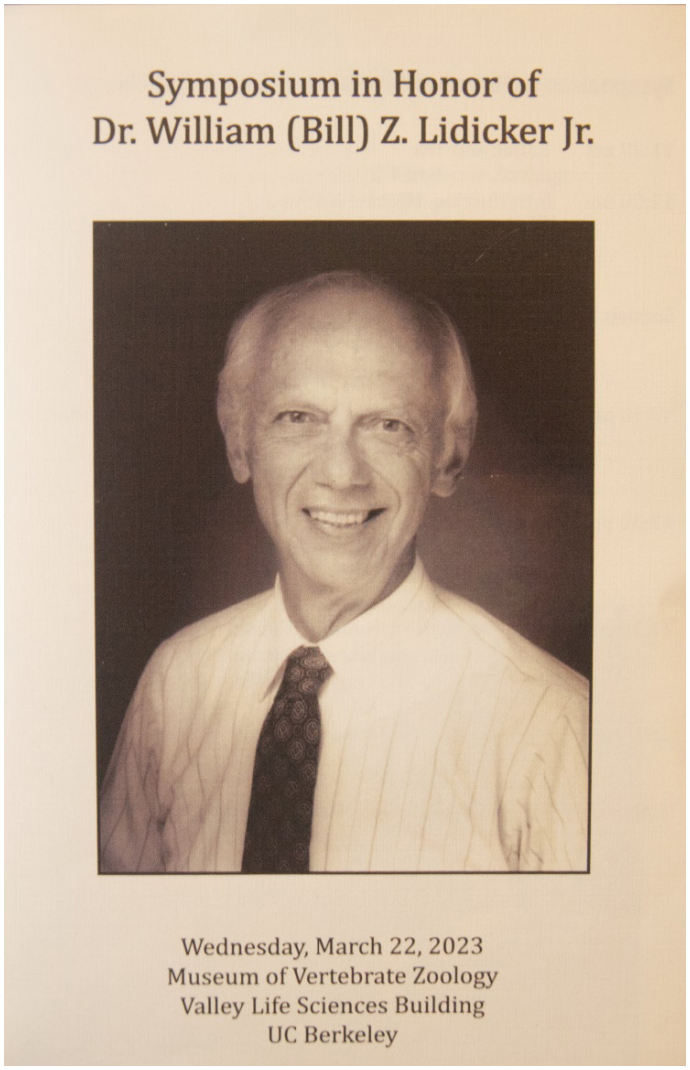

Figure 1. Cover of the flyer distributed at the MVZ Symposium in Honor of Dr. William (Bill) Z. Lidiker Jr. This one-day event comprised a morning session and an afternoon session, with three presentations in each. Morning speakers were Drs. Richard Ostfeld and Felicia Keesing ("The Lidickerian Approach to Vole Ecology"), Dr. Sergio Ticul Álvarez-Castañeda ("Chat for a Friend"), Dr. Alex Hon-Tsen Hu ("Encounters in Corridors: Reflection of my personal Interactions with Professor William Z. Lidicker, Jr."). Afternoon speakers included the author ("William Z. Lidicker, Jr., and the Development of Contemporary Mammalogy"), Dr. Eileen Lacey ("A Legacy of Service to Mammalogy"), and Dr. Jim Patton ("Bill Lidicker – Mammalian Systematist").

Act 1: Systematics and Taxonomy. North America, Australia.— As noted, Bill Lidicker's publication record began with notes on range extensions and some descriptive morphology (Davis and Lidicker 1955a, b, c; Davis *et al.* 1955; Davis and Lidicker 1956). However, he also conducted extensive field research. His dissertation was a traditional (albeit quite thorough) evaluation of morphological variation within a species, in his case Merriam's Kangaroo Rat, and included recognition of a new subspecies (*Dipodomys merriami collinus*—Lidicker 1960b). With MVZ colleagues he continued this tradition, including the discovery of a new subspecies of Cliff Chipmunk (*Neotamias dorsalis*) in Chihuahua, Mexico (Lidicker 1960a—Figs. 5, 6).

Less widely known is Bill's attempt to quantify the nature of subspecies boundaries (Lidicker 1962b). In this he devised a complex metric to quantify relative morphological change across subspecific boundaries, but as Jim Patton noted in his presentation at the Lidicker Symposium, this was published just as the field of numerical taxonomy was emerging, and Bill's contributions appear to have been lost in the flood of novel quantitative tools (Sokal 1963; Sokal and Sneath 1963). Nonetheless, as Ruedas (2020) noted in an editorial commentary, Bill's contribution was important in refuting arguments (Wilson and Brown 1953) that subspecies were neither objective nor practicable, and this paper continues to be cited in contributions addressing diverse taxa (BioSis lists 45 citing articles, Google Scholar lists 81, as of 17 August 2023).

Although Bill rapidly diversified his thematic foci, he never lost his interest in systematics, which included Australasian rodents and marsupials (Lidicker 1968; Lidicker and Follett 1968: Lidicker and Ziegler 1968; Ziegler and Lidicker 1968; Lidicker and Marlow 1970; Lidicker 1973a; Lidicker and Brylski 1987) – even describing a new genus and species of fossil rodent (Martinez R. and Lidicker 1971) – and later addressing the taxonomic status of the Southern Sea Otter (*Enhydra lutris nereis*—Davis and Lidicker 1975), and ultimately returning to the kangaroo rat of his nascent years, helping with the revision of *D. merriami* in Baja California, México (Álvarez-Castañeda *et al.* 2009).

Act 2: Population Ecology (mostly voles). Bill's interests clearly extended beyond taxonomy and evolutionary systematics, and immediately upon arriving at Berkeley he initiated studies on the local fauna. This included surveys on the House Mouse (*Mus musculus*) population on Brooks Island, located close to Richmond in the San Francisco Bay and populated at that time almost solely by house mice, but at very high abundances; Norway Rats (*Rattus norvegicus*) occupied beach areas. At about the same time, California Voles were accidentally introduced from an adjacent islet (Lidicker 1966:27), ultimately leading to the extirpation of *Mus* from the island. Observations on these and other populations of small mammals led to a brief but highly influential paper (Lidicker 1962a) that remarkably included no data. In a contribution to the *Therya* festschrift, Krebs (2022) noted that at that time, few authors had given much thought to a role for emigration in regulating populations. He noted that David Lack (1954), in his seminal book, had emphasized the role of food, predation, and disease, but gave little consideration to animal movement as a regulating factor. Nearly three decades earlier, Elton (1927) also discussed dispersal, but largely phenomenologically, as did Andrewartha and Birch (1954) in their influential contribution. Lidicker (1962a) emphasized the potential role of emigration but carried this further, addressing the selective advantages of dispersal and several corollary themes. Indeed, Krebs (2022:19) concluded: "If you go back to Lidicker (1962[a]) you will find threads of [many subsequent] developments in the study of dispersal", including: emigration, dispersal, and population regulation; social and genetic consequences of dispersal; the adaptive advantage of dispersal; selection for dispersal tendency; frustrated emigration; lack of food limitation.

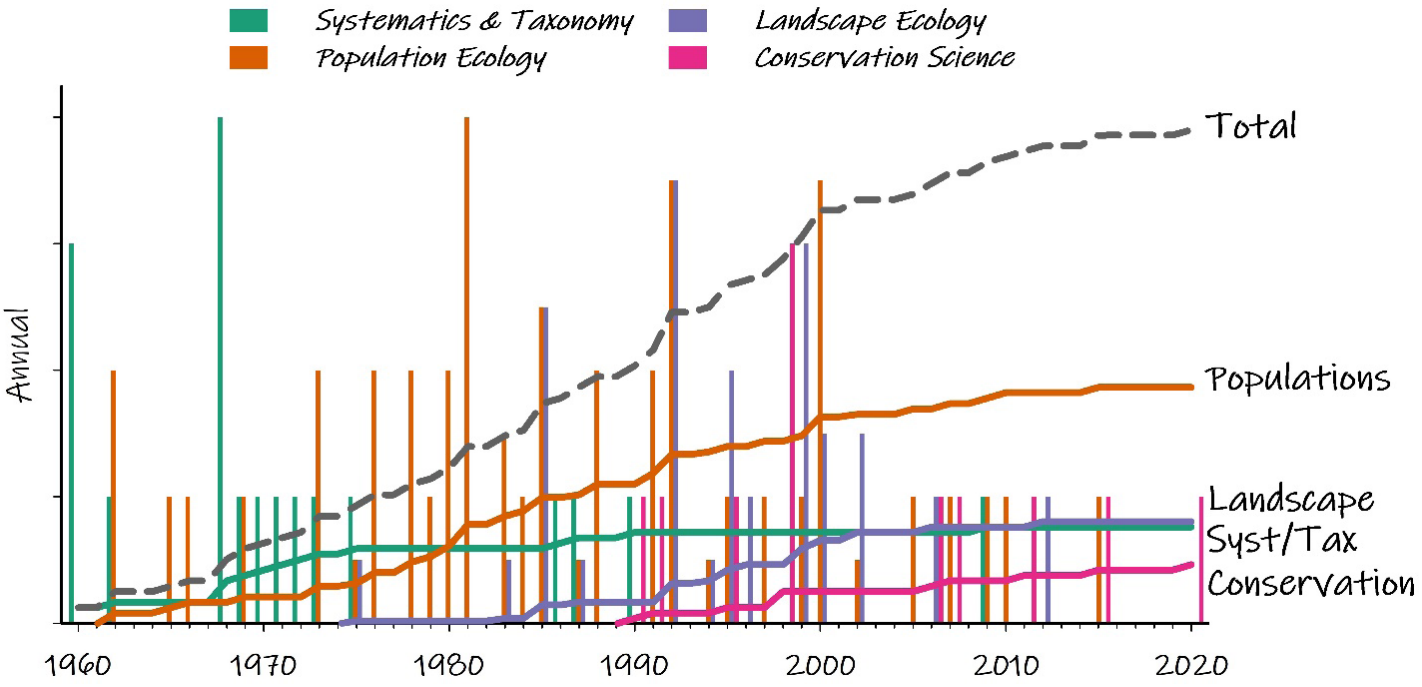

Figure 2. Bill Lidicker's research publication record, segregated in four general themes. Vertical bars illustrate the number of papers published in each year, whereas the line show the cumulative number of papers in each theme over Bill's career. What stands out is that Bill gradually transitioned from classical systematics and taxonomy to a career-dominant theme of population ecology, which in turn was complemented by papers (and books) that extended population biology to landscape scales and finally integrated conservation themes in the face of increasing societal concerns over habitat loss, climate change, and related challenges.

After collecting 13 years of data on California Voles from Brooks Island, Bill published his observations in *Ecological Monographs*, where he initiated what would become a hallmark of his legacy, as he questioned the value of single-factor models to explain regular cyclicity in these populations. Bill wrote (Lidicker 1973b:272): "The quasi 2-year cycle of regularly recurring peaks every year and alternating high and low winter densities which came to characterize the Brooks Island vole population is considered to be the result of a regulation process in which a *multiplicity of factors interact to achieve regulation*. Both density-unresponsive and responsive factors are involved" (emphasis mine). He concluded his paper by noting: "It is clearly apparent to me that one cannot triumphantly point to *the* regulating factor

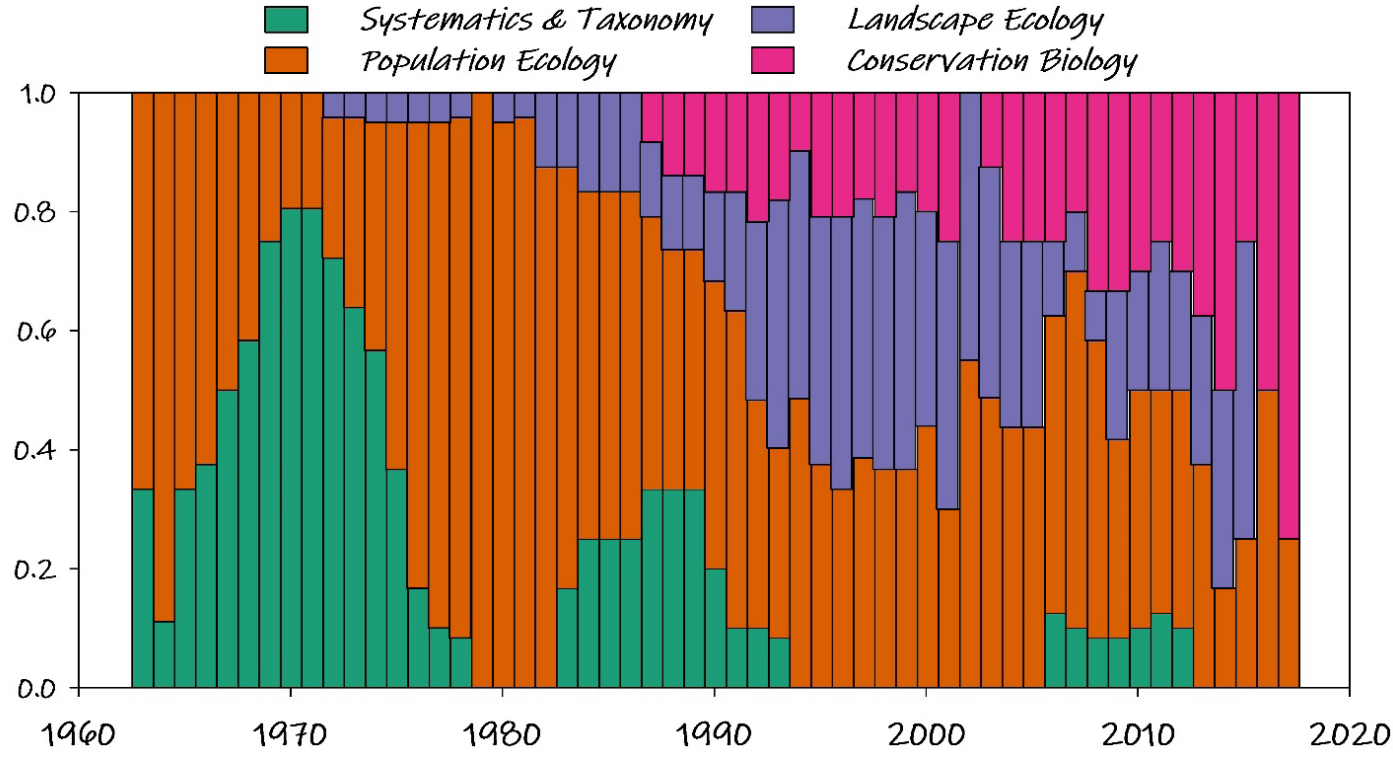

Figure 3. Using the same data as in Figure 2, this figure illustrates the proportion of Bill's publications in four themes, using a 7-year rolling window.

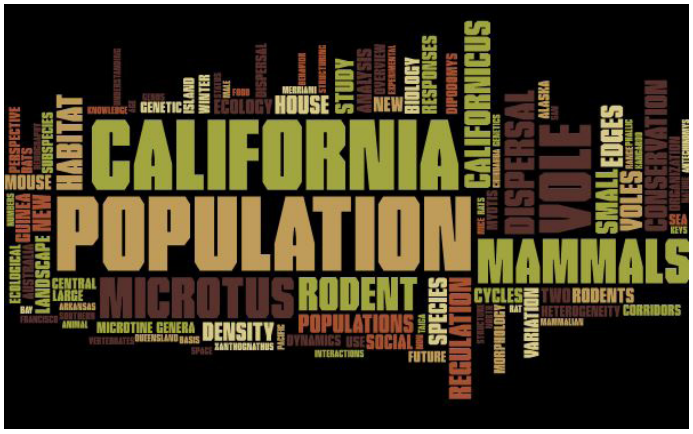

Figure 4. A word cloud based on the full titles of Bill Lidicker's research publications.

influencing vole density. Rather, a multiplicity of factors are found to be interacting, and one is led to some integrated or synthetic theory of regulation" (emphasis his).

It was in 1978, when Bill was invited to contribute to a symposium on small mammal populations (Lidicker 1978), that he formally coined the term "multi-factorial model of vole demography". He returned to this theme when the American Society of Mammalogists recognized Bill's career with the Merriam Award; in his resulting talk and publication, Bill highlighted four extrinsic factors and four intrinsic factors that he argued were important in regulating populations of California voles (Lidicker 1988). Of course, a number of these had been discussed by other authors, and Bill didn't disagree with the potential role of each of these factors individually; rather, he argued that none of them in and of themselves could explain cyclicity in California Vole numbers, and probably not in other species either.

Another seminal contribution was Bill's invited contribution of a chapter for an edited volume in the IBP book series (Lidicker 1975). In this he reiterated and built upon his developing theory of population regulation, but two key sets of concepts emerged from this paper. First, Bill formally distinguished "pre-saturation dispersal" from "saturation dispersal", noting that animals in these two phases are different in numerous respects, including rates of maturity, reproduction, and the very likelihood of their survival: whereas the former are in relatively good condition, and they have a much greater chance of surviving and re-establishing themselves elsewhere, the latter tend to be social outcasts, juveniles, very old individuals, and generally in poor condition, with limited capacity to cope with local conditions. As such, the former category includes individuals for which there may actually be "greener pastures" on the other side of the hill, whereas the latter category includes individuals faced with the immediate choice of staying in the population and almost certainly dying, versus moving out and probably dying.

A second concept that emerged from this publication was that of a "dispersal sink". For an animal to emigrate there has to be somewhere to go; in the absence of another patch where the animal could at least survive for some time, it would most likely return home, which Bill called frustrated dispersal. This concept was picked up by others and contributed significantly to the development of source/sink dynamics by Ron Pulliam (1988), which in turn has contributed to metapopulation (and metacommunity) theory.

It should be noted that pushing boundaries carries risks, and Bill was roundly denounced by many research-

Figure 5. Bill Lidicker (right) conducting field research in the Sierra del Nido, Chihuahua, Mexico, 1961. These efforts resulted in the description of a new subspecies of the Cliff Chipmunk (*Neotamias dorsalis nidoensis* —Lidicker 1960a). Other members of this photo include (left to right) Ned Johnson, Gene Christman, Mike Pontrelli, and Jim Anderson (Courtesy of the MVZ Archives; Image #10065; © Museum of Vertebrate Zoology, University of California, Berkeley).

ers on demographic cyclicity, not so much because they disagreed with his argument that no single factor could explain all cycles (neither within nor – certainly! – across species) as because Bill's multifactorial approach is exceedingly difficult to test. Hence began what Ostfeld (2015) called the "vole wars", which unfortunately pushed at least some young researchers away from this exciting field. In the face of seemingly personal attacks, however, Bill remained remarkably unperturbed, and he epitomized the heart of scientific debate by responding calmly yet succinctly to his critics (e.g., "Science without controversy would be dull indeed . . ."—Lidicker 1991b:631).

Act 3: Landscape and Corridor Ecology.—it is perhaps inevitable that Bill's interest in dispersal led to curiosity over how and where animals disperse, but understanding such dynamics required that he put population ecology into the broader spatial context of landscapes. Of course, in a world of growing appreciation of habitat fragmentation, it may seem logical that a demographer interested in dispersal would ask about the corridors through which individuals move between populations. In the 1980s, with Andy Cockburn, Bill published on the role of microhabitat heterogeneity in structuring the population dynamics of California Voles (Cockburn and Lidicker 1983). This work evidently stimulated Bill's interest in population ecology across landscapes, leading to a symposium at the sixth *International Theriological Congress* in Sydney in 1993, and a subsequent edited volume, *Landscape Approaches in Mammalian Ecology and Conservation* (Lidicker 1995a). In turn, this was followed by chapters on vertebrate responses to habitat edges and corridors in which Bill and his colleagues summarized the state of knowledge at the time. They emphasized the importance of understanding emigration and immigration in a metapopulation context, given growing anthropogenic fragmentation and degradation of habitats globally (Lidicker and Koenig 1996; Lidicker and Peterson 1999).

Figure 6. Bill Lidicker named two subspecies new to science. Heske *et al.* (2023) illustrated one of these (*Dipodomys merriami collinus*), based on his dissertation work and published in (Lidicker 1960b). His field research in Chihuahua, Mexico (Figure 5) resulted in discovery of this new subspecies of chipmunk. Photo by William Stone (Courtesy of CalPhotos and the MVZ Archives; MVZ Image #16834; © Museum of Vertebrate Zoology, University of California, Berkeley).

Perhaps culminating this section of his career, with Jodi Hilty and Adina Merenlender he co-edited the first volume on the growing field of corridor ecology (Hilty *et al.* 2006). This book has had a substantial influence on the field, and recently was updated and revised in a second edition (Hilty *et al.* 2019). This trajectory illustrates how Bill continued to expand his research focus; while remaining largely focused on small mammals and population ecology, he contributed importantly to placing this in the proper spatial framework that furthered understanding of nuance in population ecology and demographic cycles. In a retrospective article, Bill's co-editors (Merenlender *et al.* 2022) wrote that Bill repeatedly urged consideration of the *species* for whom corridors were being considered. He always emphasized the ecology and natural history of species, and how spatial dynamics and environmental structure influenced population demography and viability.

Act 4: Conservation Biology. The final broad theme to Bill's career, as I see it, is perhaps common to many contemporary scientists. Studying population ecology of small mammals in an increasingly fragmented world under the specter of desertification and climate change leads many to be concerned over the future of entire biomes, not to mention the particular taxa we have dedicated our lives to study. Bill's interest in conservation appears to have initiated in earnest in the late 1980s, when he edited the first ever global survey of rodent species of conservation concern (Lidicker 1989a). Soon thereafter he published chapters on "Impacts of non-domesticated vertebrates on California grasslands" (Lidicker 1989b) and "Introduced mammals in California" (Lidicker 1991a), and three years after that by an essay on "Biodiversity: what is it and what is it good for?" (Lidicker 1995b). Bill recognized the magnitude of this title, noting that "[t]o confront such a profound question in any substantive way is beyond the scope of this essay", but underscoring his appreciation of diverse perspectives he highlighted

Figure 7. Bill Lidicker was well known for his spatial memory. Speakers at the MVZ Symposium commented that in spite of the apparent mayhem of paperwork in his office, he could locate "just the paper you need" with ease. One has to wonder if this spatial memory contributed to the ease with which Bill integrated spatial dynamics into his population research, ultimately leading to a focus on landscape-scale processes. Photo by O. P. Pearson (Courtesy of the MVZ Archives; Unnumbered image; © Museum of Vertebrate Zoology, University of California, Berkeley).

three broad categories of reasons why biodiversity is good – "moral and aesthetic", "educational and scientific", and "mental health". Bill continued to publish papers and chapters on conservation, initially emphasizing conservation of rodents but gradually broadening his focus to all mammals and, finally, to humanity itself. A few select contributions include: "Revisiting the human dimensions of conservation biology" (Lidicker 1998); "Some neglected aspects of rodent conservation" (an extended abstract—Lidicker 2006); "Issues in rodent conservation" (Lidicker 2007); "Hope and realism in conservation biology" (Lidicker 2011); "Mammalian conservation: scientific frontiers and sociopolitical pitfalls" (Introduction to a Special Contribution on mammal conservation—Lidicker 2015); "A scientist's warning to humanity on population growth" (Lidicker 2020).

Synthesis, Conclusions, and Bill's Big Message. Bill Lidicker's passion for the biology of small mammals and his seemingly endless curiosity, combined with a legendary memory, helped to push the boundaries of mammalogy, perhaps most notably in population ecology, but also in several themes that are linked to, but distinct from, this field. Bill fended off numerous arguments concerning his multi-factorial model and he appears to have done so with good grace and diplomacy. His curiosity may inevitably have drawn him from traditional systematics to population biology, and thence to landscape and corridor ecology. As I began preparing to speak to Bill's influence on mammalogy, I was increasingly drawn to the broader message that is exemplified by his career but which has been overlooked by his biographers. Bill Lidicker was trained in classical mammalogy, but through his career he followed his passions to new intellectual arenas. Academic careers often involve intense selection for productivity, and this in turn can disincentivize intellectual diversification and personal growth and discovery – publishing more papers on a topic one knows well often is easier than pursuing novel themes, often involving a new literature. I have tried to highlight how Bill avoided being pigeon-holed or intellectually constrained. The thematic breadth illustrated through his career was founded on a deep appreciation of natural history and organismal biology, and promoted by a diverse set of personal interests and broad curiosity. If there is an overarching message from Bill Lidicker's career, it may be to remind us all that there is value in following your interests. If these lead you to new fields, then so be it – be the intellectual presaturation disperser who earns the satisfaction of experiencing new intellectual arenas, and perhaps you'll even have an impact in these fields. Even if you don't, the challenge likely is worth the effort. Nobody goes into science to be bored or to be intellectually constrained. I'll close by quoting Rick Ostfeld, who commented on this facet of Bill's career in an email to me (12 August 2023): "[Bill's] thematic breadth, derived from broad curiosity and the ability to self-inform, is in short supply these days." "[F]requency-dependence applies way beyond natural selection, and . . . rare phenotypes are often more valuable for their rarity."

Acknowledgements

I first met Bill Lidicker when, as an undergraduate, I visited MVZ to look at specimens of kangaroo rats. I still remember Bill noticing what surely was a gawking young man, and he immediately came down from his second-floor office to ask if he could help me. That such a figure would so unquestioningly offer to help left me with a career-long appreciation for the impact that one can have by simple acts of generosity (Bill then passed me to Jim Patton who was equally generous, and until I began meeting other leading mammalogists at ASM meetings I wondered if this was just something in the water at Berkeley). I am grateful to Michael Nachmann, Eileen Lacey, and Jim Patton for inviting me to speak at the Lidicker Symposium, and to all the speakers of that memorable and inspirational day. Ed Heske oversaw coordination of the *Therya* volume in honor of Bill, and subsequently built upon this to produce an outstanding obituary in the *Journal of Mammalogy*. For any readers curious to read more about Bill I highly recommend these contributions. Thanks to Peter Meserve, Ed Heske, and Jim Patton for comments on this manuscript. Finally, I owe a special thanks to Charley Krebs for his paper in *Therya*, highlighting the role of Bill's 1962 *American Naturalist* article, and to Rick Ostfeld for the elegant synthesis that I quote at the end of this manuscript.

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