

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 repasó 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.

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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. pennsylvanicus*, 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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