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Source: Journal of Mammalogy, 92(6) : 1155-1157

Published By: American Society of Mammalogists

URL: <https://doi.org/10.1644/11-MAMM-S-186.1>

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Small mammal community structure and dynamics in aridlands: overall patterns and contrasts with Southern Hemispheric systems

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Aridlands offer unique opportunities to compare effects of history, evolution, and local geography on assemblage and dynamics of small mammal communities that have severe environmental constraints. Pioneering work in Northern Hemispheric aridlands resulted in paradigms that were assumed to be general. Because the evolutionary history and biogeography of Southern Hemispheric aridlands have been distinct, they offer unusual opportunities to test this assumption. We present 6 papers in this Special Feature that show that Southern Hemispheric aridlands have developed and evolved in many unique directions.

Key words: aridland small mammals, biotic and abiotic factors, desert mammal ecology, intercontinental comparisons

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DOI: 10.1644/11-MAMM-S-186.1

The history of desert small mammal ecology is rooted in work in North America and, to a lesser and more recent extent, the Middle East. Only in the past decade or so have sufficient data emerged from arid regions in the Southern Hemisphere to allow valid comparisons to be drawn. Early studies based on ecomorphological patterns highlighted North American kangaroo rats (*Dipodomys*) and Middle Eastern gerbils (Gerbillinae) and jerboas (Allactaginae) as the epitome of desert mammals, and morphologically similar mammals elsewhere were assumed to be ecologically convergent as well. In addition, granivory was considered the most common trophic adaptation among desert small mammals (along with various physiological and behavioral means of avoiding heat and reducing water loss). Subsequent work in South America indicated a fauna lacking bipedal, saltatorial rodents, but the discovery of the Argyrolagidae provided an explanation: the South American mammal fauna simply had not responded ecologically to the extinction of these animals whose morphology suggested a kangaroo rat habit. Discovery that most jirds (*Meriones*), gerbils, and other arid-adapted bipedal small mammals were not granivorous, however, suggested that granivory and desert adaptation were not necessarily synonymous. This has been shown by intercontinental comparisons (Kelt et al. 1996; Kerley and Whitford 1994). Nonetheless, lacking sufficient data from desert systems in both hemispheres, questions remained as to the fundamental similarities

between small mammal communities in the Northern and Southern hemispheres.

In the decade following the mid-1990s several long-term studies came to fruition in the Southern Hemisphere that reveal many features of structure and function of desert small mammal communities that previously had been poorly known. Thus, it seemed timely to bring together workers from aridlands in both the Northern and Southern Hemisphere to arrive at a better understanding of the similarities and differences between small mammal communities resulting from (largely) independent evolutionary trajectories. The organization of a symposium at the 10th International Mammalogical Congress held in Mendoza, Argentina, in August 2009 provided that opportunity. In this Special Feature we present papers stemming from that symposium that include exhaustive overviews of desert mammal ecology in both hemispheres and more specific regional studies in 2 of the 3 southern continents with significant aridlands, Australia and South America. We focus on discerning patterns of assemblage composition and change, trophic structure, the relative importance of biotic compared to abiotic factors, and possible explanations for why Southern Hemispheric communities are fundamentally different in their dynamics and structure



from those in the Northern Hemisphere. Thus, we hope to arrive at a better understanding of the underlying factors that influence small mammal diversity in each realm and the role of history, climate, and evolution in structuring them.

The 1st paper in this Special Feature, by Kelt (2011), is a global review of the literature on desert small mammal ecology (excluding Australia) over the past several decades and focuses on 4 central themes: the relative importance of competition compared to predation; the role of biotic influences compared with abiotic factors; the structure and composition of small mammal assemblages; and the influence of small mammals on vegetation and habitat structure. His report emphasizes that desert small mammals have played an important role in conceptual development and hypothesis testing of important ecological paradigms in diverse settings but that some areas of investigation have been distinctly provincial, sometimes limiting the generality of the findings. Increasingly complex plant–animal interactions also are an emerging trend in such research. Kelt (2011) notes the important roles of North American desert rodents such as kangaroo rats and prairie dogs (*Cynomys*) as keystone species and ecological engineers. Although few species have been documented to play similar roles elsewhere, some notable exceptions in South America include Chilean coruros (*Spalacopus cyanus*), vizcachas (*Lagostomus maximus*), and tuco-tucos (*Ctenomys*). Recently, a common central Chilean rodent, the degu (*Octodon degus*), has been documented to have important facilitation effects on semiarid plant communities (Madrigal et al. 2011).

The 2nd paper (Fox 2011) reviews work on small mammal trophic structure and its relationship to resource availability and disturbance on aridlands in 5 continents. A single dietary category comprises nearly half or more of the small mammal assemblages in aridlands on 4 of these continents, but it is a different category on each. Whereas herbivores dominate in South America, omnivores do so in southern Africa, granivores in North America, and insectivores in Australia (Eurasia has roughly equal proportions of granivores, herbivores, and omnivores). Fire and extreme climatic events (i.e., El Niño Southern Oscillations [ENSOs]) seem to have greater effects in Southern Hemispheric aridlands, often outweighing the importance of biotic interactions such as competition and predation that have been emphasized elsewhere. Fox (2011) also notes the importance of the concept of place and history of lineage (sensu Brown 1995) in explaining the evolution of the granivorous heteromyids in the aridlands of North America and of insectivorous marsupials in those of Australia.

Contributions to this Special Feature by Dickman et al. (2011) and Letnic et al. (2011) provide illuminating perspectives on the dynamics of small mammals in aridlands of Australia. Dickman et al. (2011) consider the importance of refugia for several species of small mammals, which exhibit “boom or bust” dynamics in spinifex grasslands of the central Simpson Desert of Australia. They report that whereas 1 species uses woodlands during prolonged droughts, 2 others appear to use unidentified refugia during such periods. This, combined with the ability to maintain very low numbers, contributes to extreme fluctuations of these species and suggests that other habitats might be

important for explaining their ability to increase rapidly during pulses of significant rainfall. Further, if global climate change influences resource availability through alteration of rainfall patterns, it is likely to have a strong influence on small mammal assemblages in this system. A similar conclusion was reached by Thibault et al. (2010) for Chihuahuan Desert small mammals. Letnic et al. (2011) address the question of dramatic fluctuations in small mammals of Australian aridlands using meta-analysis. They analyzed small mammal populations at 8 widely separated sites and determined that rainfall-driven resource pulses can result in switching trophic control from predominantly bottom-up (i.e., limiting due to resource availability, and ultimately, rainfall) to eventually top-down (i.e., due to predation). Such reversals of control exist along a continuum of rainfall-driven productivity, and thus, biotic interactions are strongly affected by abiotic factors mediating productivity.

Work in South America is represented by contributions from Meserve et al. (2011) and Ojeda et al. (2011). The former documents major trends in small mammal populations from a long-term study in the northern Chilean semiarid zone. Similar to Australia, pulses of rainfall trigger dramatic increases in many small mammal species, and primary productivity is the indicated proximate factor. Membership in small mammal assemblages has not changed over more than 22 years, and refugia might play a role in enabling rapid responses of small mammals following pulses of significant rainfall. However, since about 2000 the small mammal assemblage has begun to shift from being dominated by more rapidly breeding but short-lived sigmodontine rodents to one dominated by slower reproducing, long-lived caviomorphs such as degus. This shift could represent a response to more equitable rainfall between high-rainfall years and the lack of intervening droughts, a suggested consequence of global climate change in this region. In an overview of aridlands in the Argentine Monte Desert Ojeda et al. (2011) highlight biogeographical and ecological features of the small mammals of this diverse region. Species turnover is high among ecoregions of the Monte, but within its central area assemblage composition is broadly similar. Similar to the northern Chilean semiarid zone and Australia, small mammal population abundances vary dramatically among years due to variation in rainfall. Differences in diet and microhabitat appear important in structuring Monte Desert assemblages, and in light of increasing anthropogenic disturbance, mosaics of grazed and ungrazed areas are crucial to maintaining its remarkable diversity of indigenous mammals.

We hope that these papers contribute to a broader understanding of the differences and similarities among aridlands worldwide and serve as a stimulus for further work. Certainly, we have gained a keen appreciation for the remarkable diversity of aridlands and their importance as sentinels of the ongoing effects of anthropogenic habitat transformation and climate change.

RESUMEN

Las zonas áridas ofrecen oportunidades únicas para comparar los efectos de la historia, evolución, y geografía local de ensamblajes y dinámicas de comunidades de micromamíferos

que tienen restricciones ambientales severas. Investigaciones pioneras en zonas áridas del Hemisferio Norte han resultado en paradigmas que se supusieron como generales. Como la historia evolutiva y la biogeografía de las zonas áridas del Hemisferio Sur han sido distintas, ofrecen oportunidades excepcionales para evaluar este supuesto. Presentamos 6 artículos en este Tema Especial que muestran que ellos se han desarrollado y evolucionado en muchas direcciones únicas.

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Special Feature Editor was Barbara H. Blake.