



Long-term field studies on rodents

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Long-term studies on rodents have been conducted for longer periods (up to 70 years) and more generations (up to 88 generations) than for most other mammalian taxa. These studies have been instrumental in furthering our understanding of ecophysiology, social systems, and population and community processes. Studies on African striped mice (*Rhabdomys pumilio*) revealed that basal blood glucose levels span a far greater homeostatic range than previously thought. Studies on American red squirrels (*Tamiasciurus hudsonicus*) demonstrated how endocrine pathways underlying phenotypic plasticity allow individuals to respond to different environments. Long-term studies on African striped mice, marmots (*Marmota*), tuco-tucos (*Ctenomys sociabilis*), and degus (*Octodon degus*) revealed that ecological constraints on dispersal are drivers of group formation in some species but not others. Social flexibility, when the social system of an entire population can change due to individuals changing their social tactics, has been demonstrated in striped mice. Long-term studies on prairie voles (*Microtus ochrogaster*) found that males and females often live in pairs, leading to subsequent studies of the neural mechanisms underlying social monogamy. Long-term studies on other arvicoline rodents contributed more to our understanding of the factors influencing population dynamics than studies on any other mammalian order. While food availability and predation have been identified as factors influencing population dynamics, no single factor alone drives population dynamics in any species. We encourage researchers to incorporate manipulative experiments into long-term studies and to take integrative approaches to inform cross-disciplinary theory.

Estudios de largo plazo en roedores se han realizado de manera más prolongada y abarcando un mayor número de generaciones comparado con estudios similares en otros taxa de mamíferos. Estos estudios han expandido nuestro conocimiento en ecofisiología, sistemas sociales, y procesos poblacionales y comunitarios. Estudios en el ratón rallado africano (*Rhabdomys pumilio*) han revelado niveles basales de glucosa en la sangre que abarcan un rango homeostático más amplio que lo conocido previamente. Estudios en la ardilla roja (*Tamiasciurus hudsonicus*) han demostrado cómo las vías endocrinas que median la plasticidad fenotípica permiten a los individuos responder a ambientes contrastantes. Estudios de largo plazo en el ratón rallado africano, tuco-tucos sociales (*Ctenomys sociabilis*) y degus (*Octodon degus*) han demostrado como las restricciones ambientales pueden gatillar la formación de grupos sociales en algunas especies pero no en otras. La flexibilidad social, donde el sistema social de una misma población cambia debido a cambios en las tácticas usadas por los individuos, también se ha demostrado en el ratón rallado africano. Estudios de largo plazo en ratones de la pradera (*Microtus ochrogaster*)

mostraron que machos y hembras a menudo viven juntos, y estimularon la realización de estudios sobre los mecanismos neurológicos de la monogamia social. Estudios de largo plazo en otros roedores arvicólinos han contribuido más que ningún otro estudio en mamíferos a dilucidar los factores responsables de la dinámica de sus poblaciones. Aunque se ha mostrado que tanto la disponibilidad de alimento como la depredación tienen efectos, ninguno de estos factores es responsable de la dinámica poblacional de alguna especie en forma aislada. Sugerimos que los estudios de largo plazo puedan incorporar experimentos manipulativos y utilizar aproximaciones integrativas que contribuyan a generar una teoría más interdisciplinaria.

Key words: conservation, ecophysiology, long-term studies, mating system, population and community ecology, rodents, social organization, social system

Long-term studies (defined as ≥ 10 years or ≥ 3 generations) on rodents have been and are conducted in a wide range of environments, including high-altitude and subterranean habitats, prairie and farmland ecosystems, semiarid ecosystems with highly variable climatic conditions, and boreal forests (Supplementary Data SD1 and SD2). The species examined exhibit social systems ranging from solitary to colonial living and extended family groups. Some species have a very stable form of social organization, whereas many other species show intraspecific variation in social organization. Many of the 1st long-term studies on mammals were focused on rodents. At least 93 long-term studies have been conducted, investigating > 150 rodent species, and totaling $> 1,600$ study years and $> 2,500$ generations (Supplementary Data SD1 and SD2). Twenty-five or more generations have been studied in > 50 rodent species, which would take hundreds of years for species of most taxa of large mammals which have longer generation times. Moreover, many rodents are small and breed in captivity. The ability to follow-up field studies with laboratory studies makes rodents particularly appealing study organisms. Thus, it is not surprising that long-term studies of rodents have generated important insights into the main themes of this Special Feature (ecophysiology, social systems, population and community processes) and have contributed to rodent conservation. Herein, we present examples of advances for these topics, demonstrating the importance of long-term studies on rodents. In no way can our condensed review be comprehensive. However, a list of long-term studies on rodents is provided in Supplementary Data SD1 and SD2.

ECOPHYSIOLOGY

Environmental factors influence physiology and, along with this, behavior, metabolism, osmoregulation, stress physiology, and reproduction. Long-term studies on rodents have helped us understand environment–physiology interactions in 2 different ways. First, by analyzing data from many years, which for rodents represents several generations, individuals can be observed living under varying environmental conditions. Second, long-term field studies are often built on several successive shorter studies. These short-term studies often focus in detail on a particular aspect of the larger question, leading to a deeper understanding of the physiological processes involved.

Behavior: the influence of androgens on maternal behavior.—Using 10 years of behavioral data combined with 3 years of measurements of maternal testosterone, [Dantzer et al. \(2011\)](#)

examined the influence of maternal androgens on behavior of female red squirrels (*Tamiasciurus hudsonicus*). They tested the hypothesis that androgen levels drive behavioral trade-offs, predicting that high testosterone levels lead to lower maternal care but increased territorial defense and time spent foraging. Dantzer and colleagues found that androgen levels peaked at mid-lactation, the period when territorial defense and foraging behavior also peaked for females, but maternal care (nursing) decreased. They also tested whether mothers induce early adaptive changes in offspring to face social competition ([Dantzer et al. 2013](#)). Over the 23-year study, when squirrel density was high, faster-growing offspring had greater chances of surviving the winter and being recruited into the adult population ([Dantzer et al. 2013](#)). Increased offspring growth was triggered by maternal glucocorticoids: over 6 years, population density was positively related to fecal cortisol metabolite levels, and females for which population density was experimentally increased (mimicked by playback of territorial calls) had higher fecal cortisol metabolite levels and faster-growing offspring than controls ([Dantzer et al. 2013](#)). In turn, experimentally increasing maternal androgens affected growth rates of offspring ([Dantzer et al. 2013](#)). Those results demonstrated important adaptive maternal physiological effects shaping offspring phenotype in response to social competition.

Behavior: endocrine correlates of alternative reproductive tactics.—Male striped mice (*Rhabdomys pumilio*) have 3 alternative reproductive tactics: living as philopatric nonbreeders in their natal group, living as solitary roamers trying to mate with solitary or group-living females or group-living as breeders ([Schradin and Pillay 2004](#)). Philopatric males have the lowest testosterone levels, probably induced by high corticosterone levels, while roamers have the highest testosterone levels, even though they are subordinate towards breeders ([Schradin et al. 2009](#)). Group-living breeding males, which show extensive amounts of paternal care ([Schradin and Pillay 2003](#)), have the highest levels of prolactin ([Schradin 2008a](#)), a hormone associated with paternal care ([Schradin and Anzenberger 1999](#)). These results support the relative plasticity hypothesis, predicting that alternative tactics should be characterized by different hormone profiles if these tactics are plastic ([Moore et al. 1998](#)). Accordingly, it was demonstrated that hormonal profiles of males change when males switched tactics ([Schradin and Yuen 2011](#)). This research further added 2 novel aspects for testing the relative plasticity hypothesis: first, that hormonal differences between tactics were only present during the breeding

season, indicating that differences were in fact related to reproductive, not social, tactics (Schradin 2008a, 2008b); and second, the relative plasticity hypothesis was tested for the 1st time in females. Solitary females had the lowest corticosterone levels (Hill et al. 2015), but only when they left their group and bred solitarily, and not when they became solitary because all other females had died. Thus, these long-term field studies provided good support for the relative plasticity hypothesis, extending it to peptide hormones and females, and highlighting endocrine differences between tactics that disappear in the nonbreeding season.

Metabolism: blood glucose levels as an indicator of energy balance vary more than previously believed.—One example of how environmental factors influence physiology is provided by a study using data from 6 generations of African striped mice living under different environmental conditions. Individuals had lower basal blood glucose levels when food was rare, when ambient temperatures were low, or when they were living solitarily (Schradin et al. 2015). More than 130 years ago, laboratory observations showed that blood glucose levels were regulated within a very narrow range in dogs, leading to the concept of homeostasis (Bernard 1877). However, the recent long-term study on African striped mice demonstrated that blood glucose levels can vary significantly within natural populations.

Metabolism: fitness consequences of individual variation in daily energy expenditure.—As part of a study of > 25 years on red squirrels in boreal forests, Fletcher et al. (2014) examined the fitness consequences of individual variation in daily energy expenditure by females during lactation over 7 years. They found positive selection for greater daily energy expenditure by lactating females on annual reproductive success, but no negative consequence of high daily energy expenditure on adult survival as might be expected from greater physiological costs of high daily energy expenditure (e.g., oxidative stress—Fletcher et al. 2013). Selection on daily energy expenditure during lactation was not explained by correlations with parturition date, litter size, or pup growth rates, nor was there a significant heritable component for daily energy expenditure during lactation. These results highlighted that daily energy expenditure during lactation is an important determinant of reproductive success, is not genetically correlated with other phenotypic traits examined, and that selection on this trait is apparently mediated by factors not directly related to reproductive investment (Fletcher et al. 2014).

Adaptive role of the stress axis.—Concurrently to a long-term study of > 25 years on Arctic ground squirrels (*Spermophilus parryi*—Werner et al. 2015), a series of short-term studies provided insights into the adaptive role of the stress axis (Boonstra et al. 2014). Chronic activation of the stress axis is often associated with detrimental health consequences (Sapolsky et al. 2000), but Boonstra and Boag (1992) hypothesized that chronic activation of the stress axis could be adaptive if it maximizes energy availability for reproduction, even at a cost for survival (Boonstra 2005). Male Arctic ground squirrels experience 1 short breeding opportunity per year, with intense competition, high aggression, and low interannual survival (Boonstra 2005).

Boonstra et al. (2001) compared adult breeding males, nonbreeding males, and juveniles and found that breeding males had the highest levels of free cortisol and number of eosinophils, the lowest levels of hematocrit and white blood cells, the lowest response to an immune challenge, and a slightly impaired negative stress feedback loop. In a further study comparing only breeding males at the beginning and at the end of the breeding season, Delehanty and Boonstra (2011) found opposite signatures from the stress axis and downstream physiological responses. Here, breeding males showed no increase in free cortisol over the breeding season and no impairment of the feedback loop in response to acute stress. However, they showed increased energy mobilization (higher blood glucose levels and lower free fatty acids) and decreased condition (lower hematocrit levels and lower white cell counts). Those results highlighted that downstream measures of chronic stress are not necessarily reflected in the functioning of the stress axis over the course of a breeding season, and that longitudinal studies are necessary to properly understand the adaptive role of the stress axis.

SOCIAL SYSTEMS

We review 4 major insights resulting from long-term studies on rodent social systems. First, long-term studies have not generated universal support for the ecological constraints hypotheses explaining group formation by delayed dispersal (Emlen 1982), suggesting that alternative mechanisms need to be explored (Ebensperger and Hayes 2008). Second, the observation that prairie voles (*Microtus ochrogaster*) often live in pairs set into motion revolutionary work on the neural mechanisms of exclusive social bonds between pair partners and partner preferences (Young and Wang 2004). Third, reproductive consequences of group-living are dependent on social and ecological conditions (Ebensperger et al. 2014, 2016). Finally, social flexibility, when individuals can exhibit different social tactics, may be important to species in unpredictable environments (Schradin et al. 2012).

Ecological constraints and delayed dispersal.—The ecological constraints hypothesis posits that individuals delay dispersal and remain philopatric to their natal nest (or social group) when ecological conditions do not favor independent breeding (Emlen 1982). Accordingly, striped mice are group-living during the breeding season when population density is high but leave groups and start solitary breeding when population density is low (Schradin et al. 2010) or when vacant territories are provided experimentally (Schoepf and Schradin 2012). This indicates that high population density constrains them to living in groups, whereas they can avoid costs of reproductive competition by changing to solitary living when population density is low (Schradin et al. 2010). In contrast to predictions of the ecological constraints hypothesis, the size of social groups in the common degu (*Octodon degus*) is not correlated with population density or with the quantity or quality of burrow systems (Ebensperger et al. 2011). Although some degus are philopatric to their natal group, many groups form due to the movement of adults between groups (Ebensperger et al. 2009), resulting in social groups that do not differ in relatedness compared to the rest of the population

(Davis et al. 2016). Similarly, dispersal by yearling, female yellow-bellied marmots (*Marmota flaviventris*) is not influenced by population density (Armitage et al. 2011). Rather, dispersal by yearling females is less likely when mothers are present and negatively associated with the frequency of amicable behaviors between yearling females and mothers (Armitage et al. 2011). Early observations in social tuco-tucos (*Ctenomys sociabilis*) suggested specialization for mesic, resource-rich habitats have limited dispersal and favor group-living in these caviomorphs (Lacey and Wiczorek 2003). However, subsequent studies based on a larger number of years and conducted throughout the geographic distribution of this species questioned this possibility (Tammone et al. 2012), implying that the role of constraints is scale dependent. In summary, evidence from long-term studies suggests that effects of ecological constraints on group formation are not universal in social rodents.

Social monogamy.—Adult male and female prairie voles are frequently captured together in the same trap (15% of captures of adults—McGuire and Getz 2012), suggesting that social monogamy occurs. The basic social unit of the prairie vole consists of communal groups formed by the addition of individuals to male–female pairs and single-female breeding units (Getz et al. 1993; Getz and McGuire 1997). There is also some indication of variation in the social mating system across the species range, with fewer prairie voles in Kansas displaying social monogamy than in Illinois (Roberts et al. 1998; but see Ophir et al. 2007).

Long-term field studies by Getz and colleagues on prairie voles were important because it set in motion a series of laboratory studies on molecular mechanisms underlying social bonding. In particular, research by Young and colleagues provided evidence that partner preferences are linked to the distribution of oxytocin and vasopressin receptors at specific brain areas (Young and Wang 2004). However, because field studies demonstrated that prairie voles can also live in polygynous groups, establishing how social bonds are expressed in trios of 1 male and 2 females (or of 1 female and 2 males), both on the behavioral and molecular basis, is needed. Thus, future research should not only focus on male–female pairs but also on larger groups of voles as well (e.g., trios). Such information is critical because there is evidence that the ideal group composition with respect to reproductive success is 1 adult female and 2 adult males in a study population in Illinois (McGuire et al. 2002).

Fitness consequences of group-living.—Long-term studies provide insights into the fitness correlates of group size, social status, and cooperation. In the socially monogamous alpine marmot (*Marmota marmota*), group size does not influence the production of yearlings (King and Allainé 2002). However, females in groups where dominant males remain with the group for the entire summer produce more yearlings than females in groups in which a new male takes over the group (King and Allainé 2002). Similarly, social status, competitive interactions, and a lack of social cohesion within groups have significant impacts on the reproductive success of male and female yellow-bellied marmots. Dominant males have the highest reproductive success (Huang et al. 2011). The likelihood of reproduction and

lifetime reproductive success of females decreases with increasing number of older females and the number of same-aged females in the group, but it increases with increasing number of young, adult females (Armitage 2012). Females with high affiliation strength—an indicator of social cohesion—experience reduced reproductive success, suggesting that females do not cooperate among themselves (Blumstein 2013). Females that breed earlier in life have higher reproductive success than those that delay reproduction (Oli and Armitage 2003), a cost that is not offset by increased inclusive fitness (Oli and Armitage 2008). In contrast, long-term data (16–23 years) on Columbian ground squirrels (*Urocitellus columbianus*) monitored over their lifetime show that females accrue direct (Viblanco et al. 2010, 2016) and indirect (Dobson et al. 2012) fitness benefits from breeding among close kin, highlighting the role of kin selection in the evolution of philopatry (Arnaud et al. 2012).

In degus, short-term studies of 2 or 3 years initially suggested that group-living was costly to adult females (Hayes et al. 2009). However, a study of 8 years (8 generations) revealed that females do obtain direct fitness benefits from group-living, but mostly in years with low mean food abundance (Ebensperger et al. 2014). This same long-term study reveals how fitness benefits are also dependent on social network structure, group stability, and composition (Wey et al. 2013; Ebensperger et al. 2016). Together, these observations highlight that the adaptive significance of group-living is context dependent, which is why long-term studies measuring costs and benefits under different environmental conditions are important.

Social flexibility.—Social structure varies spatially and temporally in some rodents. During the breeding season, when reproductive competition occurs within groups, striped mice are group-living when population density is high, but solitary living when population density is low. Outside the breeding season, when no reproductive competition occurs, striped mice form social groups independent of population density (Schradin et al. 2010; Schoepf and Schradin 2012). These observations lead to a more precise characterization of social flexibility (Schradin et al. 2012): both males and females have alternative reproductive tactics based on a single strategy (that is, all individuals have the same decision rules). Depending on environmental and individual conditions, individuals may live solitarily or in small or large social groups. Consequently, the social system of a species or population can change as a function of individuals of both sexes changing their tactics. It was predicted that social flexibility represents an adaptation to environments that change unpredictably, selecting for high phenotypic plasticity based on a broad reaction norm and not on genetic polymorphisms. Several rodent species are socially flexible, being solitary during the summer breeding season but forming huddling groups during winter (Webster and Brooks 1981; Madison et al. 1984; Wolton 1985). Social flexibility is a prime tool for studying ecological factors and proximate mechanisms of sociality, as it allows the comparison of solitary and group-living individuals within the same population. Social flexibility is the best-studied mechanism leading to intraspecific variation in social organization (Schradin 2013), and in

our current period of accelerated climate change, it is important to know the limits of social flexibility to predict the range of conditions to which individuals can adapt.

POPULATION AND COMMUNITY ECOLOGY

Among the most persistent themes in ecology is determining what factors control the distribution and abundance of individuals. We are far from fully understanding how populations are regulated and what causes or allows for spatial and temporal variation in population size. This is exacerbated by the occurrence of species assemblages, which integrate the regulatory processes and independent dynamics of all constituent species, including diverse interactions such as competition, predation, and disease dynamics. Long-term studies provide a venue to address part of this; in an ideal world, multiple long-term studies would allow for improved understanding across both spatial and temporal scales simultaneously.

Population cycles in arvicoline rodents.—Population cycles have long fascinated biologists (Elton 1924, 1942), and their explanation has probably been one of the dominant themes in long-term field studies (Krebs 2013). While numerous species exhibit demographic cycles, including carnivores, lagomorphs, and rodents, these cycles are most apparent and best studied among arvicoline rodents (see Supplementary Data SD2).

The most well-documented examples of cycling are those of lemmings (*Dicrostonyx*, *Lemmus*) and voles (*Microtus*, *Myodes* [formerly *Clethrionomys*]) in northern boreal and some temperate sites (Supplementary Data SD2). Lemmings are larger than voles and tend to have longer demographic cycles. For lemmings and voles, 1 statistical problem is that phases within a given cycle (increase, peak, decline, low) are not independent, and each cycle constitutes a single time series of data. Consequently, long-term studies are essential to provide the degrees of freedom needed for meaningful robust statistical inference. Because body size, reproductive timing, and behavioral characteristics vary predictably across cycle phases, Krebs and others (summarized in Krebs 2013) argued that computer modeling is a useful tool to complement field observation. However, lemming and vole cycles cannot merely be treated as variable sine waves. A long history of striving to deduce a key causal factor underlying these cycles has produced an enormous literature and numerous hypotheses treated as intrinsic or extrinsic. Intrinsic mechanisms (e.g., self-regulatory) include social and behavioral characteristics (e.g., stress, individual “quality”, density-dependent spacing behaviors), that may predispose these species to given patterns of temporal cyclicity. Related hypotheses have suggested that behavioral changes lead to short-term selection for genetic subsets (such as differential aggression or dispersal). Extrinsic mechanisms include factors such as food (quality or quantity), disease, predation, cover, and presumably climate. In general though, single-factor explanations—sought over many years—have fallen into disfavor in the face of multiple-factor explanations.

Researchers in Fennoscandia have highlighted the distinct roles of generalist as opposed to specialist predators in shaping

population cycles. Because generalist predators exhibit prey-switching behavior, they tend to stabilize prey populations, whereas specialist predators are less capable of switching prey and so their numbers track prey more directly, albeit with a lag, destabilizing them and promoting cyclical demographics. As Krebs (2013) documented, however, no single factor has been shown to be both necessary and sufficient to drive cycles in any species. For example, predation mechanisms that appear to regulate populations in some parts of northern Europe fail to do so in North America. The failure of single-factor explanations led Krebs to support multifactor hypotheses as the most practical approach to understanding the spatial and temporal complexity underlying vole and lemming cycles. He emphasized, however, that multifactor explanations offer “an invitation to multiply explanations” in a post hoc manner (Krebs 2013:208); the way to avoid this is to specify clear a priori models that are testable in the field (Krebs 2013). Adding unanticipated import to these issues is the apparent dampening and possible loss of these cycles throughout northern Europe late in the 20th Century (Hörnfeldt 2004; Hörnfeldt et al. 2005, 2006; Ims et al. 2008), with potential consequences that scale through predator populations to impact community dynamics and ecosystem structure (Schmidt et al. 2012; Millon et al. 2014). Although climate change is directly implicated in these declines, it is not clear why cycles are dampening.

Structuring of rodent populations and communities.—Long-term studies have provided key and often unexpected insights into the drivers of temporal change in communities. The relative importance of competition and predation has been widely debated, and long-term field research in arid lands highlighted the importance of competition (Brown 1998) and the transient role of predation (e.g., in Chile—Meserve et al. 2003). While no ecologist questions the importance of both of these factors, there appears to be a consensus that food is more limiting in arid (water-stressed) environments whereas predation is more important where food is not limiting. The best means of addressing this controversy is with experimental research.

Disentangling disparate causal factors in demographic studies requires lengthy time series and sophisticated statistical tools (Royama 1992; Turchin 2003). Many reports highlight the importance of density-dependent dynamics, suggesting either resource limitation or behavioral or spacing effects or both (Lima et al. 2003; Murúa et al. 2003a, 2003b; Previtali et al. 2009). In arid regions, the importance of pulsed resources, such as rainfall driven by El Niño Southern Oscillation events, has been highlighted (Lima and Jaksic 1998; Madsen et al. 2006; Lima et al. 2008; Previtali et al. 2009; Letnic et al. 2011; D’Souza et al. 2013; Greenville et al. 2014). While small mammal populations in arid regions are well known to be dominated by bottom-up dynamics generally controlled by rainfall, unusually high rainfall can be detrimental (Valone et al. 1995; Thibault and Brown 2008) and may allow these systems to shift to top-down regulation by predation as consumer populations are released from bottom-up control by rapid primary productivity (e.g., Meserve et al. 2003; Letnic et al. 2011). Another resource pulse is masting events in some deciduous

tree species, which provide pulses of food that allow for or promote demographic expansion (Wolff 1996; Elias et al. 2004; Clotfelter et al. 2007; Lobo and Millar 2013).

Species within arid communities generally respond individually to temporal variation in resources (Brown and Heske 1990; Milstead et al. 2007), reflecting complementary and non-overlapping niche space. To our knowledge, no research has assessed niche complementarity as opposed to niche overlap (or redundancy) in mesic-habitat species such as *Microtus*. Closely related to this theme of redundancy and complementarity of niche space (Thibault et al. 2010) is that of net energetic compensation by different species or groups within a community. In Arizona, small granivorous rodents did not fully compensate for the experimental exclusion of kangaroo rats (*Dipodomys*) until *Chaetodipus baileyi*, a relatively large species of pocket mouse immigrated to the study site after nearly 2 decades (Ernest and Brown 2001). Within only a few years, the pocket mouse had increased in abundance significantly more where kangaroo rats had been excluded (but not in control plots to which kangaroo rats had full access), where it consumed over 80% of the energetic resources available. This led to advocacy of “zero-sum dynamics” wherein changes in the energetic consumption of 1 species is compensated by equivalent changes in 1 or more co-occurring species, leading to no net change in energy consumption (Ernest et al. 2008). However, a similar analysis in northern Chile found no evidence of compensatory responses by any species. A subsequent macroecological assessment suggested not only that the Chilean site likely was representative of most sites in South America (thus compensation seems unlikely), but that the Arizona study was unusual in having more species with the potential for compensation by other species than most sites in North America (Kelt et al. 2015). Hence, the generality of “zero-sum dynamics” remains uncertain, although Houlahan et al. (2007) suggest that this is rare.

Disease ecology.—The broader societal value of long-term studies is highlighted in their use in tracking disease threats, both among rodents and from rodents to humans. Research in New Mexico yielded a compelling model that may allow prediction of hantavirus resurgence (Yates et al. 2002; Carver et al. 2015), and similar work in Utah has shown a negative association between disease prevalence among native reservoirs (*Peromyscus maniculatus*) and rodent species richness (Dearing et al. 2015). In their long-term research on Lyme disease, Ostfeld and Keesing (2000) proposed the dilution effect whereby prevalence of the Lyme spirochete decreases in its primary rodent host (*P. leucopus*) when numerous alternative hosts (typically incompetent reservoirs) are present (reviewed in Keesing et al. 2010; Ostfeld 2011). Further work on these and other zoonotics would be useful to allow wider generalization of the relationship between extrinsic factors and the probability of disease transmission to humans.

CONSERVATION

Long-term research programs on rodents often involve species that are of least conservation concern since repeated sampling

warrants species persistence. This might explain the scarcity of conservation-related long-term studies on rodents. Sommer et al. (2002) modeled the extinction risk of the giant jumping rat (*Hypogeomys antimena*) based on a 10-year (1992–2001) study in Madagascar and concluded that forest clearing and human disturbance were the major threats to the population persistence of this monogamous rodent. A 12-year (1999–2010) study of the root vole (*Microtus oeconomus mehelyi*) in disturbed and undisturbed habitats in Hungary showed that this subspecies was vulnerable to human impacts of mowing and burning as well as natural aridity (Horváth and Herczeg 2013). A long-term study program (1988–2005) in Mexico reported that destruction of grassland habitat by drought (Avila-Flores et al. 2012) and anthropogenic factors (Ceballos et al. 2010) contributed to population declines of the black-tailed prairie dog (*Cynomys ludovicianus*). Two endangered rodent species have been part of long-term studies. The critically endangered Vancouver Island marmot (*Marmota vancouverensis*) has been studied in British Columbia (e.g., reproductive rates from 1987 to 2004—Bryant 2005). Long-term (1987–2007) monitoring of reintroduced captive-bred Vancouver Island marmots showed that survival was high (71%), older (> 2 years) individuals survived better than yearlings, and that predation by golden eagles (*Aquila chrysaetos*) was the main contributor to mortality (Aaltonen et al. 2009). In Poland, long-term (1974–1990) studies of reintroduced free-living and captive-bred European beavers (*Castor fiber*) investigated establishment through lodge and dam construction (Żurowski 1992) and showed the existence of high mortality and reduced reproduction in older reintroduced beavers (Żurowski and Kasperczyk 1988). Although the European beaver is now listed as least concern (Halley and Rosell 2003), recent long-term (1997–2009) studies in Norway suggested that beavers are vulnerable to climatic perturbations through effects on survival and fecundity (Campbell et al. 2012).

Because they occupy a basal trophic level as primary consumers, rodents can support a complex food web (Fernández et al. 2014). Therefore, long-term studies on selected keystone rodent species could provide insight into ecosystem dysfunction and threats to biodiversity (Avila-Flores et al. 2012). Keystone species disproportionately influence community composition and diversity, relative to their population density (Power et al. 1996). For example, the activities (e.g., burrowing, selective foraging) of the kangaroo rat (*Dipodomys*—Fields et al. 1999; Brock and Kelt 2004) and Gunnison’s prairie dog (Bangert and Slobodchikoff 2000; Davidson and Lightfoot 2008) increased landscape heterogeneity within desert grasslands, promoting complex and diverse communities.

Despite the wider ecological significance of keystone species, there is some contention about whether long-term conservation studies should have a species focus or an ecosystem focus (reviewed by Lindenmayer et al. 2007). A species focus provides causal relationships that could be elevated to ecosystem level (Caughley and Gunn 1996). For example, the black-tailed prairie dog is sensitive to drought-related changes to its grassland biome. However, focusing on keystone species,

which is the case for many long-term rodent studies (as in this review), neglects vulnerable species and ecosystem processes (Lindenmayer et al. 2007). Thus, it is prudent for species-centered research to be considered alongside the role of the study species as shapers of ecosystem function, which might allow detection of ecological perturbation.

FUTURE DIRECTIONS

Long-term studies on rodents have been conducted for a longer period and for more generations than on other mammalian taxa. Although impressive, these accomplishments mask the glaring lack of information on the ecology, physiology, and behavior of most rodents. In particular, we lack long-term studies on rodents living in the tropics, especially tropical rainforests, where special adaptations in behavior and physiology may have evolved and influenced population dynamics. Similarly, we lack long-term studies on behavioral phenomena that link rodents to other taxa. For example, no one has conducted long-term studies on rodent eusociality, despite the fact that eusociality is unique to 2 African mole rats, shrimp, and insects. In light of the diversity (mostly unstudied) and ecological importance of rodents (e.g., many have large impacts on plant life and are prey to many species), we argue that additional long-term studies are critically needed.

Rodents represent the best-studied mammalian taxa in population and community ecology and have been the focus of experimental field studies (both short term—Desy et al. 1990 and long term—Gutiérrez et al. 2010). Despite these efforts, experimental manipulations of ecological conditions lasting 10 or more years are clearly lacking. Long-term experimental manipulations of ecological conditions such as food and predation risk are needed, for example, to clarify the significance of single as well as interacting factors on arvicoline population cycles. Another problem of drawing general conclusions from long-term studies on rodents is that they are typically conducted in very specific environments. For example, long-term research in southeastern Arizona has been assessing the role of competition among rodents as well as between rodents and ants (Brown 1998). Regardless of the exceptional insights offered by this 4-decade-long study, it provides only a single temporal snapshot of an otherwise highly diverse array of North American deserts and uncertain insight into deserts in other parts of the world. Additional studies in North America and other regions of the world are needed to extend observations from southeastern Arizona with confidence. Such insight would be timely in the face of climate change and expanding desertification.

Future long-term studies on rodents will benefit from taking cross-disciplinary approaches. At the simplest level, behavioral and zoonotic studies can be integrated into ongoing, long-term studies on rodent population and community ecology. Such approaches could prove critically important in informing theory on the impact of changing environments on behavior (Wong and Candolin 2015) and disease ecology, including potential transmission to humans (Ostfeld 2011; Carver et al. 2015). Based on evidence for density-dependent

stress responses and social flexibility, long-term studies that test hypotheses for the underlying mechanisms of social variation could be illuminating. Minimally invasive methods to quantify physiological responses, such as collecting blood, fecal, or hair samples continuously over many years, could generate exciting data for understanding how environmental change influences physiology and health. However, the integration of mechanism into ongoing long-term studies may be in conflict with long-term sampling procedures, as they would require changes in method or additional sampling that could impact the trajectory of long-term datasets. Most critically, some techniques, such as those used to quantify neural mechanisms of behavior, require the sacrifice of individuals, which in turn, could affect social, population, and community processes under long-term examination. Despite these challenges, long-term studies on rodents that integrate across levels of analysis have great promise to broadly inform theory and contribute to conservation and, thus, are worth the effort to implement and maintain.

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SUPPLEMENTARY DATA

Supplementary Data SD1.—Long-term studies on rodents.
Supplementary Data SD2.—Long-term studies on rodent communities.

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