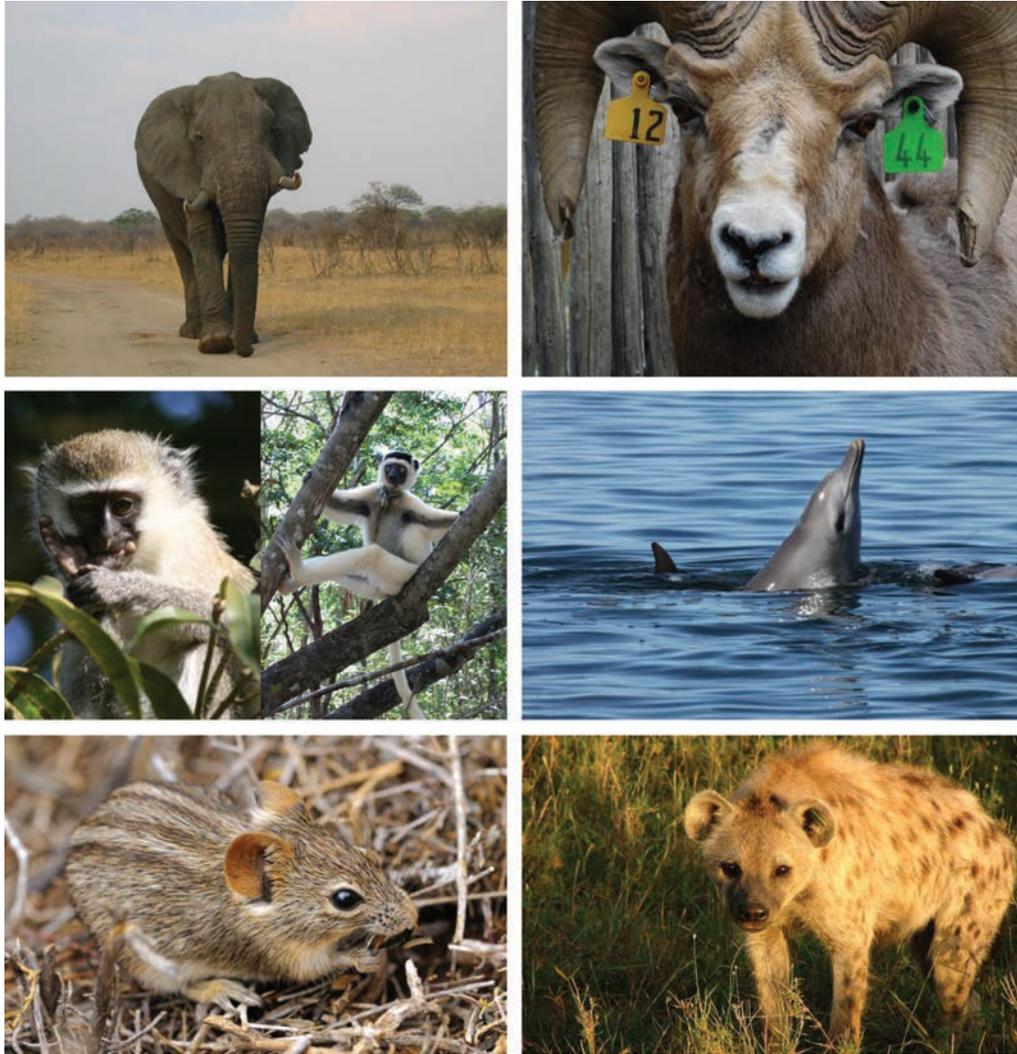




SPECIAL FEATURE: LONG-TERM STUDIES OF MAMMALS



Representative species that have been the focus of long-term studies. Clockwise: African elephant (*Loxodonta africana*), bighorn sheep (*Ovis canadensis*), bottlenose dolphin (*Tursiops aduncus*), spotted hyena (*Crocota crocuta*), striped mouse (*Rhabdomys pumilio*), vervet monkey (*Cercopithecus aethiops*), and Verreaux's sifaka (*Propithecus verreauxi*). Photo credits (clockwise): Hervé Fritz, Marco Festa-Bianchet, Ewa Krzyszczyk, Jenn Smith, Ulrike Fischer, Colin Chapman, Peter Kappeler.



Insights from long-term field studies of mammalian carnivores

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Most carnivorans (members of the mammalian order Carnivora) are elusive and long lived, so long-term studies are required to understand their basic biology and, ultimately, to conserve them. Here, we review examples of the wealth of information about the social systems, ecophysiology, and ecology of gregarious, terrestrial, carnivorous carnivorans (hereafter, carnivores) generated by long-term field studies of free-living, individually recognizable carnivores. Our synthesis yields key insights about the evolutionary forces favoring cooperation and ecological forces shaping social dynamics. The genetic assignment of parentage permits elucidation of the extent of reproductive skew in natural populations spanning multiple generations. Tracking of individuals across their life spans reveals underlying physiological, behavioral, and ecological mechanisms mediating reproductive suppression and dispersal. Long-term studies permit a comprehensive understanding of the ways in which intrinsic and extrinsic factors, including conflict with humans, regulate carnivore populations. Long-term studies also provide crucial baseline information required for the conservation of carnivores in the face of burgeoning human populations and global climate change. Notably, many conservation problems unfold on timescales only addressable with long-term data. Although we have yet to exploit the full wealth of information from long-term field studies, these valuable repositories have already yielded myriad insights about mammalian carnivores that would be unobtainable from studies conducted over shorter timescales.

Key words: carnivores, competition, cooperation, demography, disease ecology, group hunting, group living, human–wildlife conflict, long-term field studies, reproductive skew

Although most terrestrial, carnivorous members of the order Carnivora (hereafter, carnivores) are quite elusive and rare, which makes the acquisition of adequate sample sizes required for robust long-term studies of carnivores inherently difficult to implement and fund, a surprisingly large number of investigators have collected longitudinal data from free-living carnivores, particularly group-living species. These long-term studies have provided insights that would otherwise have been impossible to obtain. Many species of gregarious carnivores have complex social lives, mature slowly, and live for many years, so it often takes a decade or more to follow individuals as they advance through age and social classes. Consequently, long-term studies have unique advantages over shorter studies that take place within the period of a single funded research grant or a thesis or dissertation project. That is, long-term studies permit testing of new hypotheses as these arise while concurrently providing myriad opportunities to exploit

new data-collection technologies to address long-standing questions.

Because approximately 85–90% of carnivore species are solitary (Bekoff et al. 1984; Wilson and Mittermeier 2009), long-term studies shed considerable light on the evolutionary origins of, and selective pressures favoring, group living (reviewed by Smith et al. 2017). Social carnivores often benefit from 1 or more forms of cooperative behavior, such as cooperative hunting, breeding, coalition formation, and protection from predators (Smith et al. 2012). Following social groups across multiple generations permits researchers to assess the fitness consequences of specific phenotypic traits, particularly when researchers are able to track individual group members across their life spans; individuals may be recognizable due to their distinctive natural marks or those marked by researchers. Long-term research with individual identification has been particularly crucial to understanding the evolution of cooperation

because these important behaviors are often rare and thus likely seen only during extended periods of observation (Smith et al. 2010; Lehmann et al. in press).

Long-term field studies are teaching us a great deal about the physiological mediation of life-history patterns and how carnivores cope with extreme or variable environments such as those brought about by humans around the globe. For example, we now understand that many carnivore populations are declining due to their high energetic demands, low reproductive rates, and conflict with humans (Ripple et al. 2014). Long-term studies are particularly important for large mammalian carnivores, which typically mature slowly, have long life spans, and produce few offspring per litter at long inter-birth intervals. As a result, population responses to perturbations, either experimental or natural, may take years to measure. Elucidating the direct effects of mammalian predators on community structure (e.g., on prey abundance), as well as their indirect effects (e.g., trophic cascades), requires long-term study. Long-term studies allow biologists to track anthropogenic effects over time, suggesting possible paths for coexistence and predicting outcomes for carnivores confronting climate change. Life history and pedigree data gathered from many generations of known individuals also yield the information and sample sizes required to control for multiple sources of natural variation across temporal scales.

Here, we summarize findings generated from selected past and ongoing long-term field studies of terrestrial mammalian carnivores (see Supplementary Data SD1), regardless of their social system, and then we focus on key examples from 5 families that include gregarious species: Felidae (cats), Hyaenidae (hyenas), Herpestidae (mongooses), Mustelidae (badgers), and Canidae (dogs). We review key insights regarding social systems, ecophysiology, ecology, and conservation (Hayes and Schradin, this issue). Although several important long-term studies have focused on aquatic carnivores (Kruuk 1995; Le Boeuf et al. 2011), coverage of these taxa is beyond the scope of this review and we therefore omit them here. We focus instead primarily on studies of free-living terrestrial carnivores that span at least 10 years, and from which behavioral, demographic, and physiological data are available. In a few cases, we also refer readers to findings from important studies spanning periods < 10 years when these slightly shorter-term studies have yielded unique types of information. Because our review is not exhaustive, we focus on examples that illustrate the importance of long-term studies and their invaluable contribution to understanding the biology of these mammals.

SOCIAL AND MATING SYSTEMS

Family Felidae.—Of 40 extant felid species, the African lion (*Panthera leo*) is the only species with social groups comprised of both sexes. Although early workers (Schaller 1972; Caraco and Wolf 1975) proposed cooperative hunting as an explanation for group living in lions, subsequent long-term data contradict this theory. Lions that hunt alone benefit from higher per capita hunting success than lions hunting in large foraging

groups (Packer et al. 1990), and lions often hunt in groups of suboptimal sizes (Mosser and Packer 2009). Early results from the Serengeti Lion Project in Tanzania suggested that gregariousness among lionesses might have evolved to protect cubs from infanticidal males (Packer et al. 1990). However, data from 40 years of study have instead shown that group living in this species is favored by competition over high-quality territories and selection for numerical advantage in intergroup conflicts (Mosser et al. 2015). The largest and most cooperative prides generally reside in the highest quality habitats and enjoy the greatest reproductive success (VanderWaal et al. 2009).

Much of what we know about the social organization of cheetahs (*Acinonyx jubatus*) comes from the Serengeti Cheetah Project. Although females are solitary, associating only with dependent offspring, high-quality male cheetahs living in areas with high densities of males often form coalitions to control access of other males to territories frequented by multiple females (Caro 1994). Early studies suggested that territorial males might experience greater longevity than nomads (Caro and Collins 1987), but long-term data have revealed a more complex pattern. When male coalitions are rare, singleton males have the highest survivorship, but coalition males outlive singletons when coalitions are common (Durant et al. 2004). These contrasting results reveal how short-term studies may miss important relationships only captured by long-term data sets.

A nuanced understanding of variation in reproductive skew, defined here as the unequal distribution of reproductive output within a social group, is made possible with genetic assignment of parentage during multigenerational research. Long-term studies reveal higher reproductive skew in male lions (Packer et al. 2001) than in male cheetahs (Gottelli et al. 2007). This notable difference arises because male lions defend exclusive access to prides of females (Packer 1986). In contrast, female cheetahs move freely among male territories (Caro 1994) and mate with multiple males (Caro and Collins 1987), resulting in 43% of litters comprised of cubs from multiple fathers (Gottelli et al. 2007).

Family Hyaenidae.—Spotted hyenas (*Crocuta crocuta*) live in matrilineal groups, known as clans, comprised of several adult females and their young, along with 1 or more adult males. Spotted hyena clans are female-dominated societies (Kruuk 1972; Frank 1986). Long-term data on recognizable individuals uniquely permit tracking of shifts in the composition of clans over time, and births of new social groups via clan fission (Holekamp et al. 1993). For example, up to 4 generations may coexist within a single clan, but extinctions of entire matrilines over multiple decades may result in the surviving members of the top 2 matrilines making up 80% of the clan (Holekamp et al. 2012). Male spotted hyenas generally disperse, but females remain in their natal groups throughout their lives, where they benefit from maternal nepotism until their mothers die (Smale et al. 1997; Höner et al. 2007; Watts et al. 2009). In contrast to brown hyenas (*Hyaena brunnea*), which cooperatively rear and provision cubs at communal dens, spotted hyenas are not communal breeders and rarely provision

their own or other cubs despite the fact that multiple females rear their cubs together at a shared communal den (Mills 1990). One long-term study of spotted hyenas documented rare cases of adoption of related and unrelated cubs (East et al. 2009); this represents a prime example of how long-term studies capture rare events and other phenomena that are infrequent or difficult to observe.

Individuals belonging to a single spotted hyena clan exhibit fission–fusion dynamics; individuals regularly split apart from groups and rejoin the same or other groups over time (Smith et al. 2008). Whereas short-term studies use static snapshots of social networks, thus neglecting these temporal dynamics, Ilany et al. (2015) modeled network dynamics of spotted hyenas over 20 years and found that females maintain stable social bonds over multiple generations. Although social bonds are strongest among kin and when prey are abundant (Holekamp et al. 2012), preferred associations among pairs of unrelated adult females can nevertheless persist for many years (Smith et al. 2007).

In brown and spotted hyenas, both sexes mate with multiple partners, but reproductive skew is greater among males than females (East et al. 2003; Knowles et al. 2009; Holekamp et al. 2012). In brown hyenas, males fight to compete for mates (Mills 1990), but male spotted hyenas queue peacefully instead for mate access (East and Hofer 2001). Females prefer to mate with immigrant males, which favors dispersal by male spotted hyenas and maintains high genetic diversity within clans (Engh et al. 2002; Höner et al. 2007; Holekamp et al. 2012). Long-term behavioral and genetic data from Ngorongoro Crater in Tanzania have shown that sons of high-ranking female spotted hyenas grow faster, are more likely to disperse to clans offering better fitness prospects, start reproducing earlier, and have higher reproductive value than do lower-born sons (Höner et al. 2010). This long-term work clearly demonstrates how maternal effects can persist in male mammals long after they disperse to new social groups.

Family Herpestidae.—Long-term studies of mongooses provide clear evidence for the importance of cooperative breeding and protection from predators in promoting group living. Meerkats (*Suricata suricatta*) and dwarf mongooses (*Helogale parvula*) both live in stable, cohesive social groups containing a dominant breeding pair and multiple related helpers (Waser et al. 1995; Bell et al. 2014). In meerkat groups, the dominant breeding pair may monopolize as much as 75% of reproduction (Griffin et al. 2003). Dwarf mongoose groups have similarly high reproductive skew, where a single dominant pair performs the majority of breeding within the group (Waser et al. 1995; Creel 2013).

Meerkat helpers benefit indirectly from helping because they share genes with the breeding females, who benefit from increased survival of their pups (Clutton-Brock et al. 2001, 2002; Hodge et al. 2009). Helpers also gain direct benefits by increasing the size of their natal group; increased group size benefits individual meerkats directly because predators are most likely to be detected and successfully defended against by the largest groups (Clutton-Brock et al. 1999a, 2002). Furthermore, individuals belonging to the largest groups benefit from reduced

per capita predation risk (Clutton-Brock et al. 1999b) due to cooperative defense (e.g., sentry duty, alarm calling—Waser et al. 1995). Long-term studies thus demonstrate how the combined benefits of cooperative breeding and group defense from predation favor group living in these small carnivores.

Family Mustelidae.—Long-term studies of European badgers (*Meles meles*), complete with pedigree information, offer insights into the evolution and maintenance of sociality that would otherwise be impossible to obtain. These long-term data unequivocally demonstrate that multiple paternity within litters is common; each year only one-third of adults produce offspring and extra-group males sire roughly one-half of the cubs (Dugdale et al. 2007). Moreover, 18 years of study revealed that, on average, relatedness within groups was high ($R = 0.20$), but that pairwise relatedness was higher for females than for males due to female philopatry and high levels of extra-group paternity by neighboring males (Dugdale et al. 2008). Dominants likely lacked control over breeding opportunities because linear dominance hierarchies were inconsistent across years (Hewitt et al. 2009). Together, these data demonstrate incomplete control of dominants in monopolizing reproduction within groups or across years, but also reveal the potential for inclusive fitness benefits, especially for females.

Family Canidae.—African wild dogs (*Lycaon pictus*) live in cohesive packs that benefit from cooperative hunting in 2 ways. Specifically, the largest groups of dogs were most successful in capturing blue wildebeest (*Connochaetes taurinus*) and in reducing interspecific competition with spotted hyenas (Fanshawe and Fitzgibbon 1993). Long-term data on hundreds of kills provide strong evidence that cooperative hunting favors group living in this species, as larger packs are more successful in capturing prey (Creel and Creel 1995; Courchamp and Macdonald 2001) and defending kills (Carbone et al. 2005).

Whereas early researchers believed that a dominant pair controlled all breeding in an African wild dog pack (Frame et al. 1979), a study incorporating 8 years of data from 10 packs revealed that subordinate females bore 33% of pups, and subordinate males fathered 45% of pups (Spiering et al. 2010). When females shared reproduction, only the alpha and beta dogs gave birth, but cases of reproductive sharing among males included the 3 highest-ranking dogs (Spiering et al. 2010). These long-term data, obtained using modern genetic tools, importantly reveal substantial reproductive sharing previously missed by shorter studies.

ECOPHYSIOLOGY

Family Felidae.—Long-term data provide insights into the fitness consequences of adaptations to extreme environments, such as the constraints imposed on carnivores trying to maintain homeostasis in hot climates. For example, 36 years of data indicate that male African lions experience conflicting selection pressures to attract mates and maintain thermal homeostasis (West and Packer 2002). Females prefer males with long, dark manes, but dark-maned males suffer from poorer temperature regulation because dark manes absorb

the most heat; dark-maned males are therefore constrained in their abilities to dump excess heat and, thus, to avoid hyperthermia. Male lions with the darkest manes benefit from better offspring survival, higher circulating testosterone, better health outcomes, and greater length of their tenure with a pride of females, but they also suffer from higher body surface temperatures and greater frequency of abnormal sperm (West and Packer 2002). Interestingly, dark-maned males are less common in hot areas and seasons than are blonde-maned males, and manes disappear entirely in the hottest areas (West and Packer 2002).

Family Hyaenidae.—Long-term studies can elucidate fitness-related variation in physiology associated with social rank and ontogenetic patterns of growth. The social ranks of spotted hyenas determine their priority of access to food (Frank 1986), which in turn affects many of their physiological processes. Long-term study shows that parasite loads decrease with social rank among female spotted hyenas (East et al. 2015), whereas immune function (Flies et al. 2016) and telomere length (Lewin et al. 2015) increase with rank and resource access. Interestingly, independent of social rank, female spotted hyenas are larger than males, as females grow faster than males, rather than for a longer period of time (Swanson et al. 2013).

Family Herpestidae.—Long-term studies reveal the physiological mechanisms mediating reproductive skew in mongooses. Dominant meerkats benefit from better access to resources, foraging longer, gaining more weight, and producing heavier pups than subordinates (Bell et al. 2014). Breeding attempts by subordinate female meerkats trigger intense aggression from dominant females, resulting in infanticide or temporary eviction of subordinates (Young et al. 2006; Bell et al. 2014). These evictions trigger the chronic elevation of glucocorticoids in subordinates, suppressing their conception rates and increasing their abortion rates (Young et al. 2006). Although insufficient estrogen concentrations inhibit reproduction in nonbreeding females, reproductive suppression is independent of circulating androgen concentrations in male dwarf mongooses that fail to breed (Creel et al. 1992, 1993).

Family Mustelidae.—Dominant female badgers typically suppress the reproduction of other females, but long-term study importantly captures rare cases of plural breeding in which multiple adult females breed within the group; this occurs during times of abundant food (Woodroffe and Macdonald 1995; Rogers et al. 1997; Macdonald et al. 2002). Thus, as in spotted hyenas, food limitation constrains reproductive success among subordinate females.

Family Canidae.—Long-term research has shown that dominant African wild dogs of both sexes have higher glucocorticoid concentrations than do subordinates, indicating that stress hormones fail to mediate reproductive suppression in this species (Creel et al. 1997). Instead, elevated testosterone is associated with increased aggression and increased mating success in dominant male dogs (Creel et al. 1997). In subordinate female dogs, high baseline estrogen and high ratios of estrogen to progesterone likely prevent follicular development and ovulation, reducing mating success (Creel et al. 1997).

POPULATION AND COMMUNITY ECOLOGY

Family Felidae.—Long-term studies suggest that interspecific competition with lions and hyenas negatively affects reproductive success and recruitment among cheetahs (Kelly et al. 1998; Durant et al. 2004). Twenty years of data reveal that cheetahs lose 12.9% of their kills to other large carnivores, most often to hyenas (78% of losses) and to lions (15% of losses—Hunter et al. 2007). Cheetahs actively avoid areas occupied by lions, and to a lesser extent, spotted hyenas (Durant 2000a; Broekhuis et al. 2013). Cheetahs also avoid large congregations of their main prey, Thomson's gazelles (*Gazella thomsonii*), because these herds attract lions and hyenas (Durant 1998). Despite the evidence that lions negatively affect cheetah populations, a recent comprehensive collaboration between 3 long-term projects in the Serengeti revealed that, over the course of 30 years, lion numbers nearly tripled while the cheetah population remained stable (Swanson et al. 2014). One possible reconciliation between these conflicting results comes from Durant's (2000b) study, which suggests that the most experienced and successful female cheetahs are best at managing their relationships with lions and hyenas.

Family Hyaenidae.—Early in their long-term study of spotted hyenas in Tanzania, Hofer and East (1993) described "commuting" behavior, which appeared to occur in response to reliance on migratory prey, suggesting their subjects in the Serengeti were unique in this regard. However, recent deployment of GPS collars on spotted hyenas with abundant local prey year-round has revealed that they, too, particularly low-ranking hyenas, commute long distances as a means of avoiding intraspecific feeding competition (Green 2015).

The spotted hyena population in Ngorongoro declined over 30 years from 385 to 117 adults in response to fewer prey, and then rebounded as prey abundance increased (Höner et al. 2005). Spotted hyena populations also increased when sympatric lion numbers declined (Watts and Holekamp 2009; Green 2015). However, long-term study has revealed that multiple bottom-up and top-down processes synergistically regulate spotted hyena populations. Together, pathogens, prey scarcity, and direct mortality imposed by lions and humans limit the population sizes of spotted hyenas (Höner et al. 2005). Moreover, low-ranking hyenas are particularly vulnerable to these effects. For example, streptococcal bacterial infections most profoundly affect low-ranking hyenas during periods of prey scarcity (Höner et al. 2012).

Family Herpestidae.—Long-term study revealed an unusual pattern of dispersal in dwarf mongooses compared to the pattern observed in most mammals. That is, data on recognizable individuals across the life span suggest that dwarf mongooses of both sexes disperse, with males dispersing more often and over longer distances than females (Cant et al. 2013; Creel 2013). Documenting movement patterns at multiple life stages would be impossible without long-term demographic information on recognizable individuals.

Family Mustelidae.—Long-term data on group patterns and resources made it possible to test the resource dispersion hypothesis (Macdonald 1983), a theory proposed to explain

grouping by carnivores that typically forage alone but aggregate at clumped food. As predicted, European badgers aggregate at clumped prey (earthworms—[Kruuk and Parish 1982](#)), and group size and density increase with prey biomass ([Johnson et al. 2001](#)). Testing of this hypothesis, made possible only with long-term data, has stimulated an active area of study to explain gregariousness in species that otherwise compete with conspecifics for food.

Family Canidae.—Long-term studies generate sufficient data to explore important ecological and evolutionary concepts, such as the Allee effect. The Allee effect predicts that populations at low numbers exhibit a positive relationship between population growth rate and density ([Allee et al. 1949](#)). Populations at low densities are therefore expected to grow more slowly than those at high densities, increasing the likelihood of extinction for low-density populations ([Courchamp et al. 1999a](#)). Furthermore, theory predicts that obligate cooperative breeders such as wild dogs should be especially susceptible to the Allee effect because a critical number of helpers is necessary for reproductive success and survival, and thus for maintaining a positive population growth rate ([Courchamp et al. 1999b](#)). Long-term studies on multiple groups of African wild dogs support this hypothesis by documenting a positive relationship between pack size and breeding success as measured through litter size, pup survival, and juvenile survival ([Creel et al. 2004](#); [Buettner et al. 2007](#); [McNutt and Silk 2008](#)). In contrast, [Ginsberg et al. \(1995\)](#) and [Somers et al. \(2008\)](#) documented negative relationships between pack size and breeding success as well as between population size and growth rates, even for small populations. Conflicting findings have prompted ongoing study and debate, which push the boundaries of our knowledge of the effects of social group size on population viability ([Angulo et al. 2013](#); [Creel and Creel 2015](#)).

Long-term study of the reintroduction of gray wolves (*Canis lupus*) to Yellowstone National Park informs our understanding of community ecology. Fifteen years of data suggest that the reintroduction of these predators triggered a trophic cascade, with wolves indirectly altering plant communities by reducing herbivory by elk (*Cervus elaphus*) on plants in Yellowstone ([Ripple and Beschta 2012](#)). Specifically, predation by wolves on elk caused a decrease in elk abundance and shifts in foraging behavior, suggesting that the introduction of wolves promoted an increase in woody plants and herbaceous forage ([Ripple and Beschta 2012](#)). However, other data contradict the notion that wolves cause behavior-induced trophic cascades, and warn that if such cascades do occur, they are unlikely to operate outside boundaries of protected areas ([Mech 2012](#)).

Overall, available data have triggered ongoing debate about the extent to which regeneration of vegetation was prompted by wolf reintroduction, and whether regeneration, if it occurred, was promoted by shifts in elk behavior in response to wolf presence, abiotic factors interacting with wolf predation to limit plant growth, or predation forcing elk to seek or avoid bush cover ([Mech 2012](#)). In addition, [Mech \(2012\)](#) states that it remains unclear whether the indirect effects of wolves or alternative factors not yet tested best explain the

patterns of regeneration documented by [Ripple and Beschta \(2012\)](#). Nonetheless, these long-term data importantly quantify changes in community assemblage that would be impossible to document from short-term studies and are now motivating exciting new lines of ecological inquiry and debate.

The longest ongoing study of predator–prey dynamics to date is at Isle Royale, an isolated island in Lake Superior. Since 1958, the relationship between populations of wolves and moose (*Alces alces*) has varied considerably across years. Whereas early data suggested that wolves are the primary factor limiting moose population growth and abundance ([McLaren and Peterson 1994](#)), 40 consecutive years of study documented oscillations in moose abundance over time that were better explained by abiotic factors (e.g., winter precipitation, spring and summer temperatures) than by biotic factors. Among the biotic factors, bottom-up processes (such as density of moose and fir trees) were found to be more important predictors of inter-annual variation in moose abundance than top-down processes (e.g., wolf density—[Vucetich and Peterson 2004](#)). These long-term data emphasize the potentially strong effects of stochastic processes in driving short-term patterns, and underscore the need for long-term perspectives to understand complex ecological processes.

CONSERVATION

Family Felidae.—Although some wildlife managers tout the trophy killing of lions as a potential means for funding conservation, long-term data have documented the negative effects of trophy hunting on lion populations throughout Tanzania ([Packer et al. 2011](#)). If hunting of lions is to be permitted, then strict limits are required regarding the ages at which lions can be hunted ([Whitman et al. 2004](#)), and models based on long-term study provide reliable methods for identifying such limits ([Whitman et al. 2007](#)). Because experimental manipulations of wild carnivore populations are usually impractical, modeling is an essential tool for testing hypotheses concerning population dynamics. Because model assumptions determine the utility of models, long-term data sets provide rich opportunities to increase the reliability of model results.

Habitat encroachment represents the primary threat to cheetah populations. Cheetahs require large home ranges because they avoid areas frequented by larger carnivores ([Durant 2000a](#)) and because their primary prey can move long distances ([Durant et al. 1988](#)). Their need for large home ranges results in cheetahs occurring at lower densities than other large carnivores ([Caro 1994](#)), and it means that they are dependent on vast areas with heterogeneous predator and prey distributions ([Durant et al. 2007](#)). Areas outside or adjacent to protected areas may be particularly important for cheetahs because these areas often contain large populations of ungulates but relatively low numbers of lions and hyenas. Long-term genetic viability of cheetah populations may require a minimum effective population size far exceeding that of any particular population, so construction of wildlife corridors or translocation of cubs may be necessary to ensure sufficient genetic diversity ([Durant et al. 2007](#)).

Fortunately, cheetahs readily adopt cubs of unrelated mothers, suggesting that translocation of young cubs may be a viable alternative for maintaining gene flow (Caro 1994).

Long-term studies are also crucial for understanding disease ecology, because pathogen transmission interacts with the social structure of host animals, with traits of heterospecifics, and changing abiotic conditions (Munson et al. 2008; Craft et al. 2009). For example, Serengeti lions suffered massive mortality during 2 epidemics of canine distemper when drought preceding these epidemics caused an increase in the tick-borne pathogen, *Babesia*, which in turn exacerbated the effects of the virus (Munson et al. 2008). An outbreak of canine distemper in 1994 killed one-third of the Serengeti lion population, but the data available at the time were too sparse to deduce how the virus propagated through the lion population to achieve epidemic proportions (Roelke-Parker et al. 1996). Fifteen years after the outbreak, researchers used behavioral and movement data from a long-term data set to model a contact network to understand the dynamics of the 1994 outbreak; they found that the pattern of disease transmission was most consistent with repeated introductions from other carnivores rather than an epidemic transmitted from lion to lion (Craft et al. 2009). Finally, researchers modeled the dynamics of a multi-host canine distemper virus in the Serengeti ecosystem using decades of data on infection and vaccination rates from domestic dogs and lions (Viana et al. 2015). Whereas dog-to-lion transmission was the most common direction of cross-species transmission of canine distemper virus, the synchrony between infection peaks in domestic dogs and lions deteriorated over time (Viana et al. 2015). Large-scale vaccination campaigns decreased infection rates in dogs but failed to prevent transmission of the virus to lions. Because these data suggest that multiple wild carnivore hosts appear to maintain this virus, single-host vaccination campaigns are unlikely to succeed in controlling outbreaks.

Family Hyenidae.—There is remarkable consistency among data sets on spotted hyenas documenting effects of anthropogenic disturbance on patterns of space use and activity (Kolowski and Holekamp 2009) and stress physiology (Van Meter et al. 2009), as well as those of social dynamics and demography (Holekamp et al. 2012). After livestock depredation events, local pastoralists may retaliate with large-scale poisoning campaigns that can cause local extinctions of entire hyena populations (Holekamp et al. 1993). Nevertheless, if local lion numbers decline in heavily disturbed areas, hyena populations can burgeon at least in part due to the enormous behavioral plasticity characteristic of these animals (Holekamp et al. 2012; Green 2015). Thus, the responses of spotted hyenas to anthropogenic disturbance may represent a best-case conservation scenario compared to those unfolding for other African carnivore species, many of which are rapidly declining.

Family Mustelidae.—Long-term study of European badgers has revealed 2 surprising findings. First, this species is benefiting from warming climates; current individuals are heavier, reproducing more often, and surviving better than their recent ancestors, presumably due to an increase in prey abundance (Macdonald et al. 2002). Second, 15 years of study suggest

that the effects of badger culling might be counterproductive in controlling the potential for the spread of bovine tuberculosis to cattle; culling actually promotes badger movements in dense populations and, thus, increases the potential for the spread of tuberculosis to cattle (Vicente et al. 2007). Long-term data clearly offer important, and sometimes unexpected, insights about population and disease dynamics in wildlife.

Family Canidae.—The Serengeti wild dog population provides a prime example of the benefits of long-term monitoring, because scientists were able to observe as the population declined, was extirpated (1991–1998), and then was reestablished (1998–2001—Woodroffe 2001; Marsden et al. 2012). Researchers variably attributed the extirpation event to stress-induced immune suppression (Burrows et al. 1994), canine distemper virus (Macdonald 1992), rabies (Woodroffe 2001), stochastic events (Ginsberg et al. 1995), and lions (Swanson et al. 2014). The reestablishment allowed researchers to document the population-level changes caused by the extirpation, even surprisingly showing that the brief extirpation did not reduce genetic diversity in the Serengeti wild dog population (Marsden et al. 2012).

Long-term research and monitoring may inform conservation decisions that facilitate the survival of carnivore species in a human-dominated world. Wild dogs can coexist with people by shifting their patterns of space use and activity to avoid humans, and populations in human-dominated areas have similar demographics to those in more pristine areas (Woodroffe 2011a, 2011b). At Hwange National Park in Zimbabwe, African wild dogs preferentially moved outside the park where they had increased hunting success, reduced competition with lions and hyenas, and more suitable den sites (Van der Meer et al. 2013). However, this buffer zone may be an ecological trap if the dogs suffer increased mortality from humans at park boundaries, so further monitoring is required to understand the potential for humans and wild dogs to coexist.

The Isle Royale wolves offer insights into the value of long-term studies for making informed policy decisions because early assumptions based on an incomplete data set yielded erroneous conclusions. First, long-term data allow for the detection of negative effects of small population sizes on genetic diversity that might otherwise be missed (Räikkönen et al. 2009). Specifically, wildlife ecologists and managers relied on early data collected from the wolves of Isle Royale to argue that a small, isolated wolf population possessed adequate genetic diversity to support a healthy wolf population (United States Fish and Wildlife Service 2000). However, the original data offered an incomplete perspective because in reality wolves belonging to this small, isolated population actually suffered from a genetic abnormality; i.e., over one-half of the 36 wolf specimens collected between 1964 and 2007 suffered from congenital bone deformities (Räikkönen et al. 2009). Second, long-term data offer background information on genetic diversity required to understand the potential utility of genetic rescue as a conservation tool. For example, Adams et al. (2011) used long-term genetic data to document the profound effects of a single immigrant male on the small wolf population at Isle Royale.

Specifically, they compared genetic data for 40 years prior to the immigration event to data collected for 10 years after the event; these data show that fitness of this single male exceeded that of every native wolf in that population such that within only 10 years (2.5 generations) all living wolves had descended from this individual (Adams et al. 2011). Long-term data therefore allowed for the documentation of a genetic sweep, a process by which natural selection acts to favor the overrepresentation of a particular allelic repertoire in a population. Based on their data, Adams et al. (2011) concluded that although these effects were impressive, a genetic sweep triggered by the immigration of a single male is insufficient on its own for ensuring population viability. Thus, a comprehensive management plan that considers the long-term genetic rehabilitation and the current environmental conditions will be necessary to combat the extinction of wolf populations.

DISCUSSION AND FUTURE DIRECTIONS

As seen in the examples presented above, long-term studies elucidate the effects of developmental, physiological, and demographic processes mediating socioecological and evolutionary phenomena in ways that are impossible to understand from short-term investigations (Clutton-Brock and Sheldon 2010). Long-term research has significantly enhanced our understanding of cooperation, dispersal, grouping, and reproductive success in carnivores. For example, while grouping in large carnivores is favored by selection on resource acquisition and defense (e.g., cooperative hunting, territory defense), sociality in small carnivores is largely driven by cooperative breeding and antipredator behavior. Long-term studies on individually recognizable carnivores that can be repeatedly observed, particularly studies involving genetic assignment of parentage, help elucidate how reproductive skew varies among species and differs between sexes. These studies also offer important insights into how the specific phenotypic attributes of individuals affect lifetime fitness of free-living carnivores. Long-term data on hormones and behavior suggest that a variety of behavioral mechanisms as well as by variation in circulating levels of androgens, estrogens, or glucocorticoids in dominant and subordinate individuals impose reproductive suppression in carnivores.

A common misperception of long-term studies is that they simply continue applying the same methods to focus on the original objectives over time. This falsely suggests that researchers conducting long-term studies merely rely on increasing numbers of individuals and years to allow them to publish their results. Although standardized protocols and baseline objectives are important features of long-term studies, in reality, these studies are highly dynamic, and they push the boundaries of our understanding by generating hypotheses to explain novel phenomena and new directions of inquiry. The cases illustrated here demonstrate repeatedly how initial findings are often refined, reworked, and sometimes rejected after newly produced data from long-term studies shed better light on specific phenomena. Such insights arise from the use of powerful data sets or technological advances, such as GPS and

GIS, new molecular genetic techniques, microbiome analyses, advanced modeling techniques, and use of stable isotopes. The most successful long-term studies are constantly evolving, as are the carnivore populations under study.

Testing hypotheses proposed to explain ecological patterns is often only possible with data from free-living carnivores spanning multiple generations. Long-term studies allow researchers to determine the roles of both bottom-up (e.g., prey availability) and top-down (e.g., disease ecology) processes regulating carnivore populations, and to enhance our understanding of interspecific interactions among sympatric carnivores. Collaboration among long-term projects allows for the empirical study of large-scale dynamic systems that would be impossible to understand with isolated short-term data sets. For example, collaboration among 3 long-term projects in the Serengeti ecosystem revealed contrasting responses by wild dogs and cheetahs to changing numbers of lions (Swanson et al. 2014). In another example, collaboration between long-term projects revealed the dynamics of morbilliviruses that affect domestic and wild animals and provided insight into the effectiveness of mass vaccinations in multiple hosts (Viana et al. 2015).

Competition for resources between humans and carnivores is perhaps inevitable in contemporary human-dominated landscapes. Because many carnivores hunt living animals and range over large areas, human-wildlife conflict over livestock loss and changing land-use patterns are critical conservation issues (Treves and Karanth 2003), and population trends may reflect anthropogenic assaults over long time periods. Long-term study clearly demonstrates that anthropogenic pressures and habitat alterations affect individual carnivores, generally triggering population declines—but also occasionally facilitating population growth. Furthermore, successful conservation depends on a thorough understanding of an organism's biology, and relevant insights (e.g., adoption of unrelated cubs by cheetahs) can offer crucial solutions to difficult problems (Durant et al. 2007).

Long-term studies have provided valuable data on the variation observed within and among populations and thus suggest how behavioral and ecological flexibility is constrained in mammalian carnivores. These data continue to elucidate fundamental biological principles, yielding key insights into the evolution of sociality, mechanisms of reproductive suppression, phenotypic traits affecting fitness, life-history trade-offs, and population dynamics. In the face of burgeoning human populations, climate change, and worldwide declines in carnivore populations, long-term data are invaluable in assessing the health and management of carnivores to promote their conservation. These studies are uniquely poised to provide baseline data to inform conservation efforts and to study effects that occur at large timescales (Magurran et al. 2010). Taken together, long-term data provide unique opportunities to go back in time to ask questions that were perhaps unimaginable at their conception. We have yet to take full advantage of these repositories. Looking toward the future, these data should permit the detection of deleterious trends over large timescales, and arm us with information necessary to mitigate threats to the survival of free-living carnivores.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Long-term studies on terrestrial carnivores.

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