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Successes and challenges of long-term field studies of marked ungulates

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Studies of marked free-ranging ungulates have provided major contributions to ecology, evolution, and conservation. We focus on research areas where these studies have been particularly important: the role of individual differences in population dynamics, temporal changes in factors limiting populations, variation in reproductive success, quantitative genetics in the wild, population management, and conservation. We underline some strengths and limitations of these studies and call for more research on populations subjected to hunting, coexisting with large predators, and living in tropical or arid environments. Long-term research on ungulates requires long-term commitment, funding, access to study areas where animals can be monitored, and, usually, support from government agencies. Logistical difficulties limit the number of these important studies.

Key words: conservation, large herbivores, life-history evolution, long-term monitoring, population dynamics, population genetics, sociality, ungulates, wildlife management

Ungulates, belonging to the orders Artiodactyla and Perissodactyla, are an excellent model for long-term studies. Their philopatry and longevity mean that individuals can be observed or sampled repeatedly within a year and over multiple years. Therefore, by monitoring individuals throughout their lifespan, one can study the long-term fitness consequences of changes in internal state (age, social dominance, body condition) and environmental conditions (weather, population density, predation risk, hunting). For some bovids, age can be estimated from horn growth, a major asset because age has strong effects on life-history traits. Many ungulates can be habituated to human observers, and because of their large size they can be fitted with artificial marks recognizable from afar. These include colored ear tags in most studies, visual collars in some, and in recent years, GPS collars. Many species are economically important, increasing interest in their management and making ungulate studies effective in promoting conservation principles (Gordon et al. 2004; Hogg et al. 2006; Garel et al. 2007). Ungulate populations, however, can be affected by both legal and illegal harvest, possibly explaining why many studies are in fenced areas, small islands, or remote populations with limited human access.

Here, we illustrate the contributions of long-term studies of marked ungulates to ecology, evolution, and conservation. Rather than attempting an exhaustive review, we focus on research areas where these studies have provided key contributions, while covering all topics included in the other contributions to this Special Feature. We also discuss the limitations of these studies, underline some logistical challenges, and point to neglected areas. We only consider studies lasting at least 10 years, with detailed life-history trajectories for recognizable individuals, and with at least 1/3 of the study population individually monitored. These somewhat arbitrary criteria restrict our review to studies that covered at least 1 generation and where marked animals likely reflected sex and age structure of the population. At least 10 studies span over 3 decades (see Supplementary Data SD1), monitoring multiple generations. Many of these studies are on small populations and monitor fewer than 300 animals at a time. These studies require an accessible yet relatively undisturbed study area, often the ability to capture and recapture individuals, ease of observation, and, in most cases, cooperation with a conservation agency. Most studies were initiated to understand how different sex and age classes contribute to population dynamics and to quantify individual differences in reproductive success. As data accumulated and networks of collaborators expanded, many incorporated additional research goals in ecology, population genetics, evolution, and conservation.

Much research on population dynamics, management, and conservation of ungulates has involved time series of censuses, population estimates, and analyses of harvested animals, providing important contributions (Mysterud et al. 2002; Fryxell et al. 2005; Peterson et al. 2014). These studies suggest that predators, disease, climate, density dependence, and weather all influence ungulate populations. Studies based on a single measurement per individual, however, cannot measure how individual differences affect reproductive tactics or population responses to environmental variation. These can best be quantified with longitudinal data repeatedly collected from individually recognizable known-age animals. Long-term monitoring of marked individuals can partition the effects of age into age-specific changes at the individual level and differences in survival among individuals with different attributes (Clutton-Brock and Sheldon 2010). Both types of age effects have profound influences on the life history, population dynamics, and evolution of ungulates. Lifetime monitoring can also account for individual differences in genotype, early development, and social status, which may affect population dynamics.

Ecophysiology

Studying ecophysiology in wild ungulates presents many challenges. Because of their size, it is not possible to use classical methods such as metabolic chambers. Additionally, long-term studies typically avoid intrusive methods that could affect behavior, survival, or reproduction of marked animals. Research on ecophysiology of wild ungulates has therefore focused on noninvasive methods, including analyses of hormones from saliva, fecal, and hair samples. In bighorn sheep (*Ovis canadensis*), concentration of testosterone in feces was positively correlated with dominance status only for prime-aged rams (Martin et al. 2013), whereas in male red deer (*Cervus elaphus*), concentration of cortisol, but not testosterone, in feces was correlated with harem size (Pavitt et al. 2015). Work on eco-immunology on Soay sheep (*Ovis aries*), based on blood samples, found weak positive correlations among different concentrations of antibodies (Nussey et al. 2014). That study revealed complex links between immunology and fitness traits. A correlation of concentrations of immunoglobulin G antibodies with overwinter survival suggests a fitness effect of immunity against parasites.

Social Systems

Most female ungulates are philopatric and some form kin groups. Long-term studies of marked ungulates have revealed how social relationships among kin can weaken at high population density (Albon et al. 1992). These studies also have explored how demography affects the probability of co-existence of related females, an essential requirement for kin structuring of social systems (Festa-Bianchet 1991). Social network techniques have shown that sociality correlates positively with fitness in both sexes (Vander Wal et al. 2015), possibly because of the antipredator benefits of gregariousness.

Sociality has a strong effect on mammalian mating systems, and mating systems should affect the degree of skew in male mating success. Monitoring the reproductive success of male ungulates is challenging. With few exceptions, such as observations of copulations in fallow deer (*Dama dama*—Say et al. 2003), molecular tools are necessary to identify paternities because of the weak correlation between behavioral and genetic estimates of breeding success (Coltman et al. 1999). In many species, sperm competition is an important component of mating tactics (Hogg and Forbes 1997). Although DNA can now be extracted from feces or hair, adequate sampling remains an important issue for reliable measurement of male reproductive success. In some species, some resident males leave and nonresidents arrive for the rut, as reported in bighorn sheep and mountain goats (*Oreamnos americanus*—Hogg 2000; Mainguy et al. 2009). Nonresident males are in the study population for a short time, making it difficult to sample them for genetic analyses, and often their age and morphological characteristics are unknown. To measure reproductive success of males, a very large proportion of the young must be sampled to avoid biases from missing data, especially when the distribution of individual males during the rut is not accounted for. If juveniles cannot be sampled at birth, early mortality also may bias estimates of siring success. Consequently, reliable data on reproductive success of males currently exist for very few species, especially on lifetime or multi-year reproductive success of the same individuals (Festa-Bianchet 2012).

An assessment of the factors affecting success of males requires precise monitoring of nearly all males in a population. That is because the main factors determining reproductive success of males are the presence, number, and characteristics of competing males (Coltman et al. 2002). To understand the relationship between a trait and reproductive success of females, one only needs to measure the trait and reproduction of a sample of females, then compare the 2, accounting for other variables such as age and environmental conditions. For males, however, absolute trait size may be less important than relative value: to be successful a male must outcompete other males. Therefore, the reproductive success of males that do not overlap in time and space is difficult to compare.

Population and Community Ecology

Individual differences in age and mass are important.—Survival and reproduction are strongly age dependent in ungulates (Gaillard et al. 2000b). Survival of juveniles is much lower than survival of adults and is highly variable across years. Yearlings typically do not reproduce, and both mean and variability of their survival rates are intermediate between those of juveniles and of prime-aged adults. In contrast, prime-aged females, between 2–3 and 8–10 years of age depending on the species, usually show high survival with little yearly variation and consistently high fecundity (Gaillard et al. 1998). Ecologists and managers are very interested in determining which vital rates drive temporal changes in population growth. Detailed monitoring of marked ungulates has revealed that changes in population growth are at times driven by recruitment of juveniles, and at times by survival of adult females, both across populations and within populations over time (Coulson et al. 2005). Although survival of juveniles is always more variable than survival of adult females, and more sensitive to changes in density and weather, factors such as predation and disease can strongly affect survival of females (Gaillard and Yoccoz 2003; Coulson et al. 2005; Bourbeau-Lemieux et al. 2011).

With annual survival of prime-age ungulates typically 90–95%, many adults reach senescence. Long-term studies of ungulates have advanced our understanding of senescence in the wild (Nussey et al. 2013). They have identified characteristics of individuals such as mass that are associated with differences in longevity and in the age of onset of senescence (Gaillard et al. 2000a; Martin and Festa-Bianchet 2011a; Lemaître et al. 2014). Studies of ungulates also reveal trade-offs between growth, body reserves, and reproduction, particularly at primiparity, because females usually reproduce before completing body growth (Hamel et al. 2010; Martin and Festa-Bianchet 2011b). Changes in mass and in life-history traits with age, however, can be due to individual-level aging processes or to population-level changes through selective mortality or immigration. In ungulates, both are important (Nussey et al. 2011). The onset of senescence varies among vital rates. Survival is usually the 1st trait to decline, followed by mass (Bérubé et al. 1999). Reproductive senescence typically begins several years after survival senescence (Nussey et al. 2009; Hayward et al. 2013; Gamelon et al. 2014a). These major age-related changes in vital rates mean that age structure has important effects on population dynamics (Coulson et al. 2001). Some changes in age structure are predictable from population trajectories. For example, the proportion of older females typically increases in populations that decline because of density-dependent reductions in recruitment, leading to apparent density dependence in survival of females that is actually due to changes in age structure (Festa-Bianchet et al. 2003). Similarly, distribution of body mass within a population can affect population growth, especially in harsh years when the benefits of large body mass become more important (Pelletier et al. 2007; Ezard et al. 2009).

Males nearly always have lower survival than females and senesce faster (Loison et al. 1999). The reasons for these differences are an active area of research, as recent data challenge the assumption that survival of males is correlated with allocation to weapons used in competition over access to females (Lemaître and Gaillard 2012). Most studies suggest a decline in reproductive performance for the oldest males (Festa-Bianchet 2012). The factors that modulate senescence patterns in males remain poorly known, offering promising avenues for research (Lemaître et al. 2015). Survival and senescence of males is important for management, as in many species, mature males are sought by trophy hunters and their availability depends on survival rates (Festa-Bianchet 2003).

Population dynamics and switches in limiting factors.—The impact of environmental variability on population growth, particularly in interaction with density, is a fundamental question in population dynamics. Long-term studies of marked ungulates have advanced our understanding of density dependence, in particular its interactions with weather and sex and age structure within a population (Clutton-Brock and Coulson 2002; Bonenfant et al. 2009). Importantly, these studies also document temporal variability in population limiting factors. For example, in bighorn sheep, density dependence, disease, and predation can all become limiting at different times, sometimes in the same population (Festa-Bianchet et al. 2006). Increasingly, studies of ungulates are revealing the effects of global changes, such as reduced early survival in roe deer (*Capreolus capreolus*) caused by mismatches between reproduction and forage phenology (Gaillard et al. 2013; Plard et al. 2014), advanced breeding phenology in red deer (Moyes et al. 2011b), and weather-related declines in mass of feral sheep (Ozgul et al. 2009). As climate change becomes more evident, these monitoring programs remain essential to understanding impacts of climate on wild populations. Studies that have accumulated decades of data (see Supplementary Data SD1) can assess the effects of environmental conditions on population dynamics, phenotypic plasticity, and evolutionary potential.

A major contribution of long-term studies of marked individuals has been the quantification of maternal and cohort effects by comparing lifetime performance to maternal characteristics (Milner et al. 2000; Wilson et al. 2005) and by monitoring individuals born under contrasting environmental conditions (Douhard et al. 2014). Poor environmental conditions during early life, including adverse weather, can have long-lasting negative effects on body growth, age at primiparity, and senescence rate (Nussey et al. 2007; Douhard et al. 2013). The long-term effects of conditions in the year of birth, however, can be modulated by strong viability selection during early life. Lifetime monitoring of entire cohorts is necessary to quantify the effects of early environment on survival to maturity, and then on the performance of survivors. Sexes might display opposite responses. For instance, in roe deer, poor early-life environment increases life expectancy for females and shortens it for males (Garratt et al. 2015).

The evidence for switches in limiting factors, however, underlines a problem: most long-term studies of marked ungulates are in areas where large predators have been extirpated. There are no predators capable of killing adults in 19 of the 24 populations listed in Supplementary Data SD1. This limitation restricts our understanding of predator–prey dynamics in ungulates. It may inflate our perception of the importance of bottom-up limiting factors, including both density-dependent regulation and limitation through low resource quality or quantity. Therefore, it is difficult to predict what might happen to ungulate populations when large predators return, either naturally (Chapron et al. 2014) or through reintroductions (Middleton et al. 2013). Even where large predators persist, the study species is often not their main prey, providing limited insights on predator–prey dynamics. For example, cougar (*Puma concolor*) predation has caused drastic population declines of bighorn sheep in 3 study areas (Festa-Bianchet et al. 2006; Bourbeau-Lemieux et al. 2011). In all cases, however, predation was attributable to individual specialists: cougar populations may not respond to changes in availability of bighorn sheep, because other ungulates, mostly deer, represent the bulk of their diet (Ross et al. 1997). Populations of predators, particularly wolves (*Canis lupus*) and Eurasian lynx (*Lynx lynx*) (Chapron et al. 2014) that are increasing in size, may provide opportunities to assess their impacts on ungulate population dynamics. Although a detailed analysis of the demographic impact of lynx predation on roe deer has yet to be conducted, survival of all age classes of roe deer markedly decreased in the presence of lynx (Andersen et al. 2007), possibly leading to population declines (Andrén and Liberg 2015). The possible indirect effects of predation on population dynamics of ungulates are the object of much interest and debate (Creel et al. 2007; Middleton et al. 2013) because they may depress population growth beyond the impact of direct predation mortality. One study of bighorn sheep has quantified these indirect effects, showing reduced growth of lambs in years of high cougar predation (Bourbeau-Lemieux et al. 2011).

The limited contribution of long-term individual-based studies to our knowledge of predator–prey relationships in ungulates underlies a limitation of this approach: long-term studies requiring the marking of most individuals cannot be easily applied over broad spatial scales and very large populations. At these larger scales, which are often very relevant to management, complementary approaches include monitoring predators (Andrén and Liberg 2015).

Variation in reproductive success of individual females.—Studies of marked ungulates excel at measuring the reproductive success of females. Females drive ungulate population dynamics, and documenting their survival and reproduction is extremely important. It is often easy to monitor female reproduction because of the close mother–offspring association until weaning, the ability of many studies to mark offspring before independence, and the strong philopatry of most female ungulates. Several studies have monitored the reproductive success of females until offspring reach adulthood, a difficult task in many other taxonomic groups such as birds (Lebreton et al. 1993). We now know how reproductive success of females is affected by numerous factors: population density, environmental conditions, age, dominance, previous reproduction, litter size, sex of offspring, inbreeding, parasite load, and body mass (Gaillard et al. 2000b; Clutton-Brock and Pemberton 2004; Festa-Bianchet and Côté 2008; Martin and Festa-Bianchet 2010). Life histories of females reveal persistent individual differences in reproductive success in red deer and long-term fitness costs of catch-up growth in bighorn sheep (Moyes et al. 2011a; Marcil-Ferland et al. 2013). Finally, monitoring of mothers and daughters has allowed researchers to partition variance in fitness attributable to individuals or to their parents, showing, for example, that heavy birth mass can benefit daughters but not their mothers, and raising key questions about how to measure fitness in wild animals (Wilson et al. 2005).

There are 2 important limitations to the study of female reproductive success in ungulates. One is that in most species females can only produce 1 or 2 young per parturition and reproduce once per year. That makes it difficult to separate environmental from maternal effects. The 2nd limitation is the logistical challenge of experimental studies on reproductive effort, which have only been attempted in feral sheep (Tavecchia et al. 2005). Because of the strong mother–offspring bond, experiments such as litter size manipulation currently appear impossible in ungulates.

Conservation and Management

Sustainable harvest of wild ungulates requires knowledge of population dynamics. Although a change in survival of adult females would have a much greater impact on population growth than a similar proportional change in any other vital rate, survival of juveniles has greater variability from year to year (Gaillard et al. 1998; Gaillard et al. 2000b). Therefore, harvest should target different sex and age classes depending on management goals. The harvest of adult females is most effective in controlling populations, while harvesting juveniles can maximize hunting opportunities with minimal impact on population growth (Gamelon et al. 2012). It is likely, however, that the sex and age structures of heavily hunted populations are very different from those of well-studied populations of marked individuals, most of which are either not hunted or hunted very lightly. The wild boar (*Sus scrofa*) study at Chateauvillain (France) is an exception, as this population is subjected to very high hunting pressure (Toïgo et al. 2008). Although sustainable harvest policies assume density dependence, demographic analyses of some roe deer populations subjected to both hunting and predation reveal an increase in generation time and a population decline, because the low survival was not compensated by earlier reproduction or increased litter size (Nilsen et al. 2009). In bighorn sheep, cougar predation led to positive density dependence in population growth (Bourbeau-Lemieux et al. 2011). With moderate hunting pressure, particularly in the absence of large predators, sustainably hunted populations display a colonizing demographic regime, characterized by high recruitment, a young female age structure, few senescent individuals, and shortened generation times (Crampe et al. 2006; Nilsen et al. 2009).

Ungulates typically show density dependence, beginning with reduced recruitment (Gaillard et al. 1998). Low recruitment leads to an increase in the mean age of females (Festa-Bianchet et al. 2003) so that generation time increases as the population approaches carrying capacity. Thus, as expected from life-history theory (Charnov 1993), generation time and population growth covary negatively. Our knowledge of the demography of exploited ungulate populations, however, is in its infancy. Both generation time and population growth rate are important drivers of population responses to transient demographic regimes induced by hunting (Gamelon et al. 2014b). Those changes can include severe alterations of both the sex ratio and age structure of the population. It remains unclear, therefore, whether the response of heavily hunted populations to changes in density, weather, and resource availability differs from that documented by long-term studies of unhunted populations.

Trophy hunting leads to rapid evolution of reduced horn growth in bighorn rams, because hunters remove young males with rapidly growing horns, years before those weapons improve reproductive success (Pigeon et al. 2016). Although analyses of time series of harvested wild sheep report declines in horn length or changes in shape over time (Garel et al. 2007; Douhard et al. 2016), results for deer do not suggest an evolutionary response (Mysterud 2011), possibly because of differences in harvest pressure, harvest policies, or biological differences between horns, which grow over the lifetime, and antlers which are regrown each year. In addition, there are as yet no pedigrees available for hunted populations of deer, which would be necessary for quantifying evolutionary effects. Long-term monitoring of marked individuals in hunted populations seems particularly desirable, because most ungulate populations worldwide are harvested, sometimes heavily. The wild boar population at Chateauvillain, France, is under heavy hunting pressure (Toïgo et al. 2008). Wild boars are unusual among ungulates by combining potentially high survival of adults with an average litter size of 5 (Focardi et al. 2008). Females respond to high hunting pressure by earlier primiparity (Servanty et al. 2009), facilitated by the earlier birth dates selected for by hunting pressure (Gamelon et al. 2011). As hunting substantially reduces survival of breeders, generation time also decreases markedly. Thus, heavily hunted wild boar have a generation time of only about 2 years (Servanty et al. 2011), similar to that of small passerines and likely about half as long as in populations subjected to a lower level of harvest (Focardi et al. 2008).

The relevance of long-term studies of ungulates for wildlife management is demonstrated by the frequent collaborations between universities and government agencies. Conservation or wildlife management agencies collaborate with nearly all studies listed in Supplementary Data SD1. That collaboration often involves participation in all aspects of research, from selecting objectives to publication.

Quantitative Genetics and Evolution

The study of evolution under natural conditions is challenging. One approach is to establish detailed pedigrees over several generations (Pemberton 2008) and apply statistical methods to estimate the genetic basis of complex traits (Kruuk 2004). If a trait is genetically determined, then individuals who share the same genes should express similar phenotypes (Kruuk 2014). Ungulate populations with detailed pedigrees have produced important contributions to the study of selection and evolution in the wild. For example, long-term studies on bighorn and Soay sheep recently accounted for ~10 % of all published heritability estimates and 47% of those for mammals (Postma 2014).

An assessment of the genetic basis of complex traits is critical to evaluate the evolutionary potential of wild species. Studies of ungulates have estimated heritability and genetic correlations among morphological and life-history traits, showing, for example, that in bighorn sheep both mass and horn size are moderately heritable (Poissant et al. 2008) and under sexual selection (Coltman et al. 2002). Theory predicts that heritable traits under directional selection should evolve quickly so that genetic variation should be eroded. In nature, however, we often find persisting genetic variation and no response to selection for traits apparently under strong selection. Research on sexual selection on ungulate weapons has partly resolved this mismatch between prediction and observations. Analyses of 40 years of data on antler size and reproductive success in red deer revealed that, although antler size is heritable, selection did not result in an evolutionary change in the trait because of strong environmental effects on antler development (Kruuk et al. 2002). Antler growth is strongly affected by body condition, which varies with environmental conditions and affects the ability of males to monopolize females during the rut. Thus, under favorable environmental conditions both antler growth and fitness are enhanced, but this association is not due to causal effects of the trait on fitness, leading to an apparent mismatch between selection and response to selection (Kruuk et al. 2014).

Studies of bighorn sheep and red deer in population with deep pedigrees show that inbreeding reduces juvenile survival (Rioux-Paquette et al. 2011; Walling et al. 2011). Experimental genetic rescue of an inbred bighorn sheep population through the introduction of unrelated individuals led to dramatic improvements in population performance, with important implications for conservation biology (Hogg et al. 2006). Ungulates, however, do not always avoid inbred mating: pronghorns avoid it but bighorn sheep do not (Rioux-Paquette et al. 2010; Dunn et al. 2012), suggesting that inbreeding is important for the conservation of small populations.

Future Directions, Research Needs, and Challenges

Many years of monitoring are necessary to acquire the valuable data discussed above. That is a problem in the current climate of short-term funding focused on immediate gains, which results in the need for new studies to be productive immediately and to include short-term objectives. Funding and logistic challenges may discourage researchers from embarking on ambitious long-term plans, especially when much time and resources must be invested in the initial marking program. A possible solution is to exploit situations where preliminary work, often by management agencies, shows the possibility of capturing and monitoring many individuals. At least 15 of the studies in Supplementary Data SD1 were started by management agencies.

Long-term studies of ungulates are well placed to assess the consequences of climate change at the individual and population levels. Expanding predator populations may provide new insights on predator–prey dynamics. Collaborations among researchers are leading to more comparative studies, contrasting

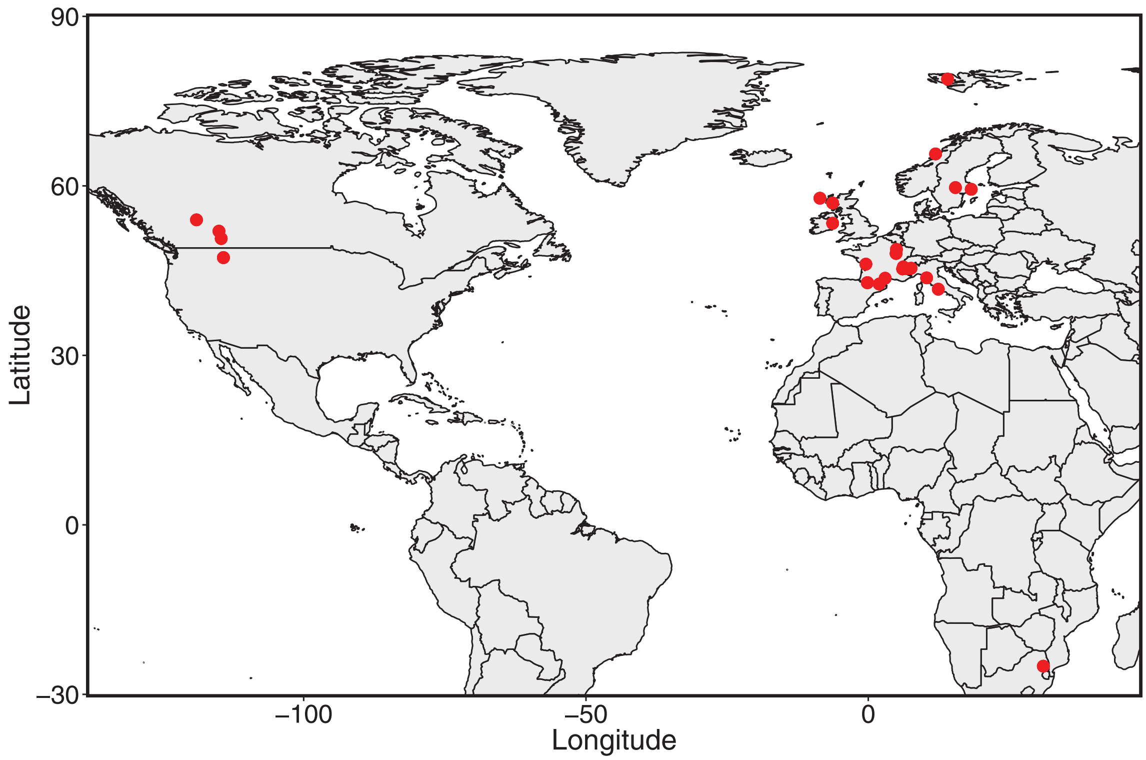

Fig. 1.—Geographical distribution of 24 long-term studies of ungulates listed in Supplementary Data SD1. Only the study in South Africa was outside Europe or North America.

populations under different ecological conditions. For most species, only 1 population has been the object of a long-term study (see Supplementary Data SD1), so we know little about among-population variability. An excellent example of synergy is the roe deer collaborative network (EURODEER—e.g., Cagnacci et al. 2011). Geographic and ecosystem coverage by long-term studies of ungulates is biased (Fig. 1): all but 1 of the studies in Supplementary Data SD1 are from North America or Europe. Research in other regions such as tropical and arid environments may produce novel findings, especially in areas with a more diverse ungulate guild or a variety of predators (Sinclair et al. 2003).

Many of the challenges of studies of ungulates are shared with long-term studies of other taxa, such as problems in maintaining funding and consistent data collection (Clutton-Brock and Sheldon 2010). The scientific impact of these studies tends to increase with their duration (Clutton-Brock and Sheldon 2010). Studies of ungulates also face specific challenges, such as maintaining access to study areas over decades despite changes in land ownership, management mandate, political structure, and aging and degrading infrastructure such as field stations. Like all ecological field research, studies of ungulates are subject to increasingly restrictive permitting requirements, often increasing costs. Ungulates are often difficult to capture, and the ability to capture a large number of individuals severely restricts the choice of study area. Many studies rely on capturing neonates or on using very expensive methods such as helicopters for captures. Only one-half of the studies in Supplementary Data SD1 include repeated captures of individuals. In some studies, baited platform scales provide measurements of body mass without recaptures (Hamel et al. 2010). There is also a need to carefully evaluate different types of artificial markings and to consider alternatives, because some large tags or collars can have deleterious consequences, raising ethical issues and possibly biasing results (Rasiulis et al. 2014). Events such as extreme weather, high predation, invasive species, and disease outbreaks present interesting research opportunities but can also drastically reduce sample sizes. Illegal harvest is a concern in some cases, especially when poachers target large dominant males because of their trophy value.

Investigators running long-term studies may be reluctant to manipulate their system experimentally. Demographic manipulations, or even feeding experiments, can compromise long-term monitoring of individuals. There are exceptions: the Ram Mountain bighorn research began as an experimental manipulation of population density (Festa-Bianchet et al. 2003), and density has been manipulated in roe deer (Gaillard et al. 2013). More experimental manipulations are desirable, to examine the effects of different harvesting strategies and explore the effects of resource availability at different life stages.

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Supplementary Data

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

Supplementary Data SD1.—Long-term studies on ungulates.

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