

TEMPORAL VARIATION IN FITNESS COMPONENTS AND POPULATION DYNAMICS OF LARGE HERBIVORES

J.-M. Gaillard,¹ M. Festa-Bianchet,² N. G. Yoccoz,³
A. Loison,¹ and C. Toïgo⁴

¹*Unité Mixte de Recherche No. 5558 "Biométrie et Biologie Evolutive,"
Université Claude Bernard Lyon 1, 69622 Villeurbanne Cedex, France;
e-mail: gaillard@biomserv.univ-lyon1.fr; loison@biomserv.univ-lyon1.fr*

²*Département de Biologie, Université de Sherbrooke, Sherbrooke, Québec,
Canada J1K 2R1; e-mail: mbianche@courrier.usherb.ca*

³*Department of Arctic Ecology, Norwegian Institute for Nature Research,
Polar Environmental Centre, N-9296 Tromsø, Norway;
e-mail: nigel.yoccoz@ninatos.ninaniku.no*

⁴*Office National de la Chasse, Division Recherche et Développement, 75017 Paris,
France; e-mail: cnerafm@mail.sky.fr*

Key Words environmental variation, density dependence, ungulates,
demography, critical life-history stage, long-term studies

■ **Abstract** In large-herbivore populations, environmental variation and density dependence co-occur and have similar effects on various fitness components. Our review aims to quantify the temporal variability of fitness components and examine how that variability affects changes in population growth rates. Regardless of the source of variation, adult female survival shows little year-to-year variation [coefficient of variation (CV <10%)], fecundity of prime-aged females and yearling survival rates show moderate year-to-year variation (CV <20%), and juvenile survival and fecundity of young females show strong variation (CV >30%). Old females show senescence in both survival and reproduction. These patterns of variation are independent of differences in body mass, taxonomic group, and ecological conditions. Differences in levels of maternal care may fine-tune the temporal variation of early survival. The immature stage, despite a low relative impact on population growth rate compared with the adult stage, may be the critical component of population dynamics of large herbivores. Observed differences in temporal variation may be more important than estimated relative sensitivity or elasticity in determining the relative demographic impact of various fitness components.

INTRODUCTION: Widespread Large Herbivores in Variable Environments

Large terrestrial mammalian herbivores (with an adult mass of ≥ 10 kg) are found in most ecosystems, from arctic tundra to tropical forest (134). They face not only very different climates, but also great variation in predation pressure, risk of disease, and human interference. Despite these potential sources of temporal variability in survival and recruitment, populations of large herbivores are often considered to be only weakly affected by temporal variation and are often described with deterministic age-structured models (46). In this review we first examine and quantify temporal variation in some fitness components for populations of large herbivores, including survival and reproduction at different stages of an individual's life cycle (Figure 1). Temporal variation in at least one fitness component has been measured for >30 species of large herbivores. We then assess the effects of taxonomic position, ecosystem, and body size on patterns of

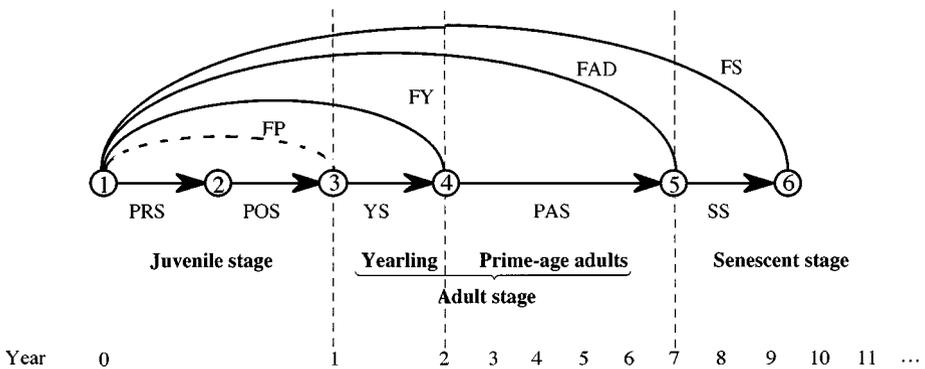


Figure 1 Life cycle graph of a large herbivore female: *Circled numbers*: 1, newborn [most ungulates are birth-pulse species (155)]; 2, weaned young (around 6 months for most species); 3, yearling; 4, 2-year-old (often the minimum age of primiparity); 5, prime-aged; and 6, senescent (older than a threshold age). *Straight lines* indicate transitions from one age group to the next, and *curved lines* indicate reproduction (and therefore production of newborns). These fitness components describe the development of individuals through the life cycle: PRS, pre-weaning survival [summer survival of young in temperate species (e.g. 29)]; POS, postweaning survival [winter survival in temperate species (e.g. 29)]; YS, yearling survival (survival probability between 1 and 2 years); PAS, prime-age adult survival [yearly survival between 2 and 7 years in small- and medium-sized species like Soay sheep (22), roe deer (64), or bighorn sheep (87); between 2 and 12 years in red deer (SD Albon, personal communication)]; SS, senescent survival [yearly survival of females older than a threshold age (7 or 10 years)]; FP, fecundity of yearling females [product of average litter size and proportion of females pregnant; differs from 0 in only a few medium-sized species like white-tailed deer or mule deer (117)]; FY, fecundity of young females [2-year-olds in most cases; in large species, primiparity is at 3 or 4 years or even older (e.g. see 56)]; FA, fecundity of prime-aged females; FS, fecundity of senescent females.

temporal variation. Finally, we propose that there may be a trade-off between the potential importance of a fitness component for changing population growth rate and its observed temporal variation: Those fitness components with the greatest potential impact on population growth rate tend to have the least temporal variability.

Populations of large herbivores display four major types of temporal variation. First, in seasonal habitats, there is predictable environmental variation over each year. Second, year-to-year fluctuations in climate lead to unpredictable, sometimes marked environmental variation. Third, density-dependent responses occur when populations overshoot a threshold density (58). Fourth, changes in abundance or in behavior of predators, prevalence of diseases, or human activities may produce environmental variation. Consequently, temporal variation should play a prominent role in the population dynamics of large herbivores (67, 156), contrary to the simplistic approach that downplays environmental stochasticity for long-lived species. Considerable progress has been made during the last 10 years to better understand demography in stochastic environments (178, 179) and to account for environmental variation, which has been shown to strongly affect estimates of population growth (178) and fitness of various life history strategies (135). It has also been suggested that, for large populations, the extinction risk from demographic stochasticity may be less important than the risk from environmental stochasticity (97), although reliable empirical data are lacking for large herbivores. Therefore, the effects of temporal variation on population dynamics are likely to have strong fundamental and applied implications.

OVERVIEW OF POPULATION DYNAMICS OF LARGE HERBIVORES

Covariation of Body Size, Lifespan, and Iteroparity

Large herbivores are among the heaviest mammals, ranging from <10 to >1000 kg [we excluded species exceeding 800 kg, because their population dynamics may differ from those of smaller species (136) and there is very little information on temporal variation of their fitness components]. Thus, the strong allometric relationships commonly found for most life history traits (144) lead large herbivores to show low fecundity and high adult survivorship (190), with only one or two offspring produced once per year (81) over a potential female lifespan exceeding 15 years (108). Large herbivores have generation times of >4 years (125) and low adult turnover (125). They are strongly iteroparous (69): Females generally reproduce >5 times (12, 13, 20, 29), and a few individuals may reproduce 15 times during a lifetime (63). Only suids deviate from this general model by having large litters (43) and short generation times, at least in heavily hunted populations (71). But because they are omnivores, we exclude suids from our review.

A Life Cycle Graph for Large Herbivores

Populations of large herbivores are strongly age- and sex-structured. In most species, a polygynous mating system leads to pronounced sexual size dimorphism (109), which correlates with marked sexual differences in life history traits (29). In particular, male survival is typically lower than female survival at all ages (29). Age has very strong effects on both reproduction and survival (Figure 1). Large herbivores fit Caughley's model of a dome-shaped age-dependent survival rate (23), with clearly identifiable juvenile (pre- and postweaning), prime-age (adults), and senescent (old adults) stages (64, 87). Here we refer to prime-aged females as those in age classes before the onset of survival senescence [often from 2 to 7–8 years (108)]. Juvenile survival can be subdivided into a preweaning component, during which mortality is mostly dependent on maternal care, and a postweaning component, when most mortality is care independent (66, 111). Yearling survival (from 1 to 2 years of age) is often lower and more variable than survival of prime-aged adults (29, 87) and therefore must be considered separately. Age-related variation in fecundity and litter size is also common, although it is often less pronounced than variation in survival (45). Primiparity is generally at 2 or 3 years, but in some small- or medium-sized species, females can breed during their first year (117). After first reproduction in most species, females attempt to reproduce every year, but in some populations females will not conceive for 1–2 years after weaning an offspring (92, 130, 176). In most ecosystems, births are highly synchronous (155), timed to maximize offspring survival by reducing predation risk (61) and synchronized with seasonal differences in vegetation quality or availability (52, 153).

Demographic Patterns of Populations of Large Herbivores

Populations of large herbivores have low growth rates (16), but compared with other vertebrates, they have high maximum population growth rates relative to their body size. Thus, monotocous species (those with a fixed litter size of one) like horses, red deer, or muskox may reach finite rates of increase (λ) of 1.25 to 1.35 (113, 148, 198), whereas polytocous species (with variable litter size and generally between 1 and 3 offspring per litter) like white-tailed deer may have $\lambda > 1.5$ (181). High potential population growth allows large herbivores to rapidly exploit areas where they may be introduced (24).

Demographic analyses reveal that the elasticity of adult survival is at least three-fold higher than that of juvenile survival or of fecundity rates (48, 83, 132, 187). Elasticity measures relative sensitivity, which can be defined as the effect on population growth rate of a proportional change in a given fitness component (39). Therefore, a proportional change in a fitness component with high elasticity will have a greater effect on population growth rate than the same change in a fitness component with low elasticity. Thus, the population growth rate of large

herbivores is much more sensitive to a given relative variation in adult survival than to the same relative variation in any other fitness component.

Temporal variation in abundance of large herbivores can have widely different sources, including density- and climate-dependent food limitation or control by humans, predation, and disease. Density-independent limitation (165) and density-dependent regulation (165) co-occur in most populations (115, 165), so that the impact on population growth of density-independent factors such as bad weather typically increases with population density (127, 146).

HOW AND WHY FITNESS COMPONENTS OF POPULATIONS OF LARGE HERBIVORES VARY OVER TIME

Heterogeneity of Data Type and Statistical Analyses: A Methodological Caveat

Ideally, our review should have included only studies based on long-term monitoring of individually recognizable animals, analyzed with methods that account for differences in recapture probability, because those studies minimize errors in estimates of fitness components and reduce the risk of sampling bias. Currently, however, only a handful of studies fit those criteria.

We included studies lasting ≥ 3 years and providing yearly estimates of at least one fitness component (see supplemental appendix at <http://www.annurev.org>). We thus faced considerable heterogeneity of data quality and statistical analyses. As a result, it was not always possible to transform the results of different studies into the fitness components defined in Figure 1. Standardized information on juvenile survival and fecundity rates was particularly difficult to extract from the literature. Several studies reported age ratios such as young:female or young:adult female. These ratios are of limited usefulness (116) because they combine juvenile survival and fecundity rate and ignore changes in female age structure. We thus analyzed age ratios separately. Studies also used widely different techniques to estimate fitness components, especially for survival. The quality of the data was highest for studies that monitored individually marked animals of known age and estimated survival by accounting for differences in detection probability of marked animals (49 of 141 studies). When juvenile and yearling survival rates were analyzed separately by sex, we used female survival. Studies based on comparing age ratios in successive years (59 of 141 studies) were of the lowest quality. Survival rates extracted from count ratios are affected by large sampling errors, partly because ratios can change after changes in either the numerator or the denominator. For example, a change in the juvenile:adult ratio could be due to changes in survival (or in sightability) of adults or of juveniles (116).

Temporal Variation in Survival

Prewearing Survival (Immature Stage 1) Most estimates of preweaning survival were based on individually marked newborns. Therefore, data quality was good [28 estimates were of high quality vs 9 of low quality (see supplemental appendix at <http://www.annurev.org>)]. Prewearing survival is generally low (mean of 0.638, $N = 46$) and varies markedly over time (CV of 0.265, $N = 39$) in most populations (Figure 2) in response to a great diversity of proximal factors. Most preweaning mortality occurs within 1 month of birth (2, 20, 76, 96, 129). It is likely that several studies overestimated preweaning survival, because unless all juveniles are caught and marked immediately after birth, some preweaning deaths, especially of neonates, will not be detected by researchers.

Survival to weaning is generally dependent on maternal care, especially when predation on neonates is not a major source of mortality. Thus, maternal attributes

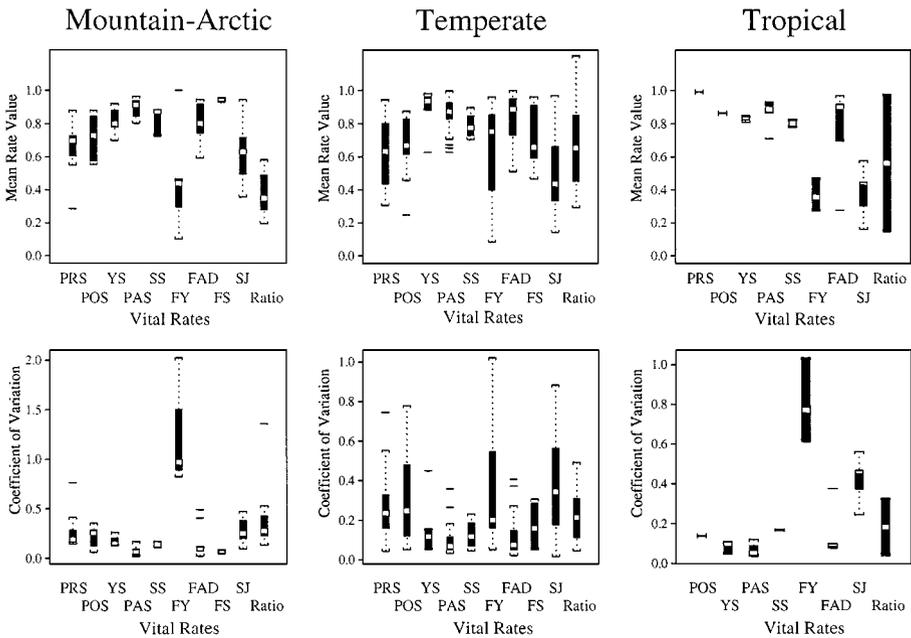


Figure 2 Temporal variation in fitness components of large herbivores. Each box-plot shows, for the mean yearly estimates and their coefficients of variation in a given population for a given ecosystem type (Mountain-Arctic, Temperate, and Tropical), the interquartile (25%–75%) range (given by the *filled box*), 1.5 times this range (*brackets*), the median (*white bar*) and the “outliers” (*horizontal bars*). Note that the scale for CVs for mountain ungulates is different from the others. PRS, preweaning survival; POS, postweaning survival; YS, yearling survival; PAS, yearly survival of prime-age adults; SS, yearly survival of old adults; FY, fecundity of young females; FAD, fecundity of prime-age adults; FS, fecundity of old females; SJ, juvenile survival; Ratio, calf:cow ratio.

such as age (3, 55, 76, 90, 96), size (21, 96, 168), reproductive experience (95, 139, 149), dominance status (31, 106), previous reproductive status (31, 53), or the size of female kin groups (138) can have strong effects on preweaning survival. Generally, the reproductive success of large multiparous prime-aged females of high social rank is much less affected by environmental conditions than is that of small, primiparous, and young females of low social rank.

Weather during gestation can affect preweaning survival. In temperate species, high snowfall and long duration of snow cover during the previous winter often reduce preweaning survival, likely by affecting maternal nutrition during late gestation (2, 114). Likewise, the amounts of precipitation during parturition and lactation cause preweaning survival to vary over years, especially for polytocous species (19, 65, 91) and at high density for monotocous species (146). Weather generally affects early survival by changing the availability of high-quality forage (19); direct effects of adverse weather on survival are exceptional (126). The strong positive correlation between preweaning survival, maternal condition, and weather during gestation and lactation is likely due to the importance of birth weight for early survival, an effect that tends to become stronger with adverse weather or high population density (3, 7, 33, 50, 65, 76, 100, 157, 171, 177). High forage quality and quantity often increase preweaning survival of large herbivores (131, 152, 197), possibly by improving milk quality (197).

Malnutrition appears to be a major cause of early mortality during some years (151) and, in extreme cases, may lead females to abandon their offspring (99). Malnutrition can also predispose juveniles to other sources of mortality. In particular, the transfer of passive immunity to newborns may be compromised at high population density (157).

Density dependence in preweaning survival has been reported in many large herbivores (26, 33, 65, 114, 120, 166), but preweaning survival of red deer (31), reindeer (171), and bighorn sheep (146) did not decrease with increasing density. Preweaning survival may therefore be more sensitive to population density in polytocous species that have a high energy expenditure per breeding attempt than in monotocous species (65).

Where predators are present, predation is often the main source of early mortality (105), and preweaning survival is generally <50% (47) and can be as low as 1% (20). Predation risk, however, is not always independent of maternal care. Maternal experience can decrease fawn vulnerability to predators (20, 139). The timing of birth may also account for temporal variation in preweaning survival. Late birth dates often lower survival in temperate ungulates (31, 33, 52) by shortening the period for access to growing forage. In the presence of predators, caribou calves born during the birth peak may enjoy higher survival than those born earlier or later (2). Finally, parasites (107), disease (126), and high levels of inbreeding (102, 162) may reduce preweaning survival to 10% in some years. Because all of these factors may vary spatially within a population in a given year, spatial heterogeneities in preweaning survival are expected to occur and have been found in pronghorn (50) and caribou (195), but not in red deer (76).

Postweaning Survival (Immature Stage 2) The data available to assess temporal variation in survival from weaning to 1 year include a narrower range of species than those available for preweaning survival. Similar to preweaning survival, data quality was good [20 estimates of high quality vs 7 of low quality (see supplemental appendix at <http://www.annurev.org>)]. Postweaning survival varied widely from year to year in most populations [mean of 0.697, $N = 30$; CV of 0.279, $N = 26$ (Figure 2)], but fewer factors were reported to affect postweaning survival than preweaning survival. Most reported causes of postweaning mortality, such as winter severity and density dependence, were care independent, and the proximate cause of mortality was usually starvation. Negative effects of severe winters have been reported for several temperate species (62, 78, 101, 166), but muskoxen seem to be highly resistant to deep snow and ice, at least in colonizing populations (86). Density dependence in postweaning survival was reported in several species (11, 31, 33, 85, 146, 166, 171) and appears to be more common in postweaning than in preweaning survival for monotocous species. Bartmann et al (11) provided the best experimental demonstration of density dependence in juvenile survival: By allowing density of mule deer to increase from 44 to 133 per km², they caused postweaning survival to decrease from 0.456 to 0.176. Predation (11) and late birth (166) can decrease postweaning survival in some years. Other factors, such as spring weather (161), birth weight (33), and maternal dominance status (31) may affect postweaning survival, but appear to be less important than for preweaning survival.

Because many studies did not distinguish pre- and postweaning survival, we examined overall variation in first-year survival. Data quality was reasonable [21 estimates of high quality vs 19 of low quality (see supplemental appendix at <http://www.annurev.org>)]. Juvenile survival displayed wide yearly variations in most populations [mean of 0.518, $N = 51$; CV of 0.346, $N = 43$ (Figure 2)]. Predation (41, 49, 73, 159, 180, 192), population density (89, 137, 160, 167, 174, 175, 189, 191), winter severity (9, 110, 146, 148, 159, 167, 192), weather affecting food supply during lactation (49, 137, 172, 189), genotype (143), and care-dependent factors such as birth weight (192), nursing time (160), or mother aggressiveness (159) affect juvenile survival. Therefore, juvenile survival is highly variable within and among populations of large herbivores (67).

Yearling Survival (Immature Stage 3) Because most studies did not estimate yearling survival separately from adult survival, there is a limited amount of reliable information [10 estimates of high quality vs 3 of low quality (see supplemental appendix at <http://www.annurev.org>)] on temporal variation for this fitness component. Yearling survival showed the same patterns of variation as postweaning survival, but the mean was higher and the variability was lower [mean of 0.872, $N = 16$; CV of 0.124, $N = 14$ (Figure 2)]. Population density (31, 33, 87, 164), adverse weather (137, 148, 175, but see 86), predation (73), and disease (164, 175) accounted for most yearly variation in yearling survival in the absence of hunting.

Adult Female Survival (Prime-Age Stage) Estimates of adult female survival are generally based on high-quality data involving long-term monitoring of recognizable individuals [28 estimates of high quality vs 19 of low quality (see supplemental appendix at <http://www.annurev.org>)]. The data reveal a striking and consistent pattern of high survivorship and very low yearly variation regardless of the sources of mortality [mean of 0.874, $N = 57$; CV of 0.087, $N = 48$ (Figure 2)].

We found very limited evidence of density dependence in adult survival of large herbivores [in buffalo (120), caused by undernutrition and affecting mainly old animals, and in island populations of Soay sheep (34) and red deer (30), although in both cases senescent animals were included in the estimate of female survival]. Stable adult survival despite wide changes in density has been reported in many species (35, 42, 68, 87, 191).

Adult survival also appears to be partly buffered against environmental sources of variation. Although winter severity (124, 128, 140, 161), adverse spring weather (161), severity of dry season (60), or severe overgrazing of the summer range (57) can decrease adult survival in some species, the survival of adult females was not correlated with any variable in roe deer (68) and was not affected by forage availability in bison (184), by severe drought in greater kudu (137), by food limitation in reindeer (167), by climate in red deer (110), moose (9), mule deer (94), and pronghorn (10), or by pneumonia in chamois (27). Disease may affect survival of adult ungulates, but there is limited evidence from long-term studies. For example, pneumonia epizootics had moderate and short-lived effects on survival of adult female bighorn sheep (87) and mouflon (36). Where large predators occur, they often account for much of the variation in adult survival, typically causing >50% of yearly mortality (73, 126, 164, 188, 194).

It appears that moderate or high levels of temporal variation in adult-female survival are mostly associated with rare events, such as epizootics of exotic diseases and high predation risk due to individual specialist predators or “predator-pit” situations, in which high levels of predation on a preferred but declining prey species can be sustained because of the availability of alternative prey species (73). In large herbivores, the stability of adult female survival relative to other fitness components may reflect a strategy of risk minimization involving a reduction of the maternal expenditure before any serious deterioration of female condition (5, 54, 82, 154).

Old Adult Female Survival (Senescent Stage) In most species of large herbivores, the ages of live females can be estimated reliably only in animals < 3 years old. Consequently, temporal variation in survival of old females can be measured only by very long-term monitoring: Typically, ≥ 10 years are required before known-age “old” females can be monitored. Very few studies have considered separately the survival of old and prime-age females, but available data were of very high quality [six estimates of high quality vs one of low quality (see supplemental appendix at <http://www.annurev.org>)]. Compared with prime-age

females, old females have lower survival and are more sensitive to environmental variation [mean of 0.811, $N = 9$; CV of 0.164, $N = 8$ (Figure 2)], possibly because of tooth wear (64, 169). Old females are more affected than prime-age females by die-offs in nyala (6), rainfall variation in greater kudu (137), and variation in food availability in reindeer (169). It has recently become evident that individual heterogeneity plays a large role in survival to old age; life expectancy is greater for larger than for smaller prime-aged females (15, 66). Failure to distinguish age classes and the widespread occurrence of survival senescence may also bias the interpretation of reported density dependence in adult survival, as unmanaged high-density populations typically include a high proportion of older females.

Temporal Variation in Reproductive Traits

Fecundity of Young Females Reproductive patterns of large mammals are easier to measure than are patterns of survivorship. Therefore, we found abundant data of high quality on temporal variation in fecundity of young females, defined as those of the youngest age at which $\geq 10\%$ of females were primiparous in a given population. Fecundity of young females is highly variable both within and among populations (8, 120, 163) and is more sensitive to adverse environmental conditions than adult fecundity in both temperate (25) and tropical (196) ungulates [mean of 0.519, $N = 32$; CV of 0.612, $N = 28$ (Figure 2)]. In populations of medium-sized species with abundant nutrition, however, the fecundity of young females can be as high and as stable from year to year as that of prime-age females (20, 63, 84). The main sources of variation in fecundity of young females are population density, weather, and food supply, especially in medium- to large-sized species. Density-dependent responses in age at primiparity have been reported in many large herbivores (25, 55, 59, 70, 85, 91, 120, 168). Female mass during the rut is often the proximate factor of variation in age at first breeding (77, 158, 170). A threshold mass must be reached before young females can reproduce (40, 51, 70, 85, 98), but in bighorn sheep, mass during the rut may play a limited role (88). Finally, adverse weather, such as drought (91) or severe winters (112), can lead to low fecundity of young females. Interpopulation variability in age of primiparity is often caused by differences in nutrition of young females, which can be independent of population density or weather. Thus, some populations in poor habitats may be characterized by late primiparity [e.g. 4–5 years instead of 2 for mountain goats (56)].

Fecundity of Prime-Age Females Many studies provide measurements of temporal variation in fecundity of prime-age females. Unfortunately, however, most studies pool prime-age and old adult females, leading to underestimation of mean values and overestimation of the magnitude of variation. The importance of these biases should depend on the proportion of old females included in the sample, and most studies did not provide that information. As previously mentioned, for most species it is impossible to know the exact age of females first marked as adults.

Fertility of prime-aged females is generally high and varies little from year to year [mean of 0.818, $N = 59$; CV of 0.125, $N = 51$ (Figure 2)]. Density dependence in adult fecundity has been reported in several species, although density effects are generally less evident than for age of primiparity (28, 85, 91, 93, 163, 184). Other species, however, show either a weak (53) or no decline of adult fecundity despite very high population densities (59, 70, 141, 147, 168). Skogland (168) suggested that the fecundity of migratory populations should be less sensitive to environmental variation than that of sedentary populations. Migratory populations of wildebeest, caribou, and elk do show stable fecundity of prime-aged females, but constant adult fecundity has also been reported in sedentary populations of roe deer (70) and fallow deer (147), indicating that adult fecundity of most large herbivores is resilient to a wide variety of environmental conditions and may be a species-specific life history trait. Studies of moose (18), pronghorn (20), and gazelles (8) confirm the high resilience of adult fecundity in ungulates. The limited density-independent, year-to-year variation in adult fecundity usually originates from yearly variation in weather such as March temperature (90), winter and spring precipitation (184), winter severity causing high fetal mortality (10), rainfall (14, 91), or snow depth and summer temperature (37). Body mass may affect adult fecundity (21, 84, 193), and poor nutrition may depress it (1, 150, 163). Body mass and population density can have an interactive effect, so that females of a given mass are less likely to conceive at high than at low population density (5), suggesting a reproductive strategy that minimizes risks to the mother. In some species, individual females may not reproduce in some years, particularly after having weaned an offspring (32, 92, 154).

Fecundity of Old Females Very few studies have investigated variation in fecundity of old females. Similar to what we found for survival, fecundity of old females is lower and more variable than that of prime-age females [mean of 0.783, $N = 7$; CV of 0.134, $N = 6$ (Figure 2)], suggesting reproductive senescence. However, reproductive senescence appears to be less precipitous and to have a later onset than survival senescence (72). Successful reproduction by all but the very oldest females has been reported in medium-sized species (15, 63, 133).

Litter Size In polytocous species, year-to-year variation in litter size is moderate for primiparous females (mean of 1.267, $N = 12$; CV of 0.164, $N = 10$), low for multiparous females (mean of 1.569, $N = 27$; CV of 0.092, $N = 26$), and mostly associated with female nutrition. For captive white-tailed deer, litter size increased from 1.11 for does on a low nutritional plane to 1.96 for those on a high nutritional plane (185). Both winter severity (121) and population density (84, 186) shape yearly variation in litter size by affecting female body mass. In moose, the largest polytocous species, twinning rates are the most variable component of fecundity and may be a sensitive indicator of habitat quality (18). Conversely, in populations of medium-sized species with abundant food, litter size may be fixed and independent of female age (20, 63).

DO TAXONOMY, PHYLOGENY, ECOSYSTEM, AND BODY SIZE AFFECT VARIATION IN POPULATION DYNAMICS OF LARGE HERBIVORES?

Temporal Variation in Fitness Components and Taxonomy: Cervids vs Bovids

Large herbivores include two major families within the order Artiodactyla: cervids and bovids. The mean duration of studies included in our survey did not differ significantly between these groups (7.5 years for cervids and 8.6 years for bovids, $P = 0.38$). Although both yearling survival and litter size of primiparous females are greater for cervids than for bovids, mean estimates of fitness components are generally close (Table 1). In both families, survivorship of yearlings, adults, and old individuals is higher than that of juveniles, while fecundity and litter size of prime-aged females are higher than those of young females (Table 1). Bovids and cervids also display the same patterns of temporal variation in fitness components, with no significant difference between groups (Table 1).

Allometric Component of Temporal Variation in Fitness Components

Allometric relationships are widespread among vertebrates (144), and we expected that body size would have a marked effect on population dynamics of large herbivores. Surprisingly, however, variation in adult mass explained little of the variation in either mean estimates ($r = 0.14$, $P = 0.53$ for prime-age survival; $r = 0.21$, $P = 0.31$ for juvenile survival; $r = -0.26$, $P = 0.24$ for fecundity of adult females; $r = -0.55$, $P = 0.05$ for fecundity of young females; Figures 3A and 3B) or temporal variation ($r = -0.04$, $P = 0.87$ for prime-age survival; $r = -0.31$, $P = 0.14$ for juvenile survival; $r = 0.40$, $P = 0.06$ for fecundity of adult females; $r = 0.48$, $P = 0.10$ for fecundity of young females; Figures 3C and 3D) of fitness components. We obtained similar results when we accounted for nonindependence of traits of related species due to phylogenetic inertia (75), using the independent contrasts method (79; Figure 3), by a taxonomy-based phylogeny (see 142 for further details). In particular, prime age ($r = -0.12$, $P = 0.60$) and juvenile survival ($r = 0.08$, $P = 0.70$), as well as their temporal variation ($r = 0.07$, $P = 0.74$ for prime-age survival; $r = -0.07$, $P = 0.74$ for juvenile survival) appeared to be independent of body mass (Figure 3A–C). On the other hand, there may be an allometric constraint on fecundity, especially for primiparous females, as longer development with increasing size prolongs the period before maturation. The progressive decrease in mean value ($r = -0.59$, $P = 0.04$; Figure 3B) and increase in variation ($r = 0.63$, $P = 0.02$; Figure 3D) of fecundity of young females as body mass increases support this allometric interpretation. A similar pattern occurs for prime-age fecundity ($r = 0.23$, $P = 0.30$; Figure 3D), suggesting that temporal variation in recruitment rates increases with adult body mass.

TABLE 1 Mean estimates (SE) and coefficients of variation (SE) of fitness components for cervids and bovids^a

Fitness Component	Mean Estimate for Bovids (SE)	Mean Estimate for Cervids (SE)	P-Value	Mean CV for Bovids (SE)	Mean CV for Cervids (SE)	P-Value
Preweaning survival	0.749 (0.084)	0.622 (0.031)	0.110	0.274 (0.098)	0.254 (0.030)	0.797
Postweaning survival	0.676 (0.048)	0.708 (0.032)	0.640	0.296 (0.066)	0.282 (0.048)	0.881
Yearling survival	0.829 (0.021)	0.929 (0.022)	0.009	0.143 (0.027)	0.095 (0.019)	0.209
Prime-aged female survival	<i>0.895 (0.013)</i>	<i>0.855 (0.015)</i>	<i>0.076</i>	0.073 (0.008)	0.094 (0.013)	0.298
Senescent-female survival	0.825 (0.025)	0.794 (0.039)	0.498	0.178 (0.026)	0.140 (0.054)	0.504
Fecundity of young females	0.495 (0.077)	0.539 (0.076)	0.712	0.693 (0.186)	0.578 (0.084)	0.526
Fecundity of adult females	0.834 (0.048)	0.851 (0.021)	0.696	0.160 (0.043)	0.101 (0.014)	0.108
Fecundity of old females	0.944 (0.013)	0.781 (0.092)	0.307	0.065 (0.021)	0.123 (0.073)	0.584
Litter size of primumparous females	1.119 (0.041)	1.372 (0.085)	0.04	0.135 (0.044)	0.183 (0.055)	0.555
Litter size of multiparous females	1.624 (0.137)	1.559 (0.057)	0.633	0.098 (0.044)	0.091 (0.012)	0.834
Calf:cow ratio	<i>0.411 (0.077)</i>	<i>0.596 (0.060)</i>	<i>0.069</i>	0.400 (0.114)	0.245 (0.027)	0.109
Juvenile survival	0.547 (0.041)	0.492 (0.039)	0.338	0.304 (0.033)	0.393 (0.052)	0.283

^aP values were obtained from one-way ANOVAs for each of the 12 fitness components surveyed in this review. Fitness components with significant between-group differences are shown in bold, and those with marginally significant between-group differences are in italics. CV, Coefficient of variation.

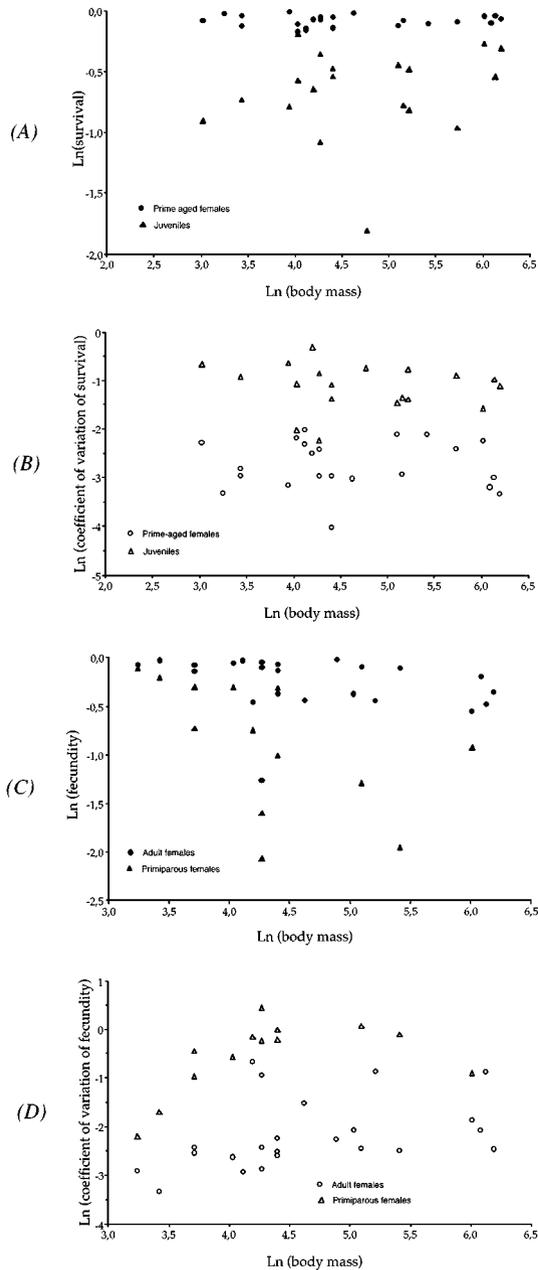


Figure 3 Allometric relationships between adult body mass of ungulate females and (A) mean log-transformed estimates of prime-age and juvenile survival, (B) log-transformed coefficients of variation of prime-age and juvenile survival, (C) mean log-transformed estimates of fecundity for adult and young females, and (D) log-transformed coefficients of variation of fecundity for adult and young females. For species with data from more than one population, the points indicate the median for each fitness component.

Temporal Variation in Fitness Components in Different Ecosystems: the Role of Seasonality and of Cover

Large herbivores in our survey have been studied in three major ecosystem types: mountains and the arctic, temperate lowlands, and tropical areas. Despite marked differences in climate and primary production, populations of large herbivores show roughly similar demographic profiles and the same patterns of temporal variation in fitness components in all ecosystems. In most populations, survival and fecundity of prime-age adults are high and constant over time, whereas juvenile survival and fecundity of young females are low and highly variable over time (Figure 2). In each ecosystem type, populations were studied in a wide range of ecological conditions, including considerable variation in food availability, population density, and predation pressure. However, there were no obvious between-ecosystem differences in temporal variation in fitness components. On the other hand, the amount of maternal energy allocated to reproduction seems to affect both magnitude and temporal variation of early survival. In temperate ecosystems, where most polytocous species occurred (81), they tended to show both lower (mean of 0.594, SE = 0.038, $N = 22$ after excluding moose and Soay sheep, whose twinning frequencies vary widely from year to year) and more variable (CV of 0.288, SE = 0.040, $N = 20$) preweaning survival than monotocous species (mean of 0.728, SE = 0.038, $N = 8$; and CV of 0.155, SE = 0.025, $N = 7$; $P = 0.10$ and 0.07 for mean and CV, respectively).

IDENTIFYING THE CRITICAL COMPONENTS OF POPULATION DYNAMICS OF LARGE HERBIVORES

Elasticity and Temporal Variability in Fitness Components: Is There a Trade-off?

The demography and population dynamics of large herbivores can be summarized as follows: Recruitment parameters (juvenile survival and some measures of fecundity) combine low elasticity with high temporal variability, whereas adult survival has the highest elasticity and the lowest temporal variability. It is important that these age-related differences in temporal variability occur regardless of whether the source of variation is stochastic (67) or density dependent (44); as we have previously reported (67), the fitness components that are more susceptible to stochastic effects are also more likely to show density dependence. These observations suggest that, in ungulates, there may be a trade-off between the potential importance of a fitness component for changing population growth rate (its elasticity) and the degree of observed temporal variation of that fitness component (its coefficient of variation). It has been suggested that a similar trade-off may also occur in other organisms (145). The resilience of adult survival to environmental variation may be an example of canalization (see 173) of a trait with a very strong influence on fitness.

The relative importance of a fitness component for changes in population growth rate depends on both its elasticity and its temporal variation; a trait such as adult survival with high elasticity but little variability may not have a greater importance in determining changes in population growth rate than a trait such as juvenile survival with low elasticity but high variability. If there was a trade-off between elasticity and temporal variation, then juvenile and adult survival could explain similar amounts of the observed variation in population growth rate. To assess this possibility, we considered three age classes of large herbivores: immature (before the minimum age of primiparity), prime age (from the age of primiparity to the onset of survival senescence), and old, and compared their contribution to temporal variation in population growth rates. We then developed a simple model based on recent developments of demography in stochastic environments (178, 179) and applied it to populations of large herbivores for which temporal variation of all fitness components had been measured.

Temporal Variation Makes the Difference

From five populations, the immature stage accounted for more of the observed variation in growth rate [from 51% to 94% (Table 2)] than either the prime-age or the old stage. For bighorn sheep and roe deer, long-term data were available for two populations. Those studies suggest that the importance of the immature stage for population growth rate may increase with environmental harshness; the

TABLE 2 Proportion of the total variation in population growth rate accounted for by the main life history stages (immature, prime-age, and old) in five populations of large herbivores monitored for > 16 years^a

Population	Species	Proportion (%) of Population Growth Rate (Accounted for) by Life Stage		
		Immature	Prime-age	Old
Ram Mountain	Bighorn sheep	69	13	18
Sheep River	Bighorn sheep	55	22	23
Chizé	Roe deer	94	5	1
Trois Fontaines	Roe deer	73	19	7
Rum	Red deer	51	44	4

^aTemporal variation in the population growth rate can be expressed as the summation of the products of squared elasticities and squared coefficient of variation of fitness components (179). Total variation in population growth rate was thus calculated as $[e^2(PRS) \times CV^2(PRS)] + [e^2(POS) \times CV^2(POS)] + [e^2(YS) \times CV^2(YS)] + [e^2(PAS) \times CV^2(PAS)] + [e^2(SS) \times CV^2(SS)] + [e^2(FY) \times CV^2(FY)] + [e^2(FAD) \times CV^2(FAD)] + [e^2(FS) \times CV^2(FS)] + [e^2(LSP) \times CV^2(LSP)] + [e^2(LSM) \times CV^2(LSM)]$, where e is the elasticity, CV is the coefficient of variation, PRS is the preweaning survival, POS is the postweaning survival, YS is the yearling survival, PAS is the yearly survival of prime-aged females, SS is the yearly survival of old adults, FY is the fecundity of young females, FAD is the fecundity of prime-aged females, FS is the fecundity of old females, LSP is the litter size of primiparous females, and LSM is the litter size of multiparous females. The contribution of each life history stage was calculated as the proportion of total variation in growth rate of a given population that was explained by that stage. (Note: the numbers represent % that sum to 100% for a given population).

contribution of this stage was higher for populations at Ram Mountain (bighorn sheep) and at Chizé (roe deer), both of which showed strong density dependence, than in the more productive populations at Sheep River (bighorn sheep) and Trois Fontaines (roe deer). Although the relative effects of elasticity and temporal variation on ungulate population dynamics have not been previously assessed, most studies suggest an overwhelming importance of the juvenile stage in accounting for between-year variation in population growth rate (32, 35, 80, 106, 123, 183). Exceptions to this pattern may include hunted populations of moose (17), declining populations of caribou (38), and ungulates in Etosha National Park (74), where hunting and predation led to high adult mortality. Elsewhere, we found remarkably similar patterns of variation, despite including in our review populations with (55) and without predators (65) and populations that were introduced or reintroduced (29, 36), feral (34), and semidomestic (7). Because the low elasticity of fitness components during the immature stage is more than compensated for by large temporal variation, for most populations of large herbivores, the immature stage is the critical component of population growth. Therefore, we conclude that temporal variation makes the difference.

PERSPECTIVES

Large herbivores have high economic value; they are often an important source of revenue through sport hunting and ecotourism but can also be agricultural pests or major traffic hazards (119). Consequently, the population dynamics of large herbivores have been the subject of considerable research, and fitness components have been measured in many populations and species. Although new technologies and recent progress in estimation procedures have improved the quality of available data, some problems persist.

Cohort Effects Lead to Interdependence Among Life-History Stages

Contrary to the assumptions of current demographic models, successive life history stages are not independent. Factors affecting fitness components during a cohort's early development may have delayed effects on that cohort's performance later in life (103). Long-term "quality effects" (65) are likely to be pervasive in populations of large herbivores (4, 65, 122, 171, 182) and may lead to an underestimation of the importance of the immature stage in shaping population dynamics.

Partitioning Biological Variability and Sampling Variability

In this review, we did not account for sampling errors that inevitably occur in the estimation of fitness components. The confusion of temporal and sampling variation may bias the assessment of temporal variation and decrease the reliability of comparisons between fitness components (104). To our knowledge, only a study

of mule deer reported temporal variation in fitness components after correcting for sampling variation (11). We recommend that future studies attempt to assess more accurately the role of temporal variation in ungulate population dynamics. The available data, however, suggest that the importance of sampling variability is likely greater for adult than for juvenile survival (67). Therefore, if sampling variation were accounted for, the difference in temporal variation between adult and juvenile survival that we reported here would be reinforced.

Data Quality, Modeling, and Population Dynamics: Where Do We Go from Here? More than 20 years ago, Eberhardt (44) suggested that, in marine mammals, an increase of population density would affect fitness components in a predictable order: first juvenile survival, then fecundity of young females, then fecundity of adult females, and last, adult survival. Based on terrestrial large herbivores, our review supports Eberhardt's hypothesis and generalizes it to all sources of temporal variation. For herbivores larger than 50 kg, however, fecundity of young females rather than juvenile survival may be the fitness component most sensitive to environmental perturbations. The production of more realistic and useful population models will require the integration of long-term cohort effects and the partitioning of temporal and sampling variation. It is clear, however, that the greatest obstacle to better understanding the population dynamics of large herbivores is the scarcity of data from long-term field studies of marked individuals. The limited amount of information limits our ability to use a scientific approach for the conservation and management of these ecologically, economically, and socially important animals. A glance at the studies included in our review shows that studies of tropical large herbivores are particularly scarce, as are studies in ecosystems with intact populations of large carnivores. We also found virtually no useful information on kangaroos and wallabies. More than 10 years ago, McNaughton & Georgiadis (118) pointed out that there was a limited amount of data available on population dynamics for the >90 species of large African herbivores. From both a fundamental and an applied viewpoint, the major challenges to improving our knowledge of populations of large herbivores are associated with field ecology. Because studies of large mammals are often costly, require large study areas, and may affect stakeholders such as hunters, farmers, and recreationists, we suggest that increased cooperation between universities and government agencies is required to fully realize the potential of long-term monitoring of marked individuals.

ACKNOWLEDGMENTS

We are grateful to Steve Albon, Mark Boyce, John Byers, Patrick Duncan, Lee Eberhardt, John Fryxell, Stephen Hall, Mark Hewison, Rolf Ims, Jean-Dominique Lebreton, Jim Nichols, Norman Owen-Smith, Dominique Pontier, Bernt-Erik Sæther, and Nils Christian Stenseth for original ideas or comments on previous drafts or for providing us with unpublished data. Financial support was provided by the Programme International de Collaboration Scientifique No. 835 of the Centre

National de Recherche Scientifique (JMG, AL, and NGY) and by the Office National de la Chasse (JMG, AL, and CT). MFB acknowledges the support of the Natural Sciences and Engineering Research Council of Canada; the Alberta Recreation, Parks and Wildlife Fund; the fonds FCAR (Québec); the Foundation for North American Wild Sheep; and the Alberta Conservation Association.

Visit the Annual Reviews home page at www.AnnualReviews.org

LITERATURE CITED

1. Adamczewski JZ, Flood PF, Gunn A. 1997. Seasonal patterns in body composition and reproduction of female muskoxen (*Ovibos moschatus*). *J. Zool.* 241:245–69
2. Adams LG, Singer FJ, Dale BW. 1995. Caribou calf mortality in Denali National Park, Alaska. *J. Wildl. Manage.* 59:584–94
3. Alados CL, Escos J. 1991. Phenotypic and genetic characteristics affecting lifetime reproductive success in female Cuvier's, dama and dorcas gazelles (*Gazella cuvieri*, *G. dama* and *G. dorcas*). *J. Zool.* 223:307–21
4. Albon SD, Clutton-Brock TH, Guinness FE. 1987. Early development and population dynamics in red deer. II. Density-independent effects of cohort variation. *J. Anim. Ecol.* 56:69–81
5. Albon SD, Mitchell B, Staines BW. 1983. Fertility and body weight in female red deer: a density-dependent relationship. *J. Anim. Ecol.* 52:969–80
6. Anderson JL. 1985. Condition and related mortality of nyala *Tragelaphus angasi* in Zululand, South Africa. *J. Zool.* 207:371–80
7. Asher GW, Adam JL. 1985. Reproduction of farmed red and fallow deer in northern New Zealand. *Bull. R. Soc. N.Z.* 22:217–24
8. Baharav D. 1983. Reproductive strategies in female Mountain and Dorcas gazelles (*Gazella gazella gazella* and *Gazella dorcas*). *J. Zool.* 200:445–53
9. Ballard WB, Miller SM, Whitman JS. 1986. Modeling a south-central Alaskan moose population. *Alces* 22:201–43
10. Barrett MW. 1982. Distribution, behavior, and mortality of pronghorns during a severe winter in Alberta. *J. Wildl. Manage.* 46:991–1002
11. Bartmann RM, White GC, Carpenter LH. 1992. Compensatory mortality in a Colorado mule deer population. *Wildl. Monogr.* 121:1–39
12. Berger J. 1986. *Wild Horses of the Great Basin. Social Competition and Population Size*. Chicago, IL: Univ. Chicago Press
13. Berger J, Cunningham C. 1994. *Bison: Mating and Conservation in Small Populations*. New York: Columbia Univ. Press
14. Berry HH. 1981. Population structure, mortality patterns and a predictive model for estimating future trends in wildebeest numbers in the Etosha National Park. *Madoqua* 12:255–66
15. Bérubé CH, Festa-Bianchet M, Jorgenson JT. 1999. Individual differences, longevity, and reproductive senescence in bighorn ewes. *Ecology* 80:2555–65
16. Blueweiss L, Fox H, Kudzma V, Nakashima D, Peters R, et al. 1978. Relationship between body size and some life history parameters. *Oecologia* 37:257–72
17. Boer AH. 1988. Moose, *Alces alces*, calf mortality in New Brunswick. *Can. Field Natl.* 102:74–75
18. Boer AH. 1992. Fecundity of North American moose (*Alces alces*): a review. *Alces Suppl.* 1:1–10
19. Boyce MS, Tate J. 1982. Pronghorn (*Antilocapra americana*) demography and hunting quotas in the Powder River Basin,

- Wyoming. *Trans. Int. Congr. Game Biol.* 14:101–6
20. Byers JA. 1997. *American Pronghorn. Social Adaptations and the Ghosts of Predators Past.* Chicago, IL: Univ. Chicago Press
 21. Cameron RD, Smith WT, Fancy SG, Gerhart KL, White RG. 1993. Calving success of female caribou in relation to body weight. *Can. J. Zool.* 71:480–86
 22. Catchpole EA, Morgan BJT, Freeman SN, Albon SD, Coulson TN. 1998. *An Integrated Analysis of Soay Sheep Survival Data. Rep. UKC/IMS/98/32.* Canterbury: Univ. Kent
 23. Caughley G. 1966. Mortality patterns in mammals. *Ecology* 47:906–18
 24. Caughley G. 1970. Eruption of ungulate populations, with emphasis on Himalayan tahr in New Zealand. *Ecology* 51:53–72
 25. Challies CN. 1985. Establishment, control, and commercial exploitation of wild deer in New Zealand. *Bull. R. Soc. N.Z.* 22:23–36
 26. Choquenot D. 1991. Density-dependent growth, body condition, and demography in feral donkeys: testing the food hypothesis. *Ecology* 72:805–13
 27. Clarke CMH, Henderson RJ. 1981. Natural regulation of a non-hunted chamois population. *N.Z. J. Ecol.* 4:126–27
 28. Clutton-Brock TH, Albon SD, Guinness FE. 1987. Interactions between population density and maternal characteristics affecting fecundity and juvenile survival in red deer. *J. Anim. Ecol.* 56:857–71
 29. Clutton-Brock TH, Guinness FE, Albon SD. 1982. *Red Deer: Behavior and Ecology of Two Sexes.* Chicago, IL: Univ. Chicago Press
 30. Clutton-Brock TH, Lonergan ME. 1994. Culling regimes and sex ratio biases in Highland red deer. *J. Appl. Ecol.* 31:521–27
 31. Clutton-Brock TH, Major M, Albon SD, Guinness FE. 1987. Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. *J. Anim. Ecol.* 56:53–64
 32. Clutton-Brock TH, Major M, Guinness FE. 1985. Population regulation in male and female red deer. *J. Anim. Ecol.* 54:831–46
 33. Clutton-Brock TH, Price OF, Albon SD, Jewell PA. 1991. Persistent instability and population regulation in Soay sheep. *J. Anim. Ecol.* 60:593–608
 34. Clutton-Brock TH, Price OF, Albon SD, Jewell PA. 1992. Early development and population fluctuations in Soay sheep. *J. Anim. Ecol.* 61:381–96
 35. Coughenour MB, Singer FJ. 1996. Elk population processes in Yellowstone National Park under the policy of natural regulation. *Ecol. Appl.* 6:573–93
 36. Cransac N, Hewison AJM, Gaillard JM, Cugnasse JM, Maublanc ML. 1997. Patterns of mouflon (*Ovis gmelini*) survival under moderate environmental conditions: effects of sex, age and epizootics. *Can. J. Zool.* 75:1867–75
 37. Crête M, Courtois R. 1997. Limiting factors might obscure population regulation of moose (Cervidae: *Alces alces*) in unproductive boreal forests. *J. Zool.* 242:765–81
 38. Crête M, Couturier S, Hearn BJ, Chubb TE. 1996. Relative contribution of decreased productivity and survival to recent changes in the demography trend of the Rivière George Caribou Herd. *Rangifer* 9:27–36
 39. de Kroon H, Plaisier A, van Groenendael J, Caswell H. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* 67:1427–31
 40. Duncan P. 1992. Horses and grasses: the nutritional ecology of equids and their impact on the Camargue. *Ecol. Stud.* New York: Springer. 87:272 pp.
 41. du Plessis SS. 1972. Ecology of blesbok with special reference to productivity. *Wildl. Monogr.* 30:1–71
 42. Dusek GL, Mackie RJ, Herriges JD, Compton BB. 1989. Population ecology of

- white-tailed deer along the lower Yellowstone River. *Wildl. Monogr.* 104:1–68
43. Dzieciolowski RM, Clarke CMH, Frampton CM. 1992. Reproductive characteristics of feral pigs in New Zealand. *Acta Theorol.* 37:259–70
44. Eberhardt LL. 1977. Optimal policies for conservation of large mammals with special reference to marine ecosystems. *Environ. Conserv.* 4:205–12
45. Eberhardt LL. 1985. Assessing the dynamics of wild populations. *J. Wildl. Manage.* 49:997–1012
46. Eberhardt LL. 1991. Models of ungulate population dynamics. *Rangifer* 7:24–29
47. Epstein MB, Feldhamer GA, Joyner RL. 1983. Predation on white-tailed deer fawns by bobcats, foxes, and alligators: predator assessment. *Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies, 37th*, pp. 161–72
48. Escos J, Alados CL, Emlen JM. 1994. Application of the stage-projection model with density-dependent fecundity to the population dynamics of Spanish ibex. *Can. J. Zool.* 72:731–37
49. Estes RD, Estes RK. 1979. The birth and survival of wildebeest calves. *Z. Tierpsychol.* 50:45–95
50. Fairbanks WS. 1993. Birthdate, birthweight, and survival in pronghorn fawns. *J. Mamm.* 74:129–35
51. Fandos P. 1989. Reproductive strategies in female Spanish ibex (*Capra pyrenaica*). *J. Zool.* 218:339–43
52. Festa-Bianchet M. 1988. Birthdate and survival in bighorn lambs (*Ovis canadensis*). *J. Zool.* 214:653–61
53. Festa-Bianchet M, Gaillard JM, Jorgenson JT. 1998. Mass and density-dependent reproductive success and reproductive costs in a capital breeder. *Am. Nat.* 152:367–79
54. Festa-Bianchet M, Jorgenson JT. 1998. Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. *Behav. Ecol.* 9:144–50
55. Festa-Bianchet M, Jorgenson JT, Lucherini M, Wishart WD. 1995. Life-history consequences of variation in age of primiparity in bighorn ewes. *Ecology* 76:871–81
56. Festa-Bianchet M, Urquhart M, Smith KG. 1994. Mountain goat recruitment: kid production and survival to breeding age. *Can. J. Zool.* 72:22–27
57. Flueck WT, Smith-Flueck JM. 1996. Kann Energiemangel ein Massensterben unter Cerviden in Sommereinständen der nördlichen Gebirge verursachen? Eine exploratorische Analyse am Schwarzwedelhirsch (*Odocoileus hemionus columbianus*). *Z. Jagdwiss.* 42:85–96
58. Fowler CW. 1987. A review of density dependence in populations of large mammals. In *Current Mammalogy*, ed. HH Genoways, 1:401–41. New York: Plenum
59. Fowler CW, Barmore WJ. 1979. A population model of the northern Yellowstone elk herd. *Proc. Conf. Sci. Res. Natl. Parks, 1st*, ed. RM Linn, 1:427–34. Washington, DC: GPO
60. Fryxell JM. 1987. Food limitation and demography of a migratory antelope, the white-eared kob. *Oecologia* 72:83–91
61. Fryxell JM. 1987. Seasonal reproduction of white-eared kob in Boma National Park, Sudan. *Afr. J. Ecol.* 25:117–24
62. Fuller TK. 1991. Dynamics of a declining white-tailed deer population in north-central Minnesota. *Wildl. Monogr.* 110:1–37
63. Gaillard JM, Andersen R, Delorme D, Linnell JDC. 1998. Family effects on growth and survival of juvenile roe deer. *Ecology* 79:2878–89
64. Gaillard JM, Delorme D, Boutin JM, Laere GV, Boisaubert B, et al. 1993. Roe deer survival patterns: a comparative analysis of contrasting populations. *J. Anim. Ecol.* 62:778–91
65. Gaillard JM, Delorme D, Van Laere G, Duncan P, Lebreton JD. 1997. Early survival in roe deer: causes and consequences

- of cohort variation in two contrasted populations. *Oecologia* 112:502–13
66. Gaillard JM, Festa-Bianchet M, Delorme D, Jorgenson JT. 2000. Bodymass and individual fitness in female ungulates: bigger is not always better! *Proc. R. Soc. London Ser. B* 267:471–77
67. Gaillard JM, Festa-Bianchet M, Yoccoz NG. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends Ecol. Evol.* 13:58–63
68. Gaillard JM, Liberg O, Andersen R, Hewison AJM, Cederlund G. 1998. Population dynamics of roe deer. In *The European Roe Deer: The Biology of Success*, ed. R Andersen, P Duncan, JDC Linnell, pp. 309–35. Oslo: Scand. Univ. Press
69. Gaillard JM, Pontier D, Allainé D, Lebreton JD, Trouvilliez J et al. 1989. An analysis of demographic tactics in birds and mammals. *Oikos* 56:59–76
70. Gaillard JM, Sempéré AJ, Boutin JM, Van Laere G, Boisaubert B. 1992. Effects of age and body weight on the proportion of females breeding in a population of roe deer (*Capreolus capreolus*). *Can. J. Zool.* 70:1541–45
71. Gaillard JM, Vassant J, Klein F. 1987. Quelques caractéristiques de la dynamique des populations de sangliers (*Sus scrofa*) en milieu chassé. *Gibier Faune Sauvage*. 4:31–47
72. Garrott RA, Eagle TC, Plotka ED. 1991. Age-specific reproduction in feral horses. *Can. J. Zool.* 69:738–43
73. Gasaway WC, Boertje RD, Grangaard DV, Kelleyhouse DG, Stephenson RO, et al. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildl. Monogr.* 120:1–59
74. Gasaway WC, Gasaway KT, Berry HH. 1996. Persistent low densities of plains ungulates in Etosha National Park, Namibia: testing the food-regulating hypothesis. *Can. J. Zool.* 74:1556–72
75. Gittleman JL, Luh HK. 1992. On comparing comparative methods. *Annu. Rev. Ecol. Syst.* 23:383–404
76. Guinness FE, Clutton-Brock TH, Albon SD. 1978. Factors affecting calf mortality in red deer. *J. Anim. Ecol.* 47:812–32
77. Hamilton WJ, Blaxter KL. 1980. Reproduction in farmed red deer. 1. Hind and stag fertility. *J. Agric. Sci.* 95:261–73
78. Hamlin KL, Mackie RJ. 1989. *Mule deer in the Missouri River Breaks, Montana. A Study of Population Dynamics in a Fluctuating Environment. Rep.* Helena: Mont. Dep. Fish, Wildl. Parks, Study No. BG-1.0
79. Harvey PH, Pagel MD. 1991. *The Comparative Method in Evolutionary Biology.* Oxford, UK: Oxford Univ. Press
80. Hatter IW, Janz DW. 1994. Apparent demographic changes in black-tailed deer associated with wolf control on northern Vancouver Island. *Can. J. Zool.* 72:878–84
81. Hayssen V, van Tienhoven A. 1993. *Asdell's Patterns of Mammalian Reproduction. A Compendium of Species-Specific Data.* Ithaca, NY: Comstock
82. Heard D, Barry S, Watts G, Child K. 1997. Fertility of female moose (*Alces alces*) in relation to age and body composition. *Alces* 33:165–76
83. Heppell SS, Caswell H, Crowder LB. 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology* 81:654–65
84. Hewison AJM. 1996. Variation in the fecundity of roe deer in Britain: effects of age and body weight. *Acta Theriol.* 41:187–98
85. Houston DB, Stevens V. 1988. Resource limitation in mountain goats: a test by experimental cropping. *Can. J. Zool.* 66:228–38
86. Jingfors KT, Klein DR. 1982. Productivity in recently established muskox populations in Alaska. *J. Wildl. Manage.* 46:1092–96
87. Jorgenson JT, Festa-Bianchet M, Gaillard JM, Wishart WD. 1997. Effects of age, sex, disease and density on survival of bighorn sheep. *Ecology* 78:1019–32

88. Jorgenson JT, Festa-Bianchet M, Lucherini M, Wishart WD. 1993. Effects of body size, population density and maternal characteristics on age of first reproduction in bighorn ewes. *Can. J. Zool.* 71:2509–17
89. Kaji K, Koizumi T, Ohtaishi N. 1988. Effects of resource limitation on the physical and reproductive condition of sika deer on Nakanoshima Island, Hokkaido. *Acta Theriol.* 33:187–208
90. Keiper R, Houpt K. 1984. Reproduction in feral horses: an eight-year study. *Am. J. Vet. Res.* 45:991–95
91. Kie JG, White M. 1985. Population dynamics of white-tailed deer (*Odocoileus virginianus*) on the Welder Wildlife Refuge, Texas. *Southwest. Nat.* 30:105–18
92. Kirkpatrick JF, McCarthy JC, Gudermuth DF, Shideler SE, Lasley BL. 1996. An assessment of the reproductive biology of Yellowstone bison (*Bison bison*) subpopulations using noncapture methods. *Can. J. Zool.* 74:8–14
93. Kirkpatrick JF, Turner JW. 1991. Compensatory reproduction in feral horses. *J. Wildl. Manage.* 55:649–52
94. Klein DR, Olson ST. 1960. Natural mortality patterns of deer in southeast Alaska. *J. Wildl. Manage.* 24:80–88
95. Kojola I. 1993. Early maternal investment and growth in reindeer. *Can. J. Zool.* 71:753–58
96. Kunkel KE, Mech LD. 1994. Wolf and bear predation on white-tailed deer fawns in northeastern Minnesota. *Can. J. Zool.* 72:1557–65
97. Lande R. 1993. Risk of population extinction from demographic and environmental stochasticity and random catastrophes. *Am. Nat.* 142:911–27
98. Langbein J, Putman R. 1992. Reproductive success of female fallow deer in relation to age and condition. In *The Biology of Deer*, ed. RD Brown, pp. 293–99. New York: Springer-Verlag
99. Langenau EE, Lerg JM. 1976. The effects of winter nutritional stress on maternal and neonatal behavior in penned white-tailed deer. *Appl. Anim. Ethol.* 2:207–23
100. Le Bel S, Salas M, Chardonnet P, Bianchi M. 1997. Rusa deer (*Cervus timorensis russa*) farming in New Caledonia: impact of different feed levels on herd breeding rate and performance of new-born fawns. *Aust. Vet. J.* 75:199–203
101. Leader-Williams N. 1980. Population dynamics and mortality of reindeer introduced into south Georgia. *J. Wildl. Manage.* 44:640–57
102. Lent PC, Davis WJ. 1991. Variables influencing survival in four generations of captive-born muskoxen. *Rangifer* 13:137–42
103. Lindström J. 1999. Early development and fitness in birds and mammals. *Trends Ecol. Evol.* 14:343–48
104. Link WA, Nichols JD. 1994. On the importance of sampling variance to investigations of temporal variation in animal population size. *Oikos* 69:539–44
105. Linnell JDC, Aanes R, Andersen R. 1995. Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. *Wildl. Biol.* 1:209–23
106. Lloyd PH, Rasa OAE. 1989. Status, reproductive success and fitness in Cape mountain zebra (*Equus zebra zebra*). *Behav. Ecol. Sociobiol.* 25:411–20
107. Logan T. 1973. Study of white-tailed deer fawn mortality on Cookson Hills Deer Refuge in Eastern Oklahoma. *Proc. Southeast. Assoc. Game Fish Comm.* 26:27–35
108. Loison A, Festa-Bianchet M, Gaillard JM, Jorgenson JT, Jullien JM. 1999. Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology* 80:2539–54
109. Loison A, Gaillard JM, Pélabon C, Yoccoz NG. 1999. What factors shape sexual size dimorphism in ungulates? *Evol. Ecol. Res.* 1:611–33
110. Loison A, Langvatn R. 1998. Short and long-term effects of winter and spring

- weather on growth and survival of red deer in Norway. *Oecologia* 116:489–500
111. Lycett JE, Henzi SP, Barrett L. 1998. Maternal investment in mountain baboons and the hypothesis of reduced care. *Behav. Ecol. Sociobiol.* 42:49–56
 112. Markgren G. 1969. Reproduction of moose in Sweden. *Viltrevy* 6:129–299
 113. McCorquodale SM, Eberhardt LL, Eberhardt LE. 1988. Dynamics of a colonizing elk population. *J. Wildl. Manage.* 52:309–13
 114. McCullough DR. 1979. *The George Reserve Deer Herd. Population Ecology of a K-Selected Species*. Ann Arbor, MI: Univ. Mich. Press
 115. McCullough DR. 1992. Concepts of large herbivore population dynamics. In *Wildlife 2001: Populations*, ed. DR McCullough, RH Barrett, pp. 967–84. London: Elsevier
 116. McCullough DR. 1994. What do herd composition counts tell us? *Wildl. Soc. Bull.* 22:295–300
 117. McCullough DR. 1997. Breeding by female fawns in black-tailed deer. *Wildl. Soc. Bull.* 25:296–97
 118. McNaughton SJ, Georgiadis NJ. 1985. Ecology of African grazing and browsing mammals. *Annu. Rev. Ecol. Syst.* 17:39–65
 119. McShea WJ, Underwood HB, Rappole JH. 1997. *The Science of Overabundance. Deer Ecology and Population Management*. Washington, DC: Smithsonian Inst. Press
 120. Mduma SAR, Sinclair ARE, Hilborn R. 1999. Food regulates the Serengeti wildebeest: a 40-year record. *J. Anim. Ecol.* 68:1101–22
 121. Mech LD, McRoberts RE, Peterson RO, Page RE. 1987. Relationship of deer and moose populations to previous winters' snow. *J. Anim. Ecol.* 56:615–27
 122. Mech LD, Nelson ME, McRoberts RE. 1991. Effects of maternal and grand-maternal nutrition on deer mass and vulnerability to wolf predation. *J. Mamm.* 72:146–51
 123. Melton DA. 1987. Waterbuck (*Kobus ellipsipyrmnus*) population dynamics: the testing of a hypothesis. *Afr. J. Ecol.* 25:133–45
 124. Merrill EH, Boyce MS. 1991. Summer range and elk population dynamics in Yellowstone National Park. In *The Greater Yellowstone Ecosystem*, ed. RB Keiter, MS Boyce, pp. 263–73. New Haven, CT: Yale Univ. Press
 125. Millar JS, Zammuto RM. 1983. Life histories of mammals: an analysis of life tables. *Ecology* 64:631–35
 126. Miller FL, Broughton E, Gunn A. 1988. Mortality of migratory barren-ground caribou on the calving grounds of the Beverly herd, Northwest Territories, 1981–83. *Can. Wildl. Serv.* 66:1–26
 127. Milner JM, Elston DA, Albon SD. 1999. Estimating the contributions of population density and climatic fluctuations to interannual variation in survival of Soay sheep. *J. Anim. Ecol.* 68:1235–47
 128. Modafferi RD, Becker EF. 1997. Survival of radiocollared adult moose in lower Susitna River Valley, Southcentral Alaska. *J. Wildl. Manage.* 61:540–49
 129. Monard AM, Duncan P, Fritz H, Feh C. 1997. Variations in the birth sex ratio and neonatal mortality in a natural herd of horses. *Behav. Ecol. Sociobiol.* 41:243–49
 130. Mundinger JG. 1981. White-tailed deer reproductive biology in the Swan River Valley, Montana. *J. Wildl. Manage.* 45:132–39
 131. Murphy DA, Coates JA. 1966. Effects of dietary protein on deer. *N. Am. Wildl. Conf.* 31:129–39
 132. Nelson LJ, Peek JM. 1982. Effect of survival and fecundity on rate of increase of elk. *J. Wildl. Manage.* 46:535–40
 133. Nichols L. 1978. Dall sheep reproduction. *J. Wildl. Manage.* 42:570–80

134. Nowak RM. 1991. *Walker's Mammals of the World*, Vol. 2. Baltimore, MD: Johns Hopkins Univ. Press. 5th ed.
135. Orzack SH, Tuljapurkar SD. 1989. Population dynamics in variable environments. VII. The demography and evolution of iteroparity. *Am. Nat.* 133:901–23
136. Owen-Smith N. 1988. *Megaherbivores. The Influence of Very Large Body Size on Ecology*. Cambridge, UK: Cambridge Univ. Press
137. Owen-Smith N. 1990. Demography of a large herbivore, the greater kudu *Tragelaphus strepsiceros*, in relation to rainfall. *J. Anim. Ecol.* 59:893–913
138. Ozoga JJ, Verme LJ. 1984. Effect of family-bond deprivation on reproductive performance in female white-tailed deer. *J. Wildl. Manage.* 48:1326–34
139. Ozoga JJ, Verme LJ. 1986. Relation of maternal age to fawn-rearing success in white-tailed deer. *J. Wildl. Manage.* 50:480–86
140. Pac DF, Mackie RJ, Jorgensen HE. 1991. *Mule Deer Population Organization, Behavior and Dynamics in a Rocky Mountain Environment*. Rep. Mont. Dep. Fish, Wildl. Parks
141. Pascual MA, Hilborn R. 1995. Conservation of harvested populations in fluctuating environments: the case of the Serengeti wildebeest. *J. Appl. Ecol.* 32:468–80
142. Pélabon C, Gaillard JM, Loison A, Portier C. 1995. Is sex-biased maternal care limited by total maternal expenditure in polygynous ungulates? *Behav. Ecol. Sociobiol.* 37:311–19
143. Pemberton JM, Albon SD, Guinness FE, Clutton-Brock TH, Berry RJ. 1988. Genetic variation and juvenile survival in red deer. *Evolution* 42:921–34
144. Peters RH. 1983. *The Ecological Implications of Body Size*. Cambridge, UK: Cambridge Univ. Press
145. Pfister CA. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. *Proc. Natl. Acad. Sci. USA* 95:213–18
146. Portier C, Festa-Bianchet M, Gaillard JM, Yoccoz NG. 1998. Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). *J. Zool.* 245:271–78
147. Putman RJ, Langbein J, Hewison AJM, Sharma SK. 1996. Relative roles of density-dependent and density-independent factors in population dynamics of British deer. *Mamm. Rev.* 26:81–101
148. Reynolds PE. 1998. Dynamics and range expansion of a reestablished muskox population. *J. Wildl. Manage.* 62:734–44
149. Robinette WL, Baer CH, Pillmore RE, Knittle CE. 1973. Effects of nutritional change on captive mule deer. *J. Wildl. Manage.* 37:312–26
150. Robinette WL, Gashwiler JS. 1950. Breeding season, productivity, and fawning period of the mule deer in Utah. *J. Wildl. Manage.* 14:457–69
151. Roffe TJ. 1993. Perinatal mortality in caribou from the Porcupine herd, Alaska. *J. Wildl. Dis.* 29:295–303
152. Rognmo A, Markussen KA, Jacobsen E, Grav HJ, Blix AS. 1983. Effects of improved nutrition in pregnant reindeer on milk quality, calf birth weight, growth, and mortality. *Rangifer* 3:10–18
153. Rosser AM. 1989. Environmental and reproductive seasonality of puku, *Kobus vardonii*, in Luangwa Valley, Zambia. *Afr. J. Ecol.* 27:77–88
154. Russell DE, Gerhart KL, White RG, van der Wetering D. 1998. Detection of early pregnancy in caribou: evidence for embryonic mortality. *J. Wildl. Manage.* 62:1066–75
155. Rutberg AT. 1987. Adaptive hypothesis of birth synchrony in ruminants: an interspecific test. *Am. Nat.* 130:692–710
156. Sæther BE. 1997. Environmental stochasticity and population dynamics of large

- herbivores: a search for mechanisms. *Trends Ecol. Evol.* 12:143–49
157. Sams MG, Lochmiller RL, Qualls CW, Leslie DM, Payton ME. 1996. Physiological correlates of neonatal mortality in an overpopulated herd of white-tailed deer. *J. Mamm.* 77:179–90
 158. Sand H. 1996. Life history patterns in female moose (*Alces alces*): the relationship between age, body size, fecundity and environmental conditions. *Oecologia* 106:212–20
 159. Sarno RJ, Clark WR, Bank MS, Prexl WS, Behl MJ, et al. 1999. Juvenile guanaco survival: management and conservation implications. *J. Appl. Ecol.* 36:937–45
 160. Sarno RJ, Franklin WL. 1999. Maternal expenditure in the polygynous and monomorphic guanaco: suckling behavior, reproductive effort, yearly variation, and influence on juvenile survival. *Behav. Ecol.* 10:41–47
 161. Sauer JR, Boyce MS. 1983. Density dependence and survival of elk in northwestern Wyoming. *J. Wildl. Manage.* 47:31–37
 162. Sausman KA. 1984. Survival of captive-born *Ovis canadensis* in North American zoos. *Zoo Biol.* 3:111–21
 163. Schladweiler P, Stevens DR. 1973. Reproduction of Shiras moose in Montana. *J. Wildl. Manage.* 37:535–44
 164. Sinclair ARE. 1974. The natural regulation of buffalo populations in East Africa. III. Population trends and mortality. *E. Afr. Wildl. J.* 12:185–200
 165. Sinclair ARE. 1989. Population regulation in animals. In *Ecological Concepts*, ed. JM Cherrett, pp. 197–241. Oxford, UK: Blackwell Sci.
 166. Singer FJ, Harting A, Symonds KK, Coughenour MB. 1997. Density-dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. *J. Wildl. Manage.* 61:12–25
 167. Skogland T. 1985. The effects of density-dependent resource limitations on the demography of wild reindeer. *J. Anim. Ecol.* 54:359–74
 168. Skogland T. 1986. Density-dependent food limitation and maximal production in wild reindeer herds. *J. Wildl. Manage.* 50:314–19
 169. Skogland T. 1988. Tooth wear by food limitation and its life history consequences in wild reindeer. *Oikos* 51:238–42
 170. Skogland T. 1989. Comparative social organization of wild reindeer in relation to food, mates and predator avoidance. *Adv. Ethol.* 29:1–71
 171. Skogland T. 1990. Density dependence in a fluctuating wild reindeer herd: maternal vs. offspring effects. *Oecologia* 84:442–50
 172. Smith RH, Lecomte A. 1979. Some factors affecting survival of desert mule deer fawns. *J. Wildl. Manage.* 43:657–65
 173. Stearns SC, Kawecki TJ. 1994. Fitness sensitivity and the canalization of life-history traits. *Evolution* 48:1438–50
 174. Swenson JE. 1985. Compensatory reproduction in an introduced mountain goat population in the Absaroka Mountains, Montana. *J. Wildl. Manage.* 49:837–43
 175. Talbot LM, Talbot MH. 1963. The wildebeest in western Masailand, East Africa. *Wildl. Monogr.* 12:1–88
 176. Thing H, Klein DR, Jingfors K, Holt S. 1987. Ecology of muskoxen in Jameson Land, northeast Greenland. *Holarct. Ecol.* 10:95–103
 177. Thorne ET, Dean RE, Hepworth WG. 1976. Nutrition during gestation in relation to successful reproduction in elk. *J. Wildl. Manage.* 40:330–35
 178. Tuljapurkar SD. 1990. *Population Dynamics in Variable Environments*. New York: Springer-Verlag
 179. Tuljapurkar S, Caswell H. 1996. *Structured-Population Models in Marine, Terrestrial, and Freshwater Systems*. New York: Chapman & Hall

180. Turner JW, Wolfe ML, Kirkpatrick JF. 1992. Seasonal mountain lion predation on a feral horse population. *Can. J. Zool.* 70:929–34
181. Van Ballenberghe V. 1983. Rate of increase of white-tailed deer on the George Reserve: a re-evaluation. *J. Wildl. Manage.* 47:1245–50
182. Van Ballenberghe V, Ballard WB. 1997. Population dynamics. In *Ecology and Management of the North American Moose*, ed. CC Schwartz, AW Franzmann, pp. 223–45. Washington, DC: Smithsonian Inst. Press
183. Van Sickle J. 1990. Dynamics of African ungulate populations with fluctuating, density-independent calf survival. *Theor. Popul. Biol.* 37:424–37
184. Van Vuren D, Bray MP. 1986. Population dynamics of bison in the Henry Mountains, Utah. *J. Mamm.* 67:503–11
185. Verme LJ. 1965. Reproduction studies on penned white-tailed deer. *J. Wildl. Manage.* 29:74–79
186. Verme LJ. 1991. Decline in doe fawn fertility in southern Michigan deer. *Can. J. Zool.* 69:25–28
187. Walsh NE, Griffith B, McCabe TR. 1995. Evaluating growth of the Porcupine Caribou Herd using a stochastic model. *J. Wildl. Manage.* 59:262–72
188. Wehausen JD. 1996. Effects of mountain lion predation on bighorn sheep in the Sierra Nevada and Granite Mountains of California. *Wildl. Soc. Bull.* 24:471–79
189. Wehausen JD, Bleich VC, Weaver RA. 1987. Mountain sheep in California: a historical perspective on 108 years of full protection. *Trans. West. Sect. Wildl. Soc.* 23:65–74
190. Western D. 1979. Size, life-history and ecology in mammals. *Afr. J. Ecol.* 17:185–204
191. White GC, Bartmann RM. 1998. Effect of density reduction on overwinter survival of free-ranging mule deer fawns. *J. Wildl. Manage.* 62:214–25
192. White GC, Garrott RA, Bartmann RM, Carpenter LH, Alldredge AW. 1987. Survival of mule deer in northwest Colorado. *J. Wildl. Manage.* 51:852–59
193. White RG, Rowell JE, Hauer WE. 1997. The role of nutrition, body condition and lactation on calving success in muskoxen. *J. Zool.* 243:13–20
194. Whitlaw HA, Ballard WB, Sabine DL, Young SJ, Jenkins RA, et al. 1998. Survival and cause-specific mortality rates of adult white-tailed deer in New Brunswick. *J. Wildl. Manage.* 62:1335–41
195. Whitten KR, Garner GW, Mauer FJ, Harris RB. 1992. Productivity and early calf survival in the Porcupine caribou herd. *J. Wildl. Manage.* 56:201–12
196. Williamson DT. 1991. Condition, growth and reproduction in female red lechwe (*Kobus leche leche* Gray 1850). *Afr. J. Ecol.* 29:105–17
197. Wilson DE, Hirst SM. 1977. Ecology and factors limiting Roan and Sable antelope populations in South Africa. *Wildl. Monogr.* 54:1–111
198. Wolfe ML. 1980. Feral horse demography: a preliminary report. *J. Range Manage.* 33:354–60