

# TEMPORAL VARIATION IN FITNESS COMPONENTS AND POPULATION DYNAMICS OF LARGE HERBIVORES

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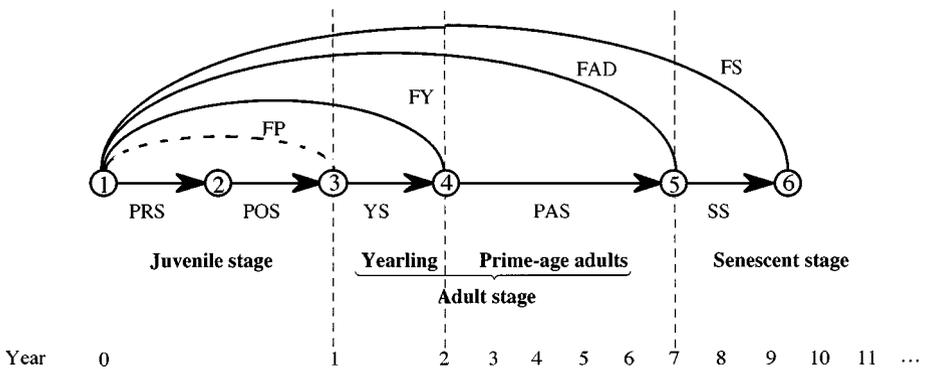
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■ **Abstract** In large-herbivore populations, environmental variation and density dependence co-occur and have similar effects on various fitness components. Our review aims to quantify the temporal variability of fitness components and examine how 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  $\geq 10$  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 ( $\lambda$ ) 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

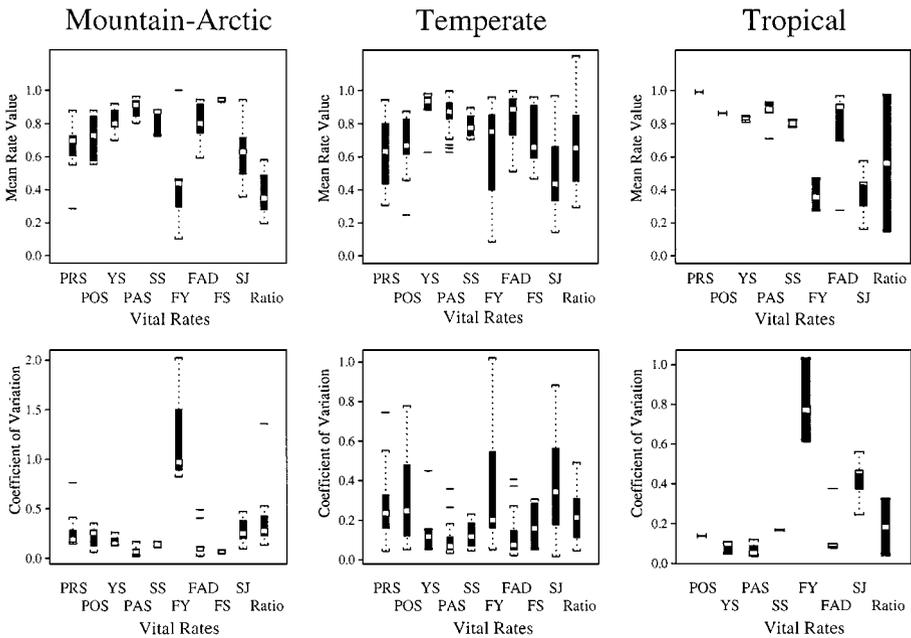
Ideally, our review should have included only studies based on long-term monitoring of individually recognizable animals, analyzed with methods that account for differences in recapture probability, because those studies minimize errors in estimates of fitness components and reduce the risk of sampling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

We included studies lasting  $\geq 3$  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 km<sup>2</sup>, 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,  $\geq 10$  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).

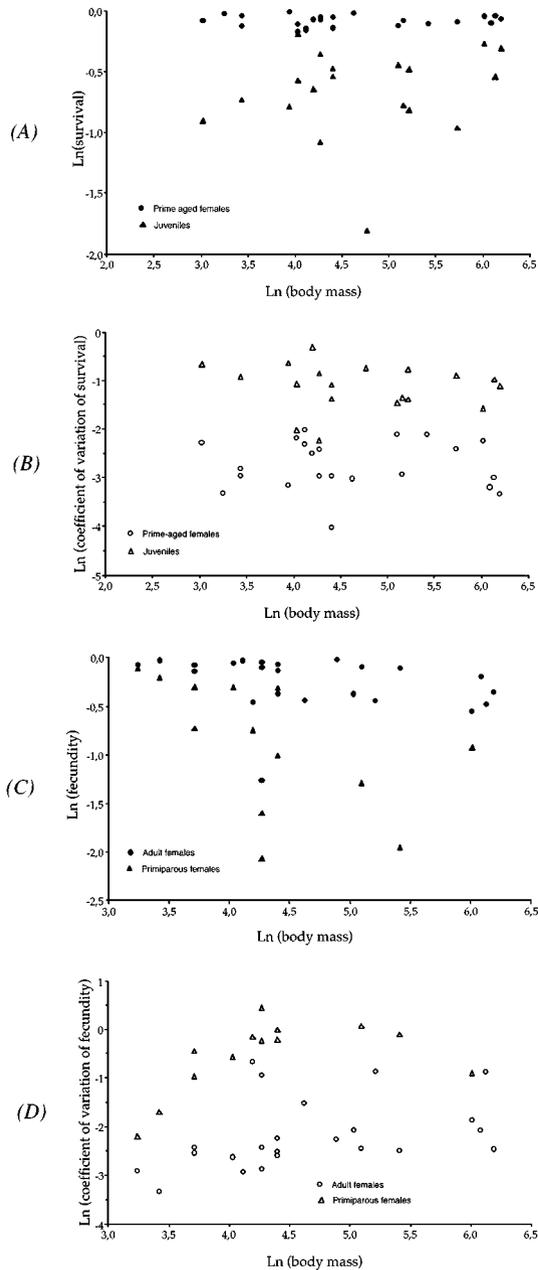
### Allometric Component of Temporal Variation in Fitness Components

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<sup>a</sup>

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	<b>0.829 (0.021)</b>	<b>0.929 (0.022)</b>	<b>0.009</b>	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 primumiparous females	<b>1.119 (0.041)</b>	<b>1.372 (0.085)</b>	<b>0.04</b>	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

<sup>a</sup>P 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<sup>a</sup>

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

<sup>a</sup>Temporal 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.

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