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Population dynamics of large herbivores: variable recruitment with constant adult survival

Jean-Michel Gaillard, Marco Festa-Bianchet and Nigel Gilles Yoccoz

The factors that explain changes in population size are a central theme in ecology, and long-term studies of population dynamics are of great interest for life history theory, population ecology, wildlife management and conservation biology^{1,2}. Studies that can identify which vital rates are more variable (variability patterns) and which ones are more likely to influence overall changes in population size (elasticity patterns) are particularly useful². Historically, large herbivores were sometimes considered unsuitable for the study of population ecology because their long generation time meant that interesting results could not be expected for several years. However, large herbivorous mammals are particularly suited to demographic studies because age classes are readily identifiable. In addition, many species are economically important or are useful indicator species for conservation. Recently, several researchers have published long-term studies of ungulates, mostly based on monitoring of marked individuals and often taking advantage of recent methodological developments of Capture–Mark–Recapture (CMR) modeling that account for differences in the probability of recapturing (or resighting) marked individuals, so that biological hypotheses can be tested reliably³.

Recent studies suggest that the population dynamics of large herbivores can be strongly affected by a combination of stochastic environmental variation and density dependence⁴. Food resources, habitat quality, weather, disease and parasites, interspecific competition, predation, human activities and population density can account for the demographic variation observed among years within a population or among populations within a species. While several studies have

Recent long-term studies of population ecology of large herbivorous mammals suggest that survival of prime-aged females varies little from year to year and across populations. Juvenile survival, on the other hand, varies considerably from year to year. The pattern of high and stable adult survival and variable juvenile survival is observed in contrasting environments, independently of the main proximal sources of mortality and regardless of whether mortality is stochastic or density-dependent. High yearly variability in juvenile survival may play a predominant role in population dynamics.

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attempted to identify the most important factor driving changes in population size (e.g. Ref. 2), less effort has been devoted to assessing the roles of different vital rates (such as age-specific survival and reproduction) in affecting population dynamics. Because large herbivores have strongly age-structured populations and markedly iteroparous life histories⁵, different vital rates may respond differently to various limiting factors (Box 1). Twenty years ago, Eberhardt⁶ proposed that the negative effects of increasing density on population growth would occur in a specific order. Among vital rates, juvenile survival (usually defined as survival over the first year of life) should change first, then the age at first reproduction, followed by the reproductive rates of prime-age adults and lastly by adult survival (Box 1).

Here, we review recent research trends on temporal variation in survival of juveniles and of prime-aged females in response to environmental stochasticity and density-dependence in large herbivores. We do not discuss demographic variation because we excluded accounts of small populations where demographic stochasticity could account for an important part of stochastic variation in vital rates.

Assessing temporal variation in vital rates in wild populations: methods and data

Two fundamental problems in population dynamics have challenged biologists and statisticians²: (1) how to measure the contribution of different vital rates to overall variability in population growth rate, and (2) how to quantify the roles of density-dependent and density-independent factors. Reliable estimates of each vital rate and a measure of the precision of these estimates (such as their variance) are key

to solving these problems. Until very recently, reliable estimates of vital rates (especially survival) for wild populations of large herbivores were uncommon, because they require long-term monitoring of marked individuals. Most published survival estimates were based on transversal life tables (for instance 14 of 17 ungulate populations in Purvis and Harvey's analysis⁷). The life-table technique assumes a stationary age distribution and equal probability of sampling for all individuals: if these assumptions are violated, survival estimates are unreliable¹. These strict assumptions are unlikely to be met in any population of wild mammals^{8,9}. Even if the assumptions were met, life-table methods do not generally provide any measure of variability in survival rates.

Fortunately, recent years have seen a rapid increase in use of CMR and radiotelemetry methods for estimating survival rates and their variability. The modeling of survival has now a firm statistical basis and allows for a flexible analysis of the roles of environmental factors and of density³. The total variability of estimates of vital rates has different components, including sampling variability. A proper measure of the precision of survival estimates is therefore required to avoid confounding sampling variability and 'biological variability' due to intrinsic and extrinsic factors (Box 2). The same problem applies to estimates of population variability or trends¹⁰. Methods based on estimation of variance components should therefore be used to separate sampling variability from 'biological variability'.

Density dependence and vital rates in large herbivores

Fowler's review¹¹ supported Eberhardt's idea that vital rates have different sensitivities to changes in population density. In 21 species of large herbivores for which density dependence was reported, juvenile survival was involved in 15, age at first breeding in 12 and adult survival in only nine. Density dependence of adult reproductive traits was reported for 17 of 21 species, but measures of reproduction, such as the number of young per adult female, usually included early juvenile survival. Fowler¹¹ pointed out that differences in the response of vital rates to changes in population density were inconclusive because adult survival is far more difficult to assess than reproductive traits. Early recruitment can be measured by female:young ratios, but adult survival is very difficult to quantify without long-term monitoring of many marked individuals.

Recent studies based mainly on monitoring individually recognized animals also support Eberhardt's suggestion. Of nine species in which adult survival and other vital rates were studied in relation to variation in population density (Table 1), all exhibited density dependence in recruitment (juvenile survival, proportion of females breeding, or a combination of both traits), yearling survival was density-dependent in four, but only two island populations (Soay sheep and red deer) exhibited density dependence in adult survival. Even for these two species, survival of adult females varies much less than juvenile survival^{12,13}. Therefore, juvenile survival is much more sensitive to density dependence than adult survival, which appears to be buffered against density effects.

Environmental variation and vital rates in large herbivores

Tables 2 and 3 summarize recent long-term studies on among-year variation in vital rates of large herbivores by focusing on juvenile survival (as a measure of recruitment) and survival of adult females. Whenever possible, we con-

Box 1. The life cycle of female large herbivores: demographic analysis of a model population

Consider a population of large herbivores just before parturition. Suppose that each year 75% of 2-year-old females produce young [yearly proportion of 2-year-old females giving birth (%B2) = 0.75] and all females 3-year-old and older produce young [yearly proportion of 3-year-old and older females giving birth (%B3+) = 1]. All reproducing females give birth to a single offspring (litter size, LS = 1). This leads to a production of 0.5 females per breeding female assuming an even sex ratio at birth. Female offspring have a mean first-year survival of 0.50 (juvenile survival, SJ = 0.50) and a second-year survival of 0.75 (yearling survival, SY = 0.75). From 2 to 7 years, the annual survival of females is 0.90 (prime-age survival, SA = 0.90). Survival probability decreases to 0.70 for females older than 7 years (senescent survival, SS = 0.70).

A Leslie-Usher matrix model² for this population is therefore:

0	0.1875	0.1875	0.1875	0.1875	0.1875	0.1875	0.1875
0.75	0	0	0	0	0	0	0
0	0.90	0	0	0	0	0	0
0	0	0.90	0	0	0	0	0
0	0	0	0.90	0	0	0	0
0	0	0	0	0.90	0	0	0
0	0	0	0	0	0.90	0	0
0	0	0	0	0	0	0.90	0.70

From this matrix, we obtain a population multiplication rate (λ) of 1.026. The elasticities of different vital rates (i.e. the change of λ due to a given proportional change in a vital rate, a_{ij}) are defined by:

$$e_{ij} = \frac{\partial \ln(\lambda)}{\partial \ln(a_{ij})} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}$$

For the above Leslie-Usher matrix, we obtain²:

$$e(\text{recruitment}) = 0.174$$

where parameters defining recruitment [SJ, LS, and (%B2 + %B3+)] all have the same elasticity because changing any of these parameters by a certain percentage will have exactly the same impact on λ (multiplicative terms in the Leslie matrix). Elasticities of %B2 and %B3+ were respectively 0.023 and 0.151.

$$e(\text{SY}) = 0.174$$

$$e(\text{SA}) = 0.513$$

where elasticity of prime-age survival is calculated as the sum of the elasticities of 5 year age classes (between 2 and 7 years of age).

$$e(\text{SS}) = 0.140$$

Variation in adult survival has the greatest effect on λ : a change in adult survival should have about three times more impact on λ than the equivalent change in recruitment.

sidered only prime-aged adults (typically those aged 2–7 years^{14,15}, but including some older age classes in larger species like red deer¹⁶), because the survival of older individuals appears to be lower^{14,15} and therefore estimates of 'adult' survival that include all age classes would be affected by population age structure. The survival of prime-aged females of 24 populations of 16 species of large herbivores monitored for a minimum of 5 years shows little among-year variation (coefficient of variation (CV) varying from 2 to 15%, Table 2). In contrast, juvenile survival shows marked temporal variation in 19 populations of 14 species (CV varying from 12 to 88%, Table 3). The differential response of adult and juvenile survival to environmental variation is clearly evident from a comparison of the same populations (numbered studies in Tables 2 and 3). In all 18 populations, yearly juvenile survival varied more than adult survival.

The high yearly variation in juvenile survival probably has multiple causes. Predation^{17–20} drought in spring and summer^{21,22} rainfall^{23,24}, harsh winters^{17,19,21,23}, low birth weight and early growth rates^{12,19,23}, late parturition^{19,23}, poor calving areas²⁵, lack of suitable bedding sites¹⁹, genetic factors²³ and altered immunocompetence of neonates²⁶ have been reported to decrease juvenile survival in ungulates. Although almost as many causes of adult mortality have been reported,

Table 1. Evidence for/against density-dependent responses in vital rates of eight species of large herbivores

Species	Refs	Evidence for density-dependence in:	No evidence for density-dependence in:	Range of density (number/km ²)
White-tailed deer (<i>Odocoileus virginianus</i>)	37	Juvenile survival in summer, reproductive success of 2 and 3 years old females and recruitment	Adult survival	14–26
Greater Kudu (<i>Tragelaphus strepsiceros</i>)	24	Juvenile survival in both populations studied, yearling survival in one population	Prime-age and senescent survival in both populations and yearling survival in one population	1.5–3 2.5–4
Roe deer (<i>Capreolus capreolus</i>)	14,22	Age at first breeding and juvenile survival in summer	Yearling, prime-age and senescent survival and fecundity	6–21
Red deer (<i>Cervus elaphus scoticus</i>)	13	Age at first breeding, fecundity of milk yield hinds, juvenile survival in winter, male yearling survival and adult survival	Summer part of juvenile survival, yearling survival of females and breeding proportion of prime age females	18–25
Wapiti (<i>Cervus elaphus canadensis</i>)	38,19	Juvenile survival	Adult survival	3–13.5
Bighorn sheep (<i>Ovis canadensis</i>)	39,15	Juvenile survival, age at first breeding and female yearling survival	Yearling male survival, prime-age and senescent survival	0.8–2.6 ^a
Reindeer (<i>Rangifer tarandus</i>)	40	Age at first breeding and recruitment	Breeding proportion of adult females and adult survival	0.5–5.5 ^b
Donkey (<i>Equus asinus</i>)	41	Age at first breeding and juvenile survival	Breeding proportion of adult females and adult survival	1.5 and 3 ^c
Soay sheep (<i>Ovis aries</i>)	12	Juvenile, yearling and adult survival	Fecundity	96–222

^aFemale density only.

^bDensity variation among contrasted populations.

^cDensity variation between two experimental sites.

including factors such as epizootics that caused significant yearly differences in adult survival^{15,27}, the available evidence indicates that, within a population, adult survival is always less variable than juvenile survival. This pattern is apparently independent of the main proximal causes of mortality and occurs in different taxa, in different continents and in widely different environments.

Juvenile survival, which determines recruitment, is highly sensitive to limiting factors, regardless of whether its variation

is caused by changes in population density or by stochastic environmental factors. Adult female survival is buffered against most limiting factors (Fig. 1). Only long-term studies of a large sample of marked individuals can detect variation in survival of large herbivores (Box 2). A large sample is required to reduce sampling variability and many years of monitoring are required to measure variability in yearly survival, over a range of densities and environmental variation. In addition, it appears that estimates of adult survival of large

herbivores are subject to greater sampling error than estimates of juvenile survival (Box 2). Therefore, analyses that partition biological and sampling variability will likely reinforce our conclusion that adult survival is much less variable than juvenile survival.

Constant adult survival or variable recruitment: which is more important for population dynamics of large herbivores?

Many demographic analyses of large vertebrates have shown that adult survival has the highest elasticity, while juvenile survival and reproductive traits have the lowest elasticity^{28,29} (Box 1). In general, elasticity of adult survival increases with generation length³⁰, which in turn increases with body

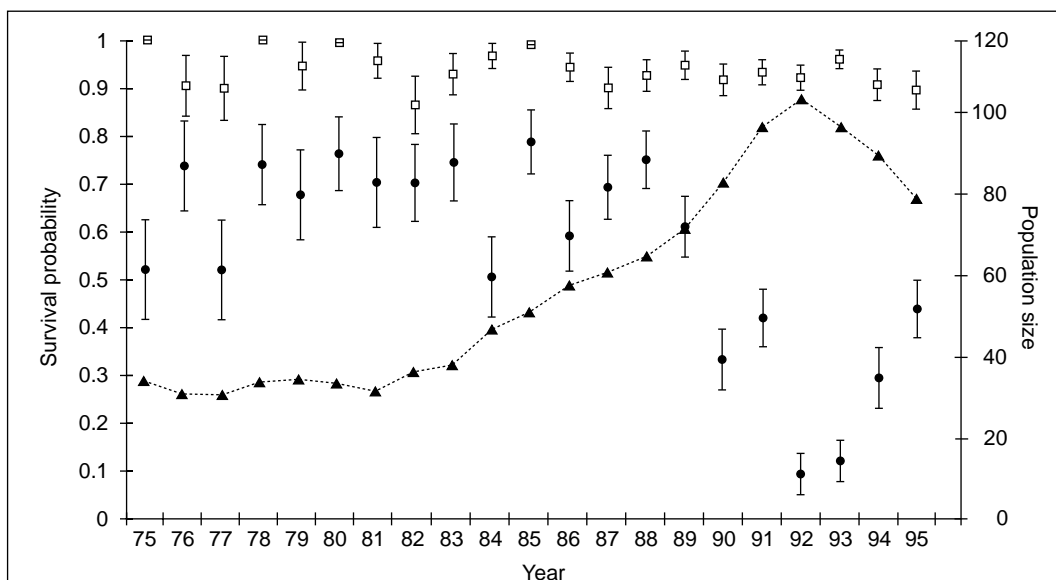


Fig. 1. An example of the contrasting variabilities in juvenile and prime-age adult survival in large herbivorous mammals: survival of bighorn sheep at Ram Mountain, Alberta, from 1975 to 1995^{15,39}. Bars indicate SE. The number of females (dashed line) increased after 1981 and density effects on juvenile survival became evident after about 1988. Survival in 1975–1988 was mostly independent of population density. Black points, yearly estimates of juvenile survival; open squares, yearly estimates of prime age survival of females (2–7 years old).

Table 2. Variation in prime-age adult survival of females in response to environmental stochasticity^a in populations of large herbivores (with at least 5 years' monitoring)

Species	Refs	Mean survival	Min	Max	CV	N ^b	Methods ^c	Analysis ^d	Number of years
Mule deer (<i>Odocoileus hemionus</i>)	43	(1) ^e 0.856	0.692	1	0.101	741	CMR	DA	13
		(2) 0.807	0.743	0.899	0.070	634	CMR	DA	9
	17	(3) 0.875	0.760	1	0.090	185	RT	CR	6
Caribou/Reindeer (<i>Rangifer tarandus</i>)	25	0.842	0.750	0.930	0.088	538	RT	CR	10
	44	0.878 ^f	0.810	0.950	0.058	532	RT	CR	9
	41	(4) 0.940 ^g	0.920	0.963	0.017		CC	DA	6 ^g
Greater Kudu (<i>Tragelaphus strepsiceros</i>)	24	(5) 0.933	0.810	1	0.061	7–57 ^h	CMR	DA	11
		(6) 0.889	0.829	0.954	0.043	27–82 ^h	CMR	DA	11
Bighorn sheep (<i>Ovis canadensis</i>)	15	(7) 0.956	0.871	1	0.033	872	CMR	CR	21
	(updated)	(8) 0.935	0.750	1	0.068	377	CMR	CR	12
Roe deer (<i>Capreolus capreolus</i>)	14	(9) 0.947	0.776	1	0.079	287	CMR	CR	10
	(updated)	(10) 0.942	0.797	1	0.077	302	CMR	CR	10
Soay sheep (<i>Ovis aries</i>)	12	(11) 0.871 ⁱ	0.696	0.980	0.151	733	CMR	DA	6
Moose (<i>Alces alces</i>)	35	(12) 0.949	0.907	1	0.033	524	RT	CR	10
Red deer (<i>Cervus elaphus scoticus</i>)	16	(13) 0.955			0.077		CMR	DA	20
Mouflon (<i>Ovis gmelini</i>)	27 (updated)	0.841 ^j	0.658	1	0.130	130	CMR	CR	7
Chamois (<i>Rupicapra rupicapra</i>)	44 (updated)	0.960					CMR	CR	6
Ibex (<i>Capra ibex</i>)	45 (updated)	0.965	0.709	1	0.086		CMR	CR	13
Dall sheep (<i>Ovis dalli</i>)	46	(14) 0.880	0.710	1	0.108		CC	DA	10
Wapiti (<i>Cervus elaphus canadensis</i>)	38	(15) 0.920					CC	DA	15
	47	0.892	0.778	1	0.117	46	RT	CR	5
Saiga (<i>Saiga tatarica</i>)	21	(16) 0.787 ^k	0.680	0.810					
Pronghorn (<i>Antilocapra americana</i>)	J. Byers (pers. commun.)	(17) 0.978	0.850	1	0.041		CMR	DA	13
Mountain goat (<i>Oreamnos americanus</i>)	Unpubl. data	(18) 0.916	0.800	1	0.079	160	CMR	DA	7

^aEnvironmental stochasticity includes here all sources of variation in the underlying vital rate. In particular, no effect was made to partition density-dependent from other variation. Then, our CVs include sampling variation as well as biological variation.

^bSample size: number of 'animal-years' used for estimating survival probabilities.

^cCMR: monitoring of individually marked animals (using collars, ear tags or natural marks) by resighting or recaptures; RT: monitoring of individually marked animals by radiotelemetry; CC: monitoring using composition counts.

^dCR: estimates based on capture–recapture modeling (see Ref. 3 for methods) accounting for capture probability less than 1; DA: direct assessment of survival from the proportion of individuals at risk known to have survived (assumes capture probability to be 1).

^eNumbers in parentheses indicate populations for which juvenile survival was also available (see Table 3).

^fWinter survival (November to May) only.

^gVariation among contrasted populations.

^hAssumed to represent the largest and smallest sample size for a given year.

ⁱWinter mortality only.

^jPrime-age females defined from 3 to 5 years of age.

^kMethods and N not detailed in the original paper. Mean survival probability was obtained using the frequency of good and bad summer/winter conditions given in the paper.

size. These modeling results, however, do not rule out the possibility that all vital rates account for similar proportions of variance in population growth rate and therefore play similar roles in ungulate population dynamics. Some studies suggest that recruitment could be a stronger determinant of changes in population size than adult survival. Thus, juvenile survival was claimed to be the most important factor influencing population responses of peccary to fluctuating food availability³¹.

Hatter and Janz³² monitored a population of mule deer before, during and after a decline, and concluded that the highly variable juvenile survival (from 0.07 to 0.41) was more important than the constant adult survival (from 0.74 to 0.76) in explaining changes in population size. Gasaway *et al.*³³, on the other hand, suggested that high mortality among adults was the primary demographic process limiting ungulate populations in Etosha. Therefore, it appears that the roles of adult survival and recruitment on population dynamics of large

herbivores cannot be assessed without further demographic analyses. Escos *et al.*²⁸ and Walsh *et al.*²⁹ underlined the difficulties of teasing apart the contributions of different vital rates to yearly changes in population size. Elasticity analyses alone cannot measure these contributions. To the theoretical estimates of what might happen (measured by elasticity) we must join empirical estimates of what happens (measured by long-term variability). This review has shown that adult survival is much less variable than juvenile survival. The next logical step will be to combine measurements of elasticity and variability to identify which vital rates are more important in causing changes in natural populations.

Prospects

In large herbivores, recruitment is the main target of limiting factors, both density-dependent and density-independent. Adult female survival appears buffered against temporal variation regardless of the causes of mortality, with

Box 2. Assessing components of variability in stochastic environments

The variability of estimates of vital rates and population size is composed of sampling variability and biological ('true') variability⁴⁰. The latter can be further partitioned in different components, such as intrinsic and extrinsic factors. To distinguish between sampling and biological variability we need a reliable measure of the sampling precision of estimates. For example, assuming a constant survival rate equal to 0.90 and estimating it by releasing each year 100 marked individuals results in a sampling standard error equal to $\sqrt{[p*(1-p)]/100} = 0.03$, and therefore observing estimates varying by $\pm 5\%$ may be due entirely to sampling variation. The variance σ_a^2 , of the estimator \hat{a} of a vital rate, a , is the sum of the biological variance, σ_a^2 , and the sampling variance, $\text{var}(\hat{a}|a)$. Methods based on estimation of variance components exist to separate sampling variability from biological variability^{40,50}.

The bias in the estimate of biological variance when ignoring sampling variance, as well as the precision of the estimate, depend on the size of both variance components, which are different for juvenile and adult survival (see Table below).

As a typical example of adult survival, we assume true survival rates equal to 0.85, 0.86, ..., 0.95, for an average survival of 0.90 and σ_a equal to 0.030. For juvenile survival, we assume that true survival rates are equal to 0.25, 0.30, ..., 0.75, for an average survival of 0.50 and σ_a equal to 0.158.

	Adult Survival			Juvenile Survival		
N	50	100	200	50	100	200
σ_a	0.051	0.042	0.036	0.166	0.162	0.160
Relative Bias	70	40	20	5	2	1
SE ($\hat{\sigma}_a$)	0.015	0.010	0.006	0.022	0.015	0.010

The sampling precision increases with the number of animals released, N , and when survival rate is close to 1 (or 0). The relative bias when ignoring sampling precision, $(\sigma_a - \hat{\sigma}_a)/\sigma_a$ is then expected to be larger for adult survival than for juvenile survival (for a given N), but the precision of the estimate, $\hat{\sigma}_a$, is higher.

the exception of disease. While this pattern is obvious from available case studies, our understanding of population dynamics in large herbivore populations suffers from a biased distribution of studies. First, reliable information exists for only 16 of about 250 extant species of large herbivores, a sampling intensity of 6%. More importantly, 15 of the 16 species are temperate ungulates, while most ungulate species occur in the tropics. We thus require detailed information about variability of vital rates for large tropical herbivores. Differences in seasonality and in predation pressure may well result in different population dynamics for temperate and tropical ungulates^{33,34}. To establish how variation in demographic variables affects population size, however, we need more studies based on marked animals monitored over several years. Such studies will enable us to combine the observed temporal variation of a given vital rate with the calculated effect of a change in this vital rate (elasticity) to correctly assess the respective roles of recruitment and adult survival on population dynamics of large herbivores. Recent intensive radio-tracking studies have been particularly useful because they often obtained information on causes of death^{17,19,35}. Knowledge of causes of death allows a better estimation of the impacts of different mortality factors.

Many long-term studies of population dynamics of large herbivores have relied almost exclusively on observational evidence. Experimental manipulations of population size³⁶ and of other ecological variables such as predation pressure would provide more reliable information. Manipulations would also provide data on the effects of population density or predation over a shorter time than observational studies. Ungulate populations that are subject to hunting or other forms of artificial control provide ideal opportunities for experimental tests of density dependence¹⁷. Predator control and predator reintroduction programs provide the opportunity to assess the role of predation. Therefore, cooperation

among researchers and government agencies in long-term studies of ungulates is likely to advance our understanding of population ecology while providing useful information for conservation and management.

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