

## TESTING THE IRRUPTIVE PARADIGM OF LARGE-HERBIVORE DYNAMICS

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**Abstract.** A dominant paradigm in understanding and managing large herbivores is that, after introduction to new range or release from harvesting, the herbivore population increases to peak abundance, crashes to a lower abundance, and then increases to a carrying capacity lower than peak abundance. However, support for the paradigm has been largely anecdotal. We first developed two mathematical models to better describe irruptive dynamics. The models differed in the form of the postcrash growth toward carrying capacity: the “Caughley model” included a time lag that generated dampening oscillations, and the “Leopold model” did not. We then evaluated which of four models ( $\theta$ -logistic, delayed-logistic, Leopold, and Caughley) best described the dynamics of seven ungulate populations either introduced to new range ( $n = 5$  populations) or released from harvesting ( $n = 2$ ). The dynamics of six of the populations were best described by irruptive models (two by the Leopold, one by the Caughley, and three by the delayed-logistic), and one of the populations did not display irruptive dynamics ( $\theta$ -logistic model). The limited data thus support the widespread existence of irruptive dynamics, and we encourage the consideration of irruptive models in studies of large-herbivore dynamics.

**Key words:** bighorn sheep; delayed-logistic growth; eruptions; ibex; irruptions; large herbivores; population dynamics; red deer; reindeer; time lags.

### INTRODUCTION

A dominant paradigm in the ecology and management of large herbivores is that, following introduction to new range or release from harvesting, the herbivore population increases to peak abundance, crashes to a lower abundance, and then increases to a carrying capacity lower than peak abundance (Leopold 1943, Riney 1964, Caughley 1970, 1976a, 1979, McCullough 1997). This phenomenon has been termed an “irruption” (Leopold 1943) or “eruption” (Riney 1964, Caughley 1970). It has been suggested that there is a greater difference between peak abundance and subsequent carrying capacity in irruptions following the introduction of a herbivore to new range than in irruptions where the herbivore has been present in the system for some time, e.g., after release from harvesting (Caughley 1979, McCullough 1997). However, inferences about irruptions have tended to be anecdotal (McCullough 1997). One reason for this is the lack of a single-species model for testing whether or not population dynamics have been irruptive. Another reason is that the quality of time series with which to make inferences from has been poor (Caughley 1970).

In this paper, we first develop single-species models describing the hypothesized irruptive dynamics of large

herbivores. We then examine the generality of the irruptive paradigm by evaluating which of the models best explain the dynamics of large herbivores either introduced to new range or released from low densities following the prohibition of harvesting.

### MODELS

#### Current models

The single-species model most used for understanding the dynamics of large-herbivore populations has been the  $\theta$ -logistic (or variants thereof; Turchin 2003):

$$N_{t+1} = N_t \exp(r_m [1 - (N_t/K)^\theta]) \quad (1)$$

where  $N_t$  is the population size at time  $t$ ,  $r_m$  is the intrinsic rate of increase,  $K$  is the carrying capacity, and  $\theta$  is the shape parameter influencing the form of density dependence (Fig. 1). However, the  $\theta$ -logistic can only generate irruptive dynamics when  $r_m > 2$  (May 1981), a value far greater than has been estimated for large herbivores (Sinclair 1996). The delayed-logistic model (Hutchinson 1948; Fig. 1) has an additional parameter,  $T$ , describing a time delay in the impact of population size on the population's growth rate:

$$N_{t+1} = N_t \exp(r_m [1 - (N_{t-T}/K)^\theta]). \quad (2)$$

The form of the dynamics of the delayed-logistic depends on the product of  $r_m$  and  $T$ , ranging from a monotonic increase to  $K$ , approach via dampened oscillations, and stable limit cycles (Caughley 1976a, Turchin 2003). Although the delayed-logistic appears to be a better descriptor of irruptive dynamics than the

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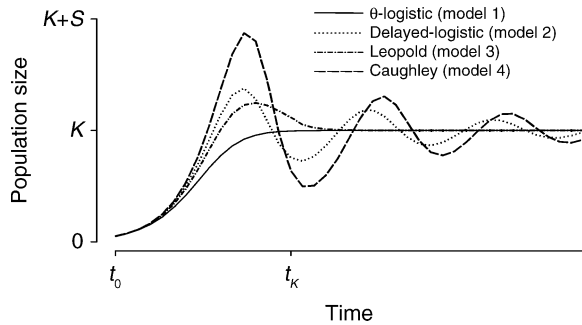


FIG. 1. The four structural models that we compared.  $K$  is the carrying capacity,  $S$  is the surplus,  $t_0$  is the time of colonization, and  $t_K$  is the time when  $S = 0$ .

$\theta$ -logistic (Caughley 1976a), it fails to capture the crash and subsequent increase to a carrying capacity lower than the initial peak envisaged by Leopold (1943), Riney (1964), and Caughley (1970).

#### New irruptive models

A key issue in irruptive dynamics is how the “capital” supply of food diminishes following colonization (Leopold 1943, Riney 1964, Caughley 1970, 1976a, 1979, McCullough 1997). We modified model 1 by adding a term describing a linear decline in “surplus” resources ( $S$ ) from time at colonization ( $t_0$ ) until all surplus is consumed (i.e.,  $S = 0$ ) at time  $t_K$  (Fig. 2):

$$N_{t+1} = \begin{cases} N_t \exp \left[ r_m \left( 1 - \left[ \frac{N_t}{K + S \left( 1 - \frac{t}{t_K} \right)} \right]^\theta \right) \right] & t \leq t_K \\ N_t \exp [r_m (1 - [N_t/K]^\theta)] & t > t_K. \end{cases} \quad (3)$$

Because Leopold (1943) was the first to describe irruptive dynamics, we term model 3 the Leopold model (see also McCullough 1997; Fig. 1).

Subsequent workers (Riney 1964, Caughley 1970, 1976a, 1979) viewed the irruption differently from Leopold (1943), believing that the postcrash equilibrium was attained via a dampened oscillation (McCullough 1997). We modeled this difference by adding a time lag ( $T$  in model 2):

$$N_{t+1} = \begin{cases} N_t \exp \left[ r_m \left( 1 - \left[ \frac{N_{t-T}}{K + S \left( 1 - \frac{t}{t_K} \right)} \right]^\theta \right) \right] & t \leq t_K \\ N_t \exp [r_m (1 - [N_{t-T}/K]^\theta)] & t > t_K. \end{cases} \quad (4)$$

The effect of  $T$  is to increase the magnitude of the population crash (Fig. 1). In deference to the contributions of Graeme Caughley to the irruptive paradigm, we term model 4 the Caughley model (Fig. 1).

#### Confronting the models with data

We believe that the most useful model will both capture the hypothesized structural dynamics of the system (Nichols 2001) and adequately fit independent data sets (Cormack [1994], cited in Morgan [2000]). Our general approach was to use the four models as representations of hypotheses and to evaluate the relative support for the models using information-theoretic model selection (Burnham and Anderson 2002). We recognize that our linear model of resource depletion is simplistic, but we believe that it is sufficient to enable model-based evaluation of hypotheses.

We first evaluated support for the four models using the data cited by Caughley (1987) as evidence for an “irruptive fluctuation typical of a herbivore colonizing a new environment.” The data were numbers of domestic sheep (*Ovis aries*) in the rangelands of western New South Wales (NSW), Australia, from 1860 to 1957 (Butlin 1962). The population would have been subject to harvesting and to predation by feral pigs (*Sus scrofa*), wild dogs (*Canis lupus*), and foxes (*Vulpes vulpes*).

We then searched the published literature for suitable data with which to test the models. We aimed to use data meeting three criteria. First, the data should have been a time series of  $\geq 20$  annual estimates of abundance from the time of introduction; Caughley (1970) suggested 20 years as the minimum period for large herbivores to undergo the increase, peak, and crash that characterizes an irruption. Second, the population should not have been subject to any mammalian predation or harvesting. Third, the annual estimates of abundance should have been based on complete annual censuses such that measurement errors were small relative to the magnitude of true changes in abundance. Only one data set satisfied all three criteria. Ibex (*Capra ibex*) were studied in the Swiss National Park, southeastern Switzerland, from 1920 to 1989 (Sæther et al. 2002). Seven animals were introduced in 1920 and the population was subsequently censused annually except during 1941–1943. Four data sets met the first and third criteria. Reindeer (*Rangifer tarandus*) were introduced to two islands in the Pribilof Group, USA, in 1911 (Scheffer 1951); 25 animals were introduced to St. Paul

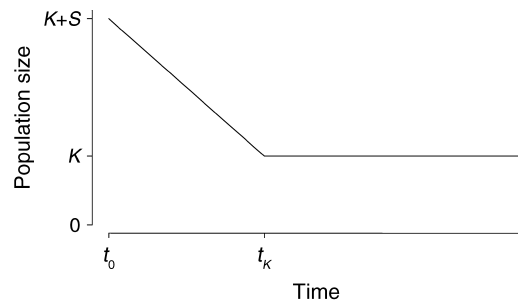


FIG. 2. Schematic representation of how surplus resources ( $S$ ) decline during an irruption.  $K$  is the carrying capacity,  $S$  is the surplus, and  $t_K$  is the time when the surplus is 0.

Island, and 15 to St. George Island. A count was undertaken annually from 1912 to 1950, with the exceptions of 1942–1945 on St. George, and 1942–1944 and 1950 on St. Paul. Scheffer (1951) thought that counts were within 10% of the true abundances. Some animals were harvested after 1916, but the percentage harvested was low on both islands (mean, 5%; range, 0–28%). Fifteen reindeer were also introduced to a peninsula on the northwestern coast of Svalbard, Norway (Aanes et al. 2000). An annual count was undertaken from 1979 to 1998. Occasional predation of reindeer by polar bears (*Ursus maritimus*) was thought not to have had a large impact on the size of the Svalbard reindeer population (Derocher et al. 2000). Because three reindeer were lost from the herd immediately after introduction, we assumed an initial population size of 12 (Aanes et al. 2000).

We included two studies in which the populations apparently had been held at low densities for many years prior to the prohibition of harvesting. Hence, the populations were predicted to exhibit irruptions of lesser magnitude than those introduced to new range (Caughley 1979, McCullough 1997). Both of these data sets met only the third criteria. Bighorn sheep (*Ovis canadensis*) were counted at Ram Mountain, Alberta, from 1975 to 1997 (Festa-Bianchet et al. 2003). From 1972 to 1980, yearly removals of 12–24% of the adult ewes kept the population density low and stable: there were no removals of adult ewes after 1980. The total number of sheep present was counted following lambing. The Ram Mountain population was isolated from other bighorn sheep populations, with only a few males sometimes migrating. Although wolves (*Canis lupus*), black bears (*Ursus americanus*), and cougars (*Puma concolor*) were present at Ram Mountain, there was almost no predation of bighorn sheep until after the 1997 count (Réale and Festa-Bianchet 2003). However, the population was still subject to a small harvest of rams (mean, 2%; range, 0–5%; M. Festa-Bianchet, *personal communication*). We used data for 1981–1997 (Festa-Bianchet et al. 2003). Red deer (*Cervus elaphus*) in the North Block of the Isle of Rum, Scotland, have been censused annually (25–61 censuses per annum) since 1971 (Clutton-Brock et al. 1997). Culling ceased in the North Block in 1972, but on the remainder of the island there was an annual cull of 14% between 1971 and 1990 (T. Coulson, *personal communication*). We used the observed numbers of deer reported annually in the North Block from 1974 (i.e., two years after culling ceased) to 1990 (Clutton-Brock et al. 1997, Coulson et al. 2004).

#### Model fitting and selection

We fitted the four models numerically using maximum likelihood, following Hilborn and Mangel (1997). We assumed that all error ( $\sigma$ ) was observational and lognormally distributed (as is the norm for population trajectories; Eberhardt 1978, Halley and Inchausti

2002). We estimated  $\theta$  only for the  $\theta$ -logistic model; for the remaining models,  $\theta$  was fixed at 1.

We used Akaike's Information Criterion corrected for sample size ( $AIC_c$ ) to rank the four models for each of the seven time series (Burnham and Anderson 2002). We report parameters only for the models having "substantial support" (i.e., within two  $AIC_c$  units; Burnham and Anderson [2002]). Model likelihoods were optimized using the nlminb algorithm in S-Plus (Insightful 2003). The nlminb algorithm uses the quasi-Newton method to identify the parameter values that minimize the negative log-likelihood for smooth nonlinear functions subject to bounds. We constrained  $r_m$  within biologically sensible values (Sinclair 1996) to assist with likelihood optimization. Potential values of  $T$  and  $t_K$  were set to integer values, and a grid search was used to identify the model(s) with the lowest  $AIC_c$ . We emphasize that we were most interested in assessing structural uncertainty in population models (i.e., the relative support for models 1–4) rather than parameter uncertainty within each population model (Nichols 2001, cf. Sæther et al. 2002).

#### RESULTS

The only model to have substantial support for explaining the dynamics of domestic sheep introduced to western New South Wales was the Caughley model (model 4 in Table 1, Fig. 3a). The next best model was the Leopold (model 3), but both the  $\theta$ - and delayed-logistic models performed very poorly (Table 1). The Caughley model estimated that the sheep population took 39 years to exhaust the surplus, and that the dampened oscillations were generated by a lag of three years (Table 2).

For the four other populations introduced to new range, the  $\theta$ -logistic (model 1) performed poorly, ranking fourth for three populations and third for one population (Table 1). The dynamics of ibex introduced to Swiss National Park were best explained by the delayed-logistic model (Table 1, Fig. 3b). The delayed-logistic model estimated a carrying capacity of 200 ibex and a lag of eight years (Table 2). The dynamics of reindeer introduced to St. George Island were best explained by the Leopold model, but there was some evidence for the existence of dampening oscillations (i.e., the Caughley model, Table 1, Fig. 3c). This population exhausted the surplus in an estimated 15 years, and the carrying capacity was estimated to be 45 reindeer (Table 2). In contrast, the dynamics of reindeer introduced to St. Paul Island were best explained by the delayed-logistic model (Table 1, Fig. 3d), with a lag of 12 years (Table 2). However, we note that the St. Paul Island population appeared to be close to extinction when the last census was conducted in 1950 ( $n = 8$  reindeer). The Leopold model best explained the dynamics of reindeer introduced to Svalbard (Table 1, Fig. 3e); the Caughley model parameters could not be estimated for this population.

TABLE 1. Comparison of the four candidate models explaining the dynamics of seven large-herbivore populations after introduction to new range (domestic sheep, ibex, and reindeer) or release from harvesting (bighorn sheep and red deer).

Species, population, and data source	Model	$K$	Log-likelihood	$AIC_c$	$\Delta AIC_c$	Rank
Domestic sheep, NSW (Butlin 1962)	1	4	-15.58	39.59	62.90	4
	2	4	-8.30	25.26	48.57	3
	3	5	14.82	-19.00	4.31	2
	<b>4</b>	<b>6</b>	<b>18.11</b>	<b>-23.31</b>	<b>0.00</b>	<b>1</b>
Ibex, Swiss National Park (Sæther et al. 2002)	1	4	9.14	-7.35	21.57	4
	<b>2</b>	4	<b>18.77</b>	<b>-28.92</b>	<b>0.00</b>	<b>1</b>
	3	5	14.50	-18.06	10.86	3
	4	6	18.77	-24.20	4.72	2
Reindeer, St. George Island (Scheffer 1951)	1	4	-32.68	74.54	36.32	4
	2	4	-27.62	64.42	26.20	3
	<b>3</b>	<b>5</b>	<b>-13.20</b>	<b>38.22</b>	<b>0.00</b>	<b>1</b>
	4	6	-13.32	41.26	3.04	2
Reindeer, St. Paul Island (Scheffer 1951)	1	4	-38.12	85.37	43.97	4
	<b>2</b>	<b>4</b>	<b>-16.13</b>	<b>41.40</b>	<b>0.00</b>	<b>1</b>
	3	5	-18.89	49.54	8.14	3
	4	6	-15.85	46.25	4.85	2
Reindeer, Svalbard (Aanes et al. 2000)	1	4	7.76	26.02	43.91	3
	2	4	1.49	13.48	31.37	2
	<b>3</b>	<b>5</b>	<b>-15.94</b>	<b>-17.89</b>	<b>0.00</b>	<b>1</b>
	4	6	no conv.			4
Bighorn sheep, Ram Mountain (Festa-Bianchet et al. 2003)	1	4	16.38	-21.43	4.44	3
	<b>2</b>	<b>4</b>	<b>18.52</b>	<b>-25.70</b>	<b>0.17</b>	<b>2</b>
	<b>3</b>	<b>5</b>	<b>20.66</b>	<b>-25.87</b>	<b>0.00</b>	<b>1</b>
	4	6	20.46	-20.51	5.36	4
Red deer, Rum (Clutton-Brock et al. 1997)	<b>1</b>	<b>4</b>	<b>27.68</b>	<b>-44.50</b>	<b>0.19</b>	<b>2</b>
	<b>2</b>	<b>4</b>	<b>27.77</b>	<b>-44.69</b>	<b>0.00</b>	<b>1</b>
	3	5	28.25	-41.88	2.81	3
	4	6	no conv.			4

Notes: Model numbers correspond to those in the text.  $K$  is the number of parameters in the model; for the log-likelihood, "no conv." means "no convergence";  $\Delta AIC_c$  is the difference between the Akaike Information Criterion ( $AIC_c$ ) for each model and that of the best-fitting model. Models within two  $AIC_c$  units are shown in boldface.

Of the two populations released from harvesting, only one (bighorn sheep) showed irruptive dynamics (Fig. 3f). Although the dynamics of bighorn sheep at Ram Mountain were similarly well described by the delayed-logistic (model 2) and the Leopold models (model 3, Table 1), the estimated surplus for the Leopold model (43 281 sheep; Table 2) was unreasonably large; we believe that the delayed-logistic is the most realistic model for this population. The delayed-logistic model estimated a carrying capacity of 86 sheep and a lag of nine years for this population (Table 2). There was little support for either the  $\theta$ -logistic or the Caughley model (Table 1, Fig. 3f). Red deer on Rum did not exhibit irruptive dynamics (Fig. 3g). The  $\theta$ -logistic (model 1) and the delayed-logistic (model 2) models had similar support for explaining the population dynamics of red deer on Rum (Table 1, Fig. 3g), and there was some support for the Leopold model. The Caughley model could not be fitted to the Rum data. Estimates of the intrinsic rate of increase and carrying capacity for red deer on Rum were similar for the  $\theta$ -logistic and the delayed-logistic models (Table 2).

#### DISCUSSION

Of the seven data sets that we examined, the dynamics of all but one (red deer on Rum) were clearly best described by at least one of the three irruptive models (i.e.,

models 2–4). Hence, the limited data support Caughley's (1979: 5) contention that "eruption is the basic pattern of growth for populations of large herbivores."

The difficulties of obtaining multiple data sets for testing models in which the predicted dynamics take many decades are obvious. All but one of the seven populations included in this study were subject to some harvesting and/or predation, and size estimates of the domestic sheep population in NSW also may have been subject to greater measurement error than for the other six populations. Hence, only one data set strictly met all three criteria for testing the dynamics of populations introduced to new range: ibex in Swiss National Park. However, providing that the limitations of the data are recognized, we believe that all seven populations provide useful tests of the models.

The question of which is the "best" irruptive model depends upon the purpose for using the model (Nichols 2001). Although the delayed-logistic was the model with substantial support for the most data sets (Table 1), this outcome may have been at least partly due to the short length of the data sets relative to the time required for the hypothesized irruptive dynamics to occur ( $\geq 20$  years; Caughley 1970, 1979). For example, differentiating between the Leopold and the Caughley model will require many years of postcrash data. Because the Caughley model contains one more parameter

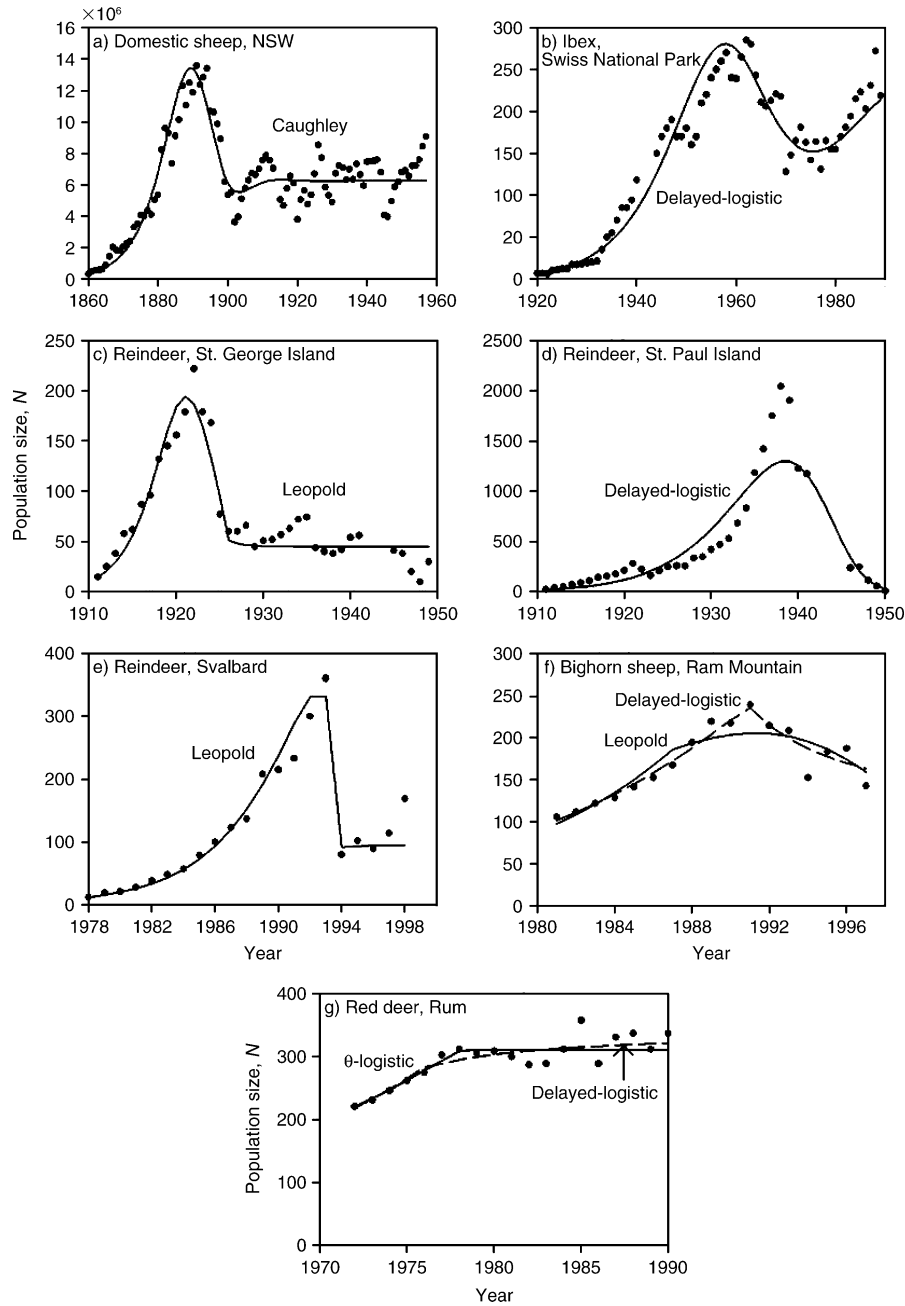


FIG. 3. The seven data sets and the model(s) of best fit (see Tables 1 and 2): (a) domestic sheep introduced to the rangelands of New South Wales (in millions,  $\times 10^6$ ); (b) ibex introduced to the Swiss National Park; reindeer introduced to (c) St. George Island, (d) St. Paul Island, and (e) Svalbard; (f) bighorn sheep at Ram Mountain following release from harvesting; and (g) red deer at Rum following release from harvesting (dashed line shows the delayed-logistic model).

( $T$ ) than the Leopold model, it is unsurprising that the former was the best model (as determined by  $AIC_c$ ) only for the longest data set (domestic sheep in NSW, 98 years). The second-longest time series (ibex, 67 censuses spanning 70 years) was of insufficient length to differentiate between a postcrash stable equilibrium (model 3) or dampening oscillation (model 4). Thus, in the absence of quantitative measures of food avail-

ability, it appears that there seldom will be sufficient data to discriminate the postcrash dynamics of large-herbivore irruptions.

We note the existence of many other time series of abundance estimates that qualitatively support the irruptive paradigm (e.g., reindeer introduced to St. Matthew [Klein 1968] and South Georgia Islands [Leader-Williams 1988], and moose *Alces alces* on Isle Royale

TABLE 2. Parameter estimates for the best-fitting model(s) identified in Table 1.

Population	Model	$\hat{r}_m$	$\hat{K}$	$\hat{S}$	$\hat{\theta}$ or $\theta^\dagger$	$\hat{\sigma}$	$\hat{T}$	$\hat{t}_K$
Domestic sheep, NSW	4	0.171	6.27‡	24.66‡	1.0	0.20	3	39
Ibex, Swiss National Park	2	0.138	200	na	1.0	0.18	8	na
Reindeer, St. George Island	3	0.422	45	500	1.0	0.35	na	15
Reindeer, St. Paul Island	2	0.194	343	na	1.0	0.39	12	na
Reindeer, Svalbard	3	0.296	96	3830	1.0	0.11	na	16
Bighorn sheep, Ram Mountain	2	0.085	86	na	1.0	0.08	9	na
	3	0.085	116	43 281	1.0	0.07	na	2
Red deer, Rum	1	0.059	310	na	36.6	0.05	na	na
	2	0.057	323	na	1.0	0.05	5	na

Notes: Model numbers correspond to those in text. Key to abbreviations:  $r_m$  is the intrinsic rate of increase,  $K$  is the carrying capacity,  $S$  is the surplus,  $\theta$  is the shape parameter,  $\sigma$  is the error,  $T$  is the time lag (yr), and  $t_K$  is the time (yr) when  $S$  is 0; na, not applicable to this model.

† The parameter  $\theta$  was estimated for model 1 and fixed at 1 for models 2–4.

‡ In millions ( $\times 10^6$ ).

[Peterson 1999]). McCullough (1997) also describes several case studies of deer irruptions in North America. Although it is tempting to cite these examples in support of the dominance of irruptive dynamics, there are few data points within each of these time series. There also may be publication bias, with studies of populations that do exhibit irruptive dynamics more likely to be published than those that do not. Our criteria attempted to minimize these potential biases. As Caughley (1970) showed in his “classic” (May 1994) refutation of the supposed irruption of mule deer (*Odocoileus hemionus*) on the Kaibab plateau (Arizona, USA), it is tempting to cite data that support one’s preferred paradigm.

There was some evidence to support the contention that the magnitude of the irruption is greater for herbivores introduced to new range than for those that had been present for some time and were released from lower densities (Caughley 1979, McCullough 1997). Red deer on Rum did not exhibit irruptive dynamics following their release from harvesting (Table 1), and the bighorn sheep population at Ram Mountain did not undergo the dramatic crash that typified the populations introduced to new range (Fig. 3). Caughley (1979) argued that a lesser irruption was likely for a population released from harvesting (or other limiting factors) because the capital, food, and hence the potential for overshoot of  $K$ , had already been eliminated from the system. Although we find Caughley’s logic compelling, more and longer data sets are required to reliably test his hypothesis.

Our irruptive models include an initial surplus ( $S$ ) of nonrenewable food that is eventually completely consumed by the herbivore population. Hence, a key issue in irruptive dynamics is how food diminishes after the herbivore is introduced or released from harvesting. Unfortunately, none of the published studies (Table 1) measured food. Characteristics of the food supply other than biomass are likely to be important determinants of  $S$  and  $K$ . In particular, the rates of consumption and renewal of the food supply appear to be of fundamental impor-

tance for understanding the dynamics of large herbivores (Caughley 1976a, b). Interestingly, despite high peak abundances of the herbivore,  $K$  may effectively be zero for some systems. For example, the reindeer populations introduced to the St. George and St. Paul islands apparently fed almost entirely on lichens, which have a low rate of renewal (Leader-Williams 1988). Although there are many possible elaborations to the irruptive models proposed here, the ability to discriminate between them is likely to be limited by the length of available time series. Better model fits than reported here (Table 1) might be obtained by including other variables in the models (e.g., precipitation for sheep in NSW and ibex in Swiss National Park [Sæther et al. 2002]), but we emphasize that the objective of our study was to identify which of the four structural models were best supported by the available data.

Caughley (1976a, b) considered that the  $\theta$ - and delayed-logistic models did not adequately represent the dynamics of the food supply during an irruption, and modified the Lotka-Volterra equations into an “interactive” model that related the dynamics of the herbivore to the dynamics of the food supply. Caughley considered that his interactive model was a more informative representation of ungulate population dynamics than either the logistic or delayed-logistic models. The Leopold and Caughley irruptive models developed here thus summarize potentially complex higher order community processes in a single-species framework. Testing interactive models of irruptive dynamics would require time series of changes in the abundance of both herbivores and their food supply; such data are not available.

Caughley (1970) observed differences in several parameters (survival, fecundity, and rate of increase) among populations of Himalayan tahr (*Hemitragus jemlahicus*) introduced to New Zealand; these differences were consistent with his predictions about the demographic changes that occur during irruptions. More recently, Eberhardt (2002) proposed a predictable sequence of changes in vital rates “as populations ap-

proach maximal levels”: juvenile survival decreases, followed by lower reproductive rates and, ultimately, lower female survival rates. The changes in age- and sex-specific vital rates observed in the red deer population at Rum following release from harvesting (Coulson et al. [2004]; see Fig. 3g) broadly support Caughley (1970) and Eberhardt (2002). The challenge is to understand how food interacts with age- and sex-specific vital rates to generate the postpeak irruptive dynamics observed in the other time series reported here (Fig. 3a–f).

Most previous investigations of large-herbivore population dynamics have assumed model structures that cannot describe irruptions. For example, Sæther et al. (2002) assumed that the underlying dynamics of the ibex population introduced to Swiss National Park were  $\theta$ -logistic (i.e., model 1), whereas our results indicate that irruptive models (i.e., models 2–4) are more appropriate (Table 1). Given the predominance of irruptions in the limited available data, we encourage the consideration of irruptive models in studies of large-herbivore population dynamics.

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#### LITERATURE CITED

- Aanes, R., B.-E. Sæther, and N. A. Øritsland. 2000. Fluctuations of an introduced population of Svalbard reindeer: the effects of density dependence and climatic variation. *Ecography* **23**:437–443.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodal inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.
- Butlin, N. G. 1962. Distribution of the sheep population: preliminary statistical picture, 1860–1957. Pages 281–307 in A. Barnard, editor. *The simple fleece: studies in the Australian wool industry*. Melbourne University Press, Parkville, Victoria, Australia.
- Caughley, G. 1970. Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. *Ecology* **51**: 53–72.
- Caughley, G. 1976a. Wildlife management and the dynamics of ungulate populations. Pages 183–246 in T. H. Coaker, editor. *Applied biology*. Academic Press, London, UK.
- Caughley, G. 1976b. Plant–herbivore systems. Pages 94–113 in R. M. May, editor. *Theoretical ecology: principles and applications*. Blackwell Scientific, Oxford, UK.
- Caughley, G. 1979. What is this thing called carrying capacity? Pages 2–8 in M. S. Boyce and L. D. Hayden-Wing, editors. *North American elk: ecology, behavior and management*. University of Wyoming Press, Laramie, Wyoming, USA.
- Caughley, G. 1987. Introduction to the sheep rangelands. Pages 1–13 in G. Caughley, N. Shepherd, and J. Short, editors. *Kangaroos: their ecology and management in the sheep rangelands of Australia*. Cambridge University Press, Cambridge, UK.
- Clutton-Brock, T. H., A. W. Illius, K. Wilson, B. T. Grenfell, A. D. C. MacColl, and S. D. Albon. 1997. Stability and instability in ungulate populations: an empirical analysis. *American Naturalist* **149**:195–219.
- Coulson, T., F. Guinness, J. Pemberton, and T. Clutton-Brock. 2004. The demographic consequences of releasing a population of red deer from culling. *Ecology* **85**:411–422.
- Derocher, A. E., Ø. Wiig, and G. Bangjord. 2000. Predation of Svalbard reindeer by polar bears. *Polar Biology* **23**:675–678.
- Eberhardt, L. L. 1978. Appraising variability in population studies. *Journal of Wildlife Management* **42**:207–238.
- Eberhardt, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. *Ecology* **83**:2841–2854.
- Festa-Bianchet, M., J.-M. Gaillard, and S. Côte. 2003. Variable age structure and apparent density dependence in survival of adult ungulates. *Journal of Animal Ecology* **72**: 640–649.
- Halley, J., and P. Inchausti. 2002. Lognormality in ecological time series. *Oikos* **99**:518–530.
- Hilborn, R., and M. Mangel. 1997. *The ecological detective*. Princeton University Press, Princeton, New Jersey, USA.
- Hutchinson, G. E. 1948. Circular causal systems in ecology. *Annals of the New York Academy of Sciences* **50**:221–246.
- Insightful. 2003. S-Plus. Version 6.2. Insightful Company, Seattle, Washington, USA.
- Klein, D. R. 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. *Journal of Wildlife Management* **32**:350–367.
- Leader-Williams, N. 1988. *Reindeer on South Georgia*. Cambridge University Press, Cambridge, UK.
- Leopold, A. 1943. Deer irruptions. *Wisconsin Conservation Bulletin* **8**:3–11.
- May, R. M. 1981. Models for single populations. Pages 2–25 in R. M. May, editor. *Theoretical ecology: principles and applications*. Blackwell, Oxford, UK.
- May, R. M. 1994. Graeme Caughley and the emerging science of conservation biology. *Trends in Ecology and Evolution* **9**:368–369.
- McCullough, D. R. 1997. Irruptive behavior in ungulates. Pages 69–98 in W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. *The science of overabundance: deer ecology and management*. Smithsonian Institution Press, Washington, D.C., USA.
- Morgan, B. J. T. 2000. *Applied stochastic modelling*. Arnold, London, UK.
- Nichols, J. D. 2001. Using models in the conduct of science and management of natural resources. Pages 11–34 in T. M. Shenk and A. B. Franklin, editors. *Modeling in natural resource management: development, interpretation, and application*. Island Press, Washington, D.C., USA.
- Peterson, R. O. 1999. Wolf–moose interaction on Isle Royale: the end of natural regulation? *Ecological Applications* **9**: 10–16.
- Réale, D., and M. Festa-Bianchet. 2003. Predator-induced natural selection on temperament in bighorn ewes. *Animal Behaviour* **65**:463–470.
- Riney, T. 1964. The impact of introductions of large herbivores on the tropical environment. IUCN (International Union for the Conservation of Nature) Publication New Series **4**:261–273.
- Sæther, B.-E., S. Engen, F. Filli, R. Aanes, W. Schröder, and R. Andersen. 2002. Stochastic population dynamics of an introduced Swiss population of the ibex. *Ecology* **83**:3457–3465.
- Scheffer, V. B. 1951. The rise and fall of a reindeer herd. *Scientific Monthly* **73**:356–362.
- Sinclair, A. R. E. 1996. Mammal populations: fluctuation, regulation, life history theory and their implications for conservation. Pages 127–154 in R. B. Floyd, A. W. Shepherd, and P. J. De Barro, editors. *Frontiers of population ecology*. CSIRO Publishing, Melbourne, Australia.
- Turchin, P. 2003. *Complex population dynamics: a theoretical/empirical synthesis*. Princeton University Press, Princeton, New Jersey, USA.