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STABILITY AND INSTABILITY IN UNGULATE POPULATIONS: AN EMPIRICAL ANALYSIS

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Abstract.—While many populations of large mammals are stable from year to year, some show persistent oscillations associated with high mortality. This article investigates the causes of variation in population stability in ungulates by comparing the contrasting dynamics of two naturally regulated island populations: the Soay sheep population of Hirta (St. Kilda), where numbers fluctuate by 60%–70% every 3 or 4 yr as a result of overcompensatory winter mortality, and the red deer population of the North Block of Rum, where numbers have been stable for over a decade. We suggest that the contrasting dynamics of these two populations are caused by differences in fecundity and maturation rate. Red deer show relatively low fecundity and slow maturation, and increases in population density depress both fecundity and juvenile survival. In contrast, the relatively rapid development of Soay sheep allows them to evade density-dependent effects on reproduction and survival until the population exceeds winter carrying capacity by a substantial margin, subsequently triggering overcompensatory mortality in late winter in all age classes.

While many populations of large mammals show considerable stability (Clutton-Brock et al. 1982; Fowler 1987; Sinclair 1989), recent studies of several ungulate populations provide evidence of oscillations that vary widely in regularity and periodicity. Periods of rapid decline followed by recovery have also been documented in populations of wild sheep, temperate deer, and tropical antelope (Geist 1971; Sinclair 1979; Fowler 1981; Bergerud 1983; Spraker et al. 1984; Prins and Weyerhauser 1987; Leader-Williams 1988; Tyler 1989; Fryxell et al. 1991), while persistent instability occurs in several populations of feral sheep and goats (Boyd 1981; Clutton-Brock et al. 1991; Boussès et al. 1992). However, the reasons that some populations remain stable while others oscillate are unknown.

Detailed demographic studies of two naturally regulated ungulate populations on Hebridean islands provide an unusual opportunity to investigate the causes of variation in stability. During the 1960s (Grubb 1974) and the 1980s (Clutton-Brock

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et al. 1991), the Soay sheep (*Ovis aries*) population of Hirta in the St. Kilda archipelago has oscillated from approximately 700 to 1,500 every 3 or 4 yr (see fig. 1A). The instability of the Hirta sheep population is in marked contrast to the relative stability of the red deer (*Cervus elaphus*) population of Rum in the Inner Hebrides (Clutton-Brock et al. 1985). Here, numbers of deer in the 12-km² North Block increased after the cessation of culling in 1972 and subsequently stabilized at about 300, fluctuating by less than 20% between 1980 and 1994 (see fig. 1B).

In this article, we combine analyses of empirical data with theoretical predictions derived from two different modeling approaches in an attempt to identify the proximate causes of the contrast in stability between the Soay population of St. Kilda and the (relatively) stable population of red deer on Rum. We initially describe demographic changes in both populations using age- and sex-structured Leslie matrix formulations that include accurate estimates of the key density-dependent parameters to ask under what circumstances the dynamics of the two populations converge. Subsequently, we use an energetic model to examine factors affecting the timing and distribution of mortality in these two populations, showing that these are related to differences in life-history parameters between the two species.

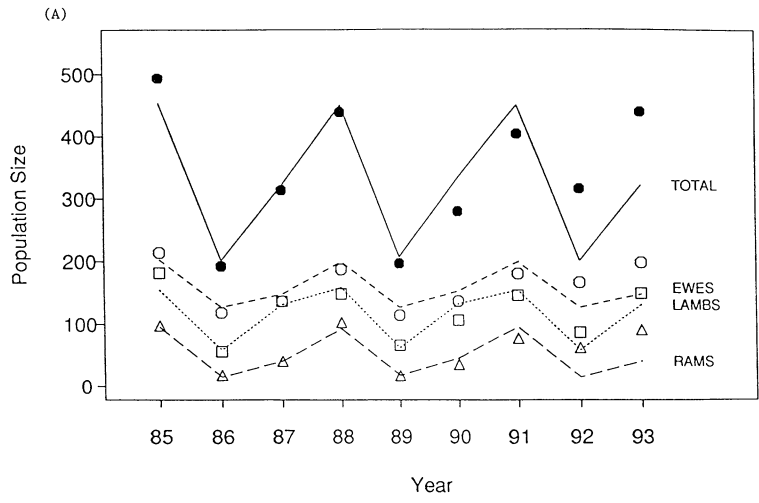
METHODS

Study Populations

Soay sheep (*Ovis aries* L.) are the most primitive domestic sheep in Europe, closely resembling domestic neolithic sheep first brought to Britain in approximately 5000 B.C. (Clutton-Brock 1981; Ryder 1983). They may have been introduced to the St. Kilda archipelago (57°49' N, 08°34' W) in the second millennium B.C. (Boyd and Jewell 1974) but, by historical times, were restricted to the uninhabited and virtually inaccessible island of Soay (99 ha). Following the evacuation of the human population of St. Kilda in 1930, 107 Soay sheep (20 rams, 44 ewes, 22 ram lambs, some of which may have been castrated, and 21 ewe lambs) were introduced from Soay to Hirta, the largest island of the archipelago (638 ha) in 1932. Numbers on Hirta increased rapidly: by 1939 the summer population was estimated to have reached 500; by 1948 numbers had risen to between 650 and 700, while the first organized census produced an estimate of 1,114 sheep in 1952 (Boyd 1974). Though the sheep are distributed throughout Hirta, intensive research has concentrated on animals living in the Village Bay area that make up about one-third of the island's population. Changes in population size in this area are closely correlated with changes in the total population of the island (Clutton-Brock et al. 1991). The Village Bay area is unfenced, and animals are free to emigrate or immigrate from other parts of the island. No mammalian predators are present on St. Kilda, though great skuas (*Stercorarius skua*) and greater black-backed gulls (*Larus marinus*) may occasionally kill lambs. The analysis described in this article is confined to the period 1985–1993.

Red deer (*Cervus elaphus* L.) were present on Rum (57° N, 6°20' W) from the early sixteenth century but were shot out by 1800. In approximately 1945, the island was restocked with deer from the mainland, and, since 1957 when the

Soay Sheep (Village Bay, Hirta)



Red Deer (North Block, Rum)

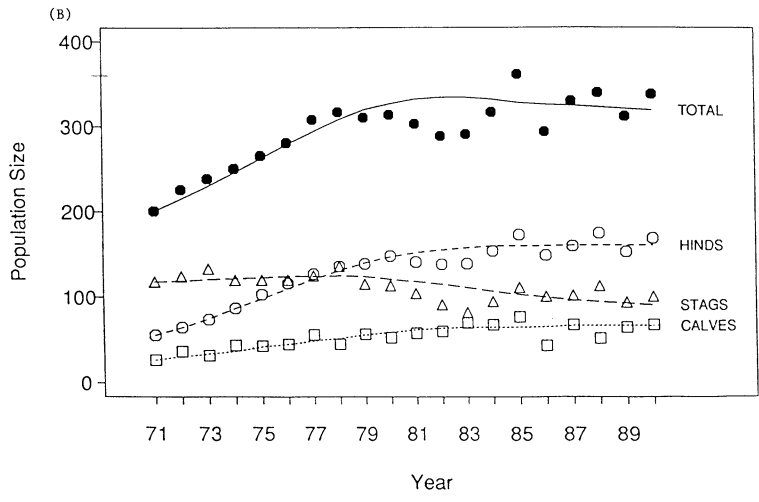
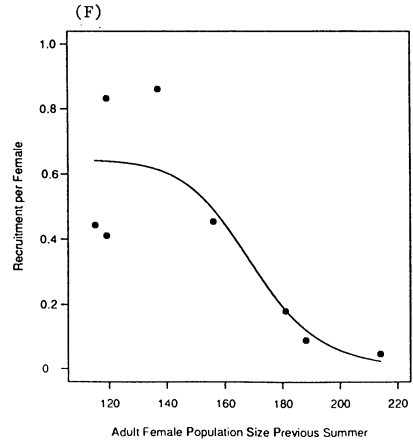
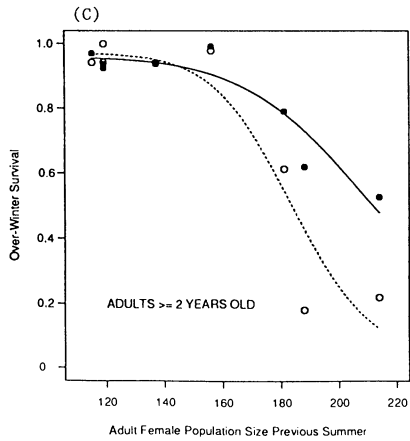
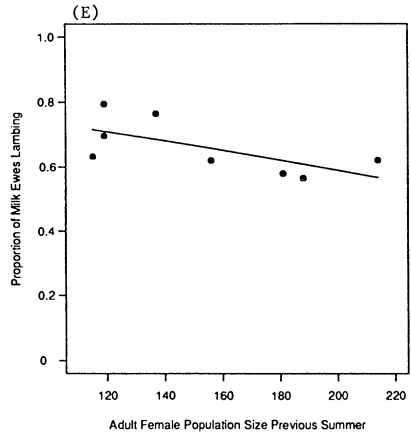
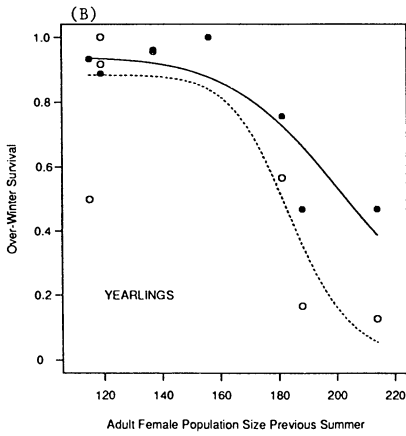
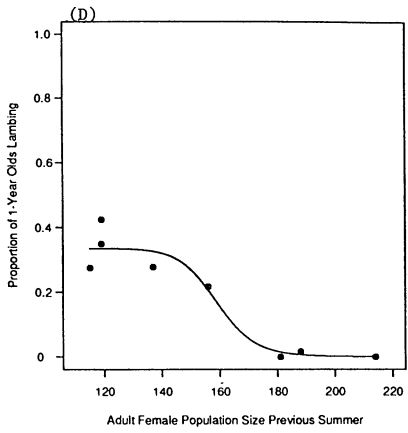
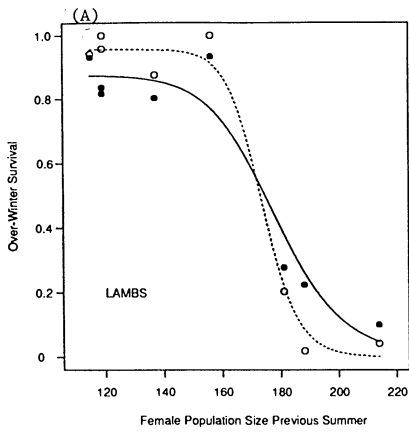


FIG. 1.—Numbers of (A) Soay sheep (*Ovis aries*) on Hirta, St. Kilda, 1985–1993 (Clutton-Brock et al. 1991; T. H. Clutton-Brock, unpublished data), and (B) red deer (*Cervus elaphus*) in the North Block of Rum, Inner Hebrides, 1971–1990 (Clutton-Brock and Albon 1989; T. H. Clutton-Brock, unpublished data). In each graph, the symbols represent the observed numbers of animals, and the lines indicate the yearly estimates predicted by a modified Leslie matrix model (see the appendix). The open squares are the observed numbers of juveniles (calves or lambs) in the summer population; the open circles are the number of female yearlings and adults (≥ 2 yr old); the open triangles are the number of male yearlings and adults (≥ 2 yr old); the solid circles are the total number of animals (adults, yearlings, and juveniles).



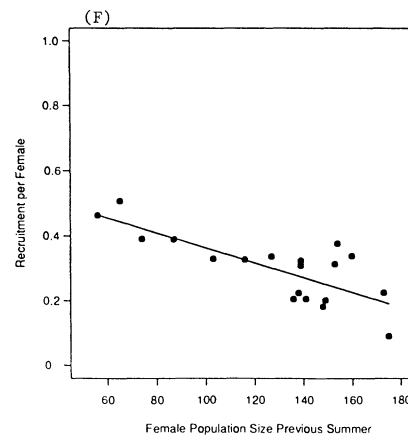
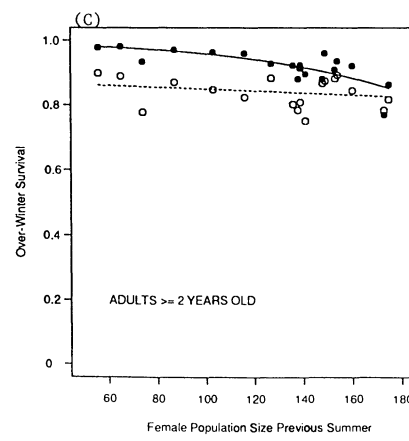
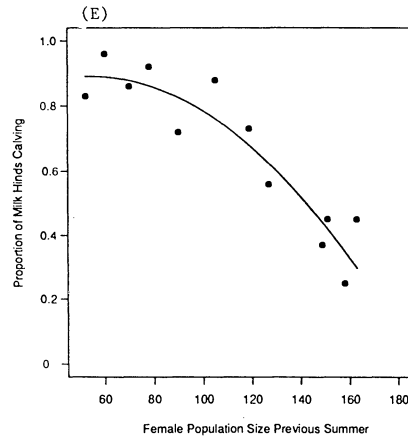
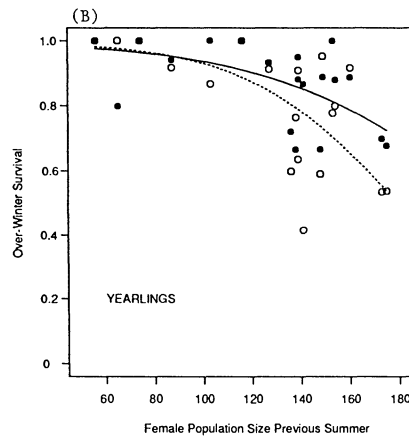
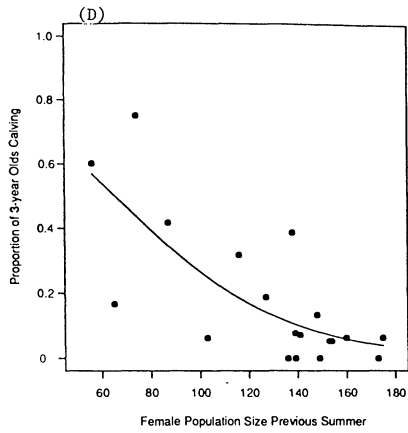
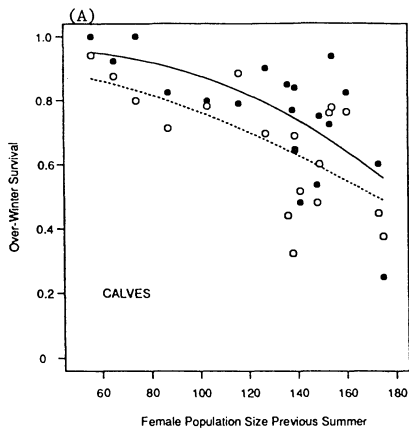
island became a nature reserve, numbers have usually been between 1,400 and 1,600. The entire population was culled annually until 1972 when culling ceased in the 12-km² North Block and detailed studies of reproduction and survival began (Clutton-Brock et al. 1982). Analysis is restricted to the period 1971–1993. Like that on St. Kilda, the study area is not fenced, and animals are free to emigrate or immigrate from other parts of the island. Emigration rates of females born in the study area are very low (Clutton-Brock et al. 1982). On Rum, too, no mammalian predators are present, but golden eagles sometimes kill calves (Clutton-Brock and Guinness 1975).

Recording Techniques

Between 1985 and 1993, over 95% of lambs born in the Village Bay area of Hirta were caught, weighed, and tagged each year (Clutton-Brock et al. 1991). As a result, the ages of most animals in the study population were known precisely throughout the later years of the study period, and more than 95% of animals were individually recognizable. Ages of animals marked as adults but not as lambs were estimated after their death by counting annuli in the cementum of the first incisor tooth (Clutton-Brock et al. 1991). We categorize animals as lambs until the beginning of their second summer. Individuals aged 13–24 mo are called yearlings and animals older than 24 mo, adults. Regular censuses of the study area enable us to follow individuals from birth to death. The size of the population resident in the study area is based on counts of individuals known to be alive on October 1 of each year. Fecundity in the Hirta population is high: most animals conceive in their first year of life and conceive each year thereafter (Grubb 1974; Clutton-Brock et al. 1991). However, crashes are followed by birth seasons when fecundity, birth weights, and juvenile survival are depressed (Clutton-Brock et al. 1992), probably as a result of the poor body condition of females that have survived the crash (fig. 2A–F). Depending on population density, between 5% and 23% of ewes ≥ 1 yr old bear twins (Clutton-Brock et al. 1992).

Similar data have been collected for the red deer population of the 12-km² North Block of Rum since 1972 (Clutton-Brock et al. 1982). Following the cessation of

FIG. 2.—Effects of population density on the survival and fecundity of Soay sheep on Hirta, 1985–1993. Except where stated, survival curves were estimated by fitting equation (1); see the text. Parameter values a , b , and d are given to three significant figures. Open symbols and dotted lines represent values for males; closed symbols and solid lines, values for females. *A*, Changes in survival of lambs (males, $a = 0.00576$, $b = 28.7$, $d = 0.956$; females, $a = 0.00562$, $b = 15.3$, $d = 0.875$). *B*, Changes in the survival of yearlings (males, $a = 0.00544$, $b = 17.8$, $d = 0.884$; females, $a = 0.00484$, $b = 9.46$, $d = 0.939$). *C*, Changes in the survival of adults (> 24 mo old) (males, $a = 0.00542$, $b = 13.0$, $d = 0.970$; females, $a = 0.00467$, $b = 8.93$, $d = 0.959$). *D*, Changes in the proportion of lambs that successfully give birth at approximately 12 mo ($a = 0.00629$, $b = 24.1$, $d = 0.335$). *E*, Changes in the proportion of milk ewes lambing (logistic regression, $a = 1.68$, $b = -0.00657$). *F*, Changes in the recruitment of lambs the following season per female surviving the winter ($a = 0.00589$, $b = 14.1$, $d = 0.643$). Milk ewes are those that successfully reared a lamb the previous year. Measures of reproduction and survival are plotted against adult female density to make plots comparable with those in figure 4.



culling in 1972, numbers of deer in the North Block initially rose from 57 hinds and 121 stags to 141 hinds and 155 stags in 1978 (Clutton-Brock et al. 1985). Throughout the 1980s, total numbers remained between 290 and 350, varying in relation to winter weather and late-winter mortality (fig. 1B).

In contrast to the Soay sheep, red deer hinds on Rum do not conceive until they are at least 2 yr old, and the number bearing calves at 3 yr old declines with population density from 60% to 10% (fig. 3D). Subsequently, virtually all hinds that failed to rear a calf the previous year conceived in the October rut, while the proportion of successful breeders that conceived again the following season declined from 90% to 30% (Clutton-Brock and Albon 1989).

In the red deer, adult males and females are largely segregated (Clutton-Brock et al. 1987), and male numbers probably exert little effect on female breeding performance and survival (Clutton-Brock et al. 1985). When plotting demographic variables against density, we consequently use female density only. In the sheep, there is less segregation between the sexes, but, to maintain comparability with figures for deer, we have plotted demographic variables on female density, too. Because female numbers and total numbers are closely correlated ($r = 0.83$), this has little effect on the form of relationships.

Leslie Matrix Model

To explore the dynamics of both populations, we used a modified Leslie matrix model (see the appendix). Seasonally reproducing ungulate populations are generally modeled using discrete, age-structured, deterministic formulations (Leslie 1945, 1948; Caswell 1989). These models, which are based on Leslie matrices (Leslie 1945, 1948), can be expressed as

$$n_{t+1} = M_t n_t,$$

where n_t and n_{t+1} are age- (and possibly sex-) structured vectors of population abundance in the subscripted years and M_t is the transition matrix, expressing the operation of survival and fecundity in year t . A crucial factor in any such model is how we model density-dependent limitations on survival and fecundity.

FIG. 3.—Effects of population density on the survival and fecundity of red deer in the North Block of Rum, 1972–1990. Except where stated, survival curves were estimated by fitting equation (2). Parameter values a and b are given to three significant figures. Open symbols and dotted lines represent values for males; closed symbols and solid lines, values for females. *A*, Changes in survival of calves (males, $a = 2.81$, $b = 0.0163$; females, $a = 4.28$, $b = 0.0232$). *B*, Changes in the survival of yearlings (males, $a = 5.82$, $b = 0.0323$; females, $a = 4.97$, $b = 0.0229$). *C*, Changes in the survival of adults (> 24 mo old) (males, $a = 1.96$, $b = 0.00228$; females, $a = 5.02$, $b = 0.0187$). *D*, Changes in the proportion of hinds that successfully give birth at approximately 3 yr ($a = 1.91$, $b = 0.0292$; see also Langvatn et al. 1996). *E*, Changes in the proportion of milk hinds calving (quadratic regression, $Y = 0.744 + 0.00541X - 0.0000500X^2$; see also Clutton-Brock et al. 1985). *F*, Changes in the recruitment of calves the following season per female surviving the winter (linear regression, $Y = 0.5937 - 0.0023X$). Milk hinds are those that successfully reared a calf the previous year. Measures of reproduction and survival are plotted against female density (adults and yearlings) since the sexes are extensively segregated (Clutton-Brock et al. 1987).

A variety of simple functional forms have been proposed to capture the spectrum of possible density-dependent responses, from undercompensatory via perfectly compensatory to overcompensatory. Here we adapt the following:

$$S = \frac{d}{1 + (aN)^b} \quad (1)$$

(Maynard-Smith and Slatkin 1973; Bellows 1981; Grenfell et al. 1992). Density-independent survival or fecundity is determined by the parameter d (thus, in the absence of density dependence, survival or fecundity is equal to d); parameter a represents the reciprocal of the population density (N) above which density dependence occurs; and parameter b determines the form of density dependence, from undercompensation ($0 < b < 1$) and perfect compensation ($b = 1$) to overcompensation ($b > 1$). This nonlinear model describes well the asymmetric density-dependent survival curve of Soay sheep, and parameter estimates can be determined using maximum-likelihood methods. However, in the red deer, density dependence is approximately linear, and maximum-likelihood models using equation (1) often fail to converge. Thus, for red deer, density dependence in survival and fecundity was determined by a simpler, logistic model:

$$S = \frac{e^{(a - bN)}}{1 + e^{(a - bN)}}, \quad (2)$$

where a and b are constants. Parameter values were estimated by binomial maximum likelihood. For the reasons described earlier, density dependence in survival and reproduction was calculated with respect to the total number of adult females (≥ 1 yr old) in the population. For each sex, there are six age classes: calves or lambs, yearlings, 2-yr-olds, 3-yr-olds, 4-yr-olds, and 5-yr-olds and older. Values used in these models are described in the appendix.

Energetic Modeling

To investigate the causes of population crashes on St. Kilda, we constructed a numerical model of the movement of energy through the St. Kilda sheep population using empirical measures collected there or estimated from other studies of sheep (table 1). The model calculates the daily flux of material and energy through compartments representing the vegetation and the sheep population. The plant component of the model was adapted from Johnson and Thornley's (1983) model of vegetative grass growth and consists of four state variables, representing the biomass of new, expanding, mature, and decaying leaf biomass. Monthly averages of daily net aboveground primary production, as estimated on Hirta by D. Bazely (unpublished data), were used as inputs to the new leaf compartment. This was not varied with grazing intensity, on the conservative assumption that net production is insensitive to all but the extremes of sward conditions arising from variation in grazing pressure (Bircham and Hodgson 1983). The rate of tissue maturation determining the flow of leaf biomass through successive leaf age compartments is governed by a temperature-dependent first-order process, with rate constant, γ , given by

TABLE 1

SYNOPSIS OF PROCESSES AND VARIABLES INCLUDED IN THE MODEL

Process	State Variable Affected	Parameter	Causal Variables	Data	Reference
Grass:					
Growth	Young leaf, L1	Net aboveground primary production	D. Bazely, unpublished data
Maturation	Expanding leaf, L2	γ_m	Temperature	...	Johnson and Thornley 1983
Senescence	Mature leaf, L3	γ_m	Temperature	...	Johnson and Thornley 1983
Decomposition	Dead leaf, D	γ_d	Temperature	...	Floate 1970; Cayley 1980; Dickinson 1983
Sheep:					
Energy intake	Herbage mass, height, and digestibility; body mass of sheep	Digestibility of leaf: live, .77; dead, .44	Illius and Gordon 1987; Armstrong et al. 1986
Heat loss to environment	Fat-free mass per sheep; fat mass per sheep	...	Temperature; wind speed; body mass	...	A. W. Illius and T. H. Clutton-Brock, unpublished manuscript
Maintenance energy expenditure	Fat-free mass; fat mass	...	Body mass; time spent grazing	...	Agriculture and Food Research Council 1980
Growth	Fat-free mass; fat mass	...	Degree of maturity in body mass; nutrient balance	...	Taylor and Murray 1987
Reproduction	Sheep numbers per sex and age class	γ	...	All females have one lamb	...
Male reproductive investment	Fat-free mass; fat mass	...	Degree of maturity in body mass	Reproduction in time spent grazing	Grubb and Jewell 1974; I. R. Stevenson, unpublished data
Female reproductive investment	Fat-free mass; fat mass	...	Degree of maturity in body mass	Nutrient costs of pregnancy and lactation	Agriculture and Food Research Council 1980
Mortality	Sheep numbers in each age and sex class	σ	Energy balance; fat mass	Variation in body mass in February	T. H. Clutton-Brock, unpublished data

$$\gamma(T) = \gamma(20) \frac{T - T_0}{20 - T_0}, \quad (3)$$

where T ($^{\circ}\text{C}$) is the mean daily temperature, T_0 is the temperature at which leaf maturation ceases (taken to be 0°C), and $\gamma(20) = 0.15$ (Johnson and Thornley 1983). The mean value thus estimated for summer 1991 corresponds closely to the estimated rate of tiller appearance on Hirta (D. Bazely, unpublished data). Data collected by Floate (1970) on decomposition of *Agrostis/Festuca* litter were found to conform to the temperature relationship (eq. [3]) and, together with the data of Cayley et al. (1980) and Dickinson (1983), were used to derive the decomposition constant governing the loss of material from the system as $\gamma(20) = 0.023$. Mean monthly temperatures recorded at Benbecula from 1971 to 1990 were adjusted for St. Kilda according to Campbell (1974, p. 17).

The animal component of the model consists of three state variables, representing animal numbers, fat-free body mass, and fat mass, in each of three age classes (lambs, yearlings, and adults) in both sexes. The animal processes are described in terms of the flow of material from the vegetation (offtake) and the metabolism and expenditure of energy in activity, heat loss to the environment, body growth, depletion of fat reserves, and reproduction. Reproductive investment is described in terms of reduced food intake, increased locomotion and consequent loss of body reserves in rutting males, and the flow of energy and protein from ewes to lambs during pregnancy and lactation. This constitutes the energy balance of each animal and is calculated using models described in detail elsewhere (Illius and Gordon 1987). Mortality during winter, when intake is depressed by low vegetation biomass and when climatic heat loss is high, is determined by the exhaustion of body reserves. Mean body fat in each age and sex class is predicted for each day from the calculated energy balance and is assumed to be normally distributed with standard deviation σ . Mortality occurs in the proportion of animals in the tail of this distribution that projects below zero. Variance in body weight measured in February 1992 is used to estimate σ within age and sex classes in animals caught in cleits.

RESULTS

Comparative Dynamics of Soay Sheep and Red Deer

Fluctuations in the size of Soay sheep populations on Hirta (fig. 1A) are a consequence of sharply focused, overcompensatory density-dependent mortality (fig. 2A–C). When autumn population size in the study area is below 350 total (or 160 adult females), overwinter survival is high, whereas survival falls sharply once it exceeds a total of 400 (180 females). Lambs of both sexes, male yearlings, and adult males are disproportionately affected (fig. 2A–C). Following years when autumn numbers of females exceed 180 and winter mortality is high, recruitment is depressed (fig. 2F), partly as a result of a decline in the proportion of lambs that breed (fig. 2D), adult ewes that twin (Clutton-Brock et al. 1991), and neonates that survive (Clutton-Brock et al. 1991), whereas fecundity in mature ewes

changes little (fig. 2E). In other years, both fecundity and neonatal survival are uniformly high with the effect that recruitment shows little or no decline before crash years.

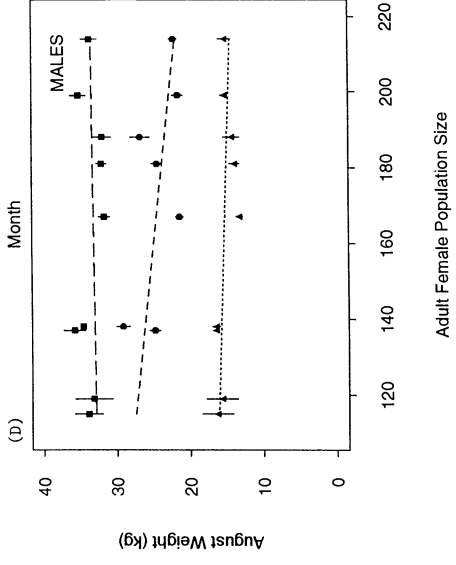
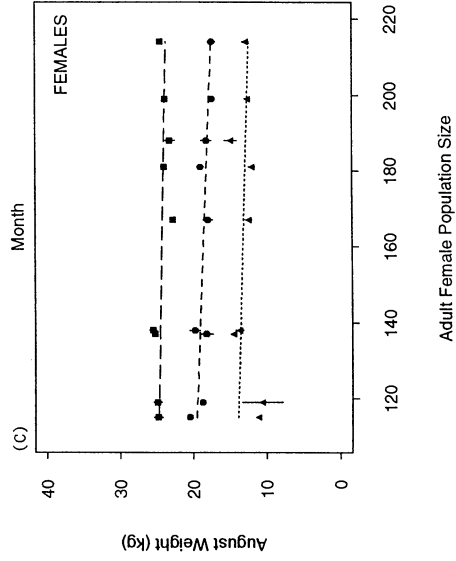
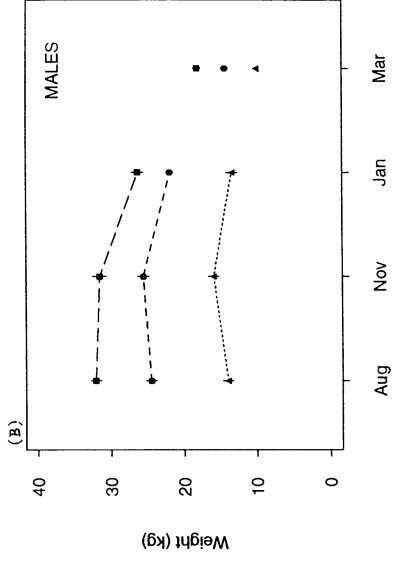
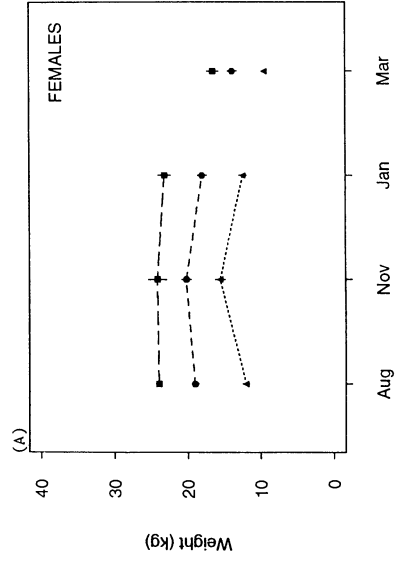
In contrast, the relative stability of the Rum deer population (fig. 1B) is associated with approximately linear density-dependent declines in the survival of calves and yearlings (fig. 3A, B) and smaller changes in adult survival (fig. 3C). Unlike the Soay sheep, neonatal mortality is unrelated to density (Clutton-Brock and Albon 1989), and density-dependent changes in calf survival (fig. 3A) are caused by changes in mortality during the first winter (Clutton-Brock and Albon 1989). In addition, both age at first breeding and fecundity decline with density in the deer (fig. 3D, E) so that recruitment is depressed (fig. 3F).

The Leslie matrix model was both qualitatively and quantitatively successful in generating dynamics that resembled those observed in the Soay sheep population on Hirta and red deer population on Rum (fig. 1). We subsequently investigated what changes would be necessary to stabilize sheep numbers and to destabilize deer numbers by multiplying the age-specific fecundity and density dependence parameters in each version of the model by a parameter representing a scaling constant. These analyses indicated that, to destabilize the red deer model, either fecundity would need to be at least three times higher than its present value, or density dependence would have to be at least twice as large as its current value. Thus, the dynamics of the red deer on Rum appear to be very stable. In contrast, analysis of the sheep model suggests that a reduction in fecundity of just 10% or in density dependence of 15% would be sufficient to stabilize the Soay sheep population on St. Kilda. Although this type of analysis is crude, it suggests that, under most conditions, ungulate populations can be expected to show considerable stability.

Why Is Winter Mortality Overcompensatory in Soay Sheep?

The underlying cause of death of most sheep dying in winter is starvation (Gulland 1992). During crash years, body weight declines by as much as 30% between January and March (fig. 4A, B). Autopsies show that sheep dying in late winter have virtually no fat reserves and that marrow fat is severely depleted (Gulland 1992).

Our energetic model's estimates of the availability of vegetation per head during the winter (fig. 5A) indicate that this is insufficient to cover the animals' requirements when summer numbers exceed a critical value and predict a rapid decline in body weight, which is particularly marked when total autumn numbers exceed 450 or female numbers exceed 200 (fig. 5B). The greater average population size predicted by the model can probably be accounted for by the fact that no account is taken of competition by sheep from outside the study area. If animals that exhaust their fat reserves die, these patterns predict a sudden increase in mortality from starvation as total autumn population size rises above 400 or female numbers rise above 170 (fig. 5C). Lambs, being smaller than adults, are more susceptible to starvation because they have smaller body fat reserves and because these are depleted at a higher rate through energy expenditure in thermoregulation



(a consequence of having a larger ratio of surface area to body mass). Adult males are expected to reach critical weights before females on account of heavy expenditure and reduced food intake during the autumn rut.

Relative mortality in different sex and age groups (fig. 2A–C) closely resembles the predictions of our model (fig. 5C). Mortality of yearlings is slightly higher than predicted, probably because the model underestimates the proportion of resources devoted to growth. The relative timing of mortality also resembles the predictions of our model: lambs of both sexes show elevated levels of mortality during the early winter, followed by yearling and adult males and adult females (fig. 5C; table 2). Mortality is not as closely synchronized in red deer, which also show a relatively early rise in mortality in yearling and adult females and greater variance in death dates in most categories (table 2).

Summer conditions and density-dependent changes in August body weight probably have relatively little effect on density-dependent changes in survival. As sheep density rises, August standing crop declines ($r = -0.692$, $n = 6$, $P = .029$). The August body weight of most categories of animals shows a significant decline with increasing density, but the magnitude of the change is small (fig. 4C, D). Several different processes may contribute to this. Although net aboveground primary production (NAPP) is not significantly depressed in precrash years, increased grazing pressure on St. Kilda is associated with an increase in the growth of shoot endophytes, which may reduce the digestibility of the vegetation (Vicari 1993). In addition, the sheep carry substantial populations of gastrointestinal nematodes (mostly *Teladorsagia* and *Nematodirus*), and the prevalence and number of strongyle eggs found in the feces rise with summer population density (Gulland 1991). Experimental removal of worm burdens during the summer and early winter before crashes increases the survival of treated animals (Gulland 1991; Gulland et al. 1993).

Why Does the Soay Sheep Population Exceed Winter Carrying Capacity?

The capacity of the sheep to exceed winter carrying capacity (thus generating periodically high mortality) is a consequence of three principal biological characteristics. First, their fecundity is unusually high for an ungulate since most females conceive in their first year of life and a substantial proportion of adult ewes

FIG. 4.—Changes in the mean (\pm SE) live weights of female (A) and male (B) sheep between August and March in a crash year (1991–1992). The last point on all lines is for dead animals only that were found in March and April. Changes in the mean live weight of female (C) and male (D) sheep of different age and sex categories in August in different years. Triangles represent lambs; circles, yearlings; and squares, adults ≥ 2 yr old. Regression analyses for females (C) are as follows: lambs, $Y = 15.590 - 0.015X$, $F = 5.515$, $df = 1, 228$, $P = .0197$, $r^2 = 0.024$; yearlings, $Y = 21.899 - 0.020X$, $F = 8.106$, $df = 1, 126$, $P = .0052$, $r^2 = 0.060$; adults, $Y = 25.810 - 0.010X$, $F = 5.109$, $df = 1, 472$, $P = .0243$, $r^2 = 0.010$. Regression analyses for males (D) are as follows: lambs, $Y = 17.969 - 0.016X$, $F = 5.096$, $df = 1, 200$, $P = .0250$, $r^2 = 0.024$; yearlings, $Y = 33.726 - 0.055X$, $F = 23.960$, $df = 1, 128$, $P < .0001$, $r^2 = 0.158$; adults, $Y = 32.165 + 0.006X$, $F = 0.179$, $df = 1, 100$, $P = .673$, $r^2 = 0.002$.

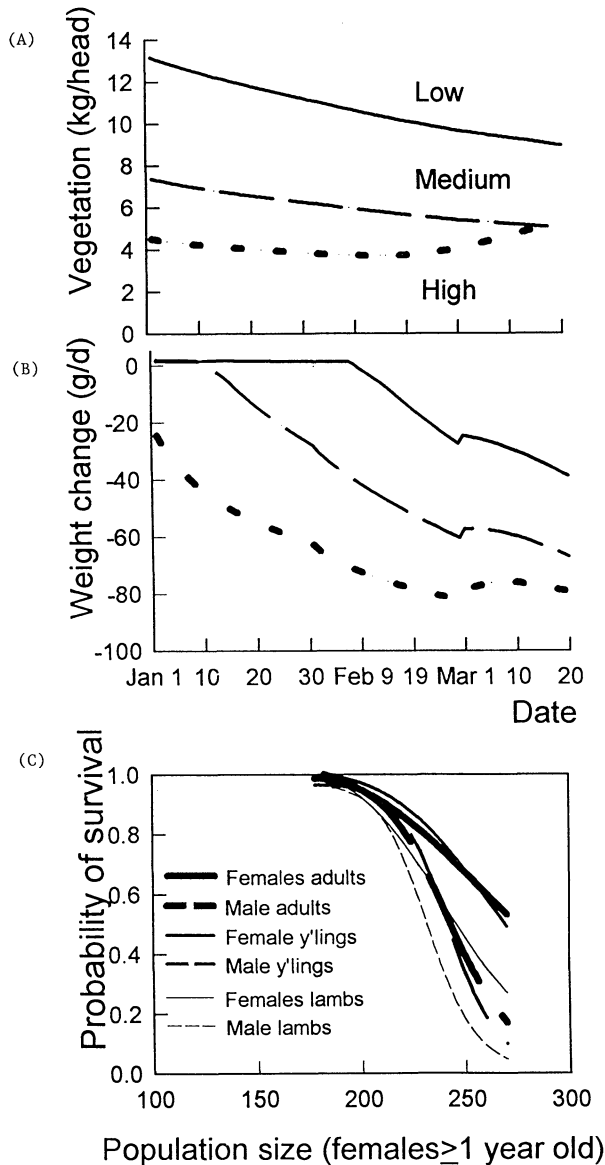


FIG. 5.—*A*, Predicted amount of vegetation available per head of sheep in Village Bay, Hirta, between January and March under low (solid line), medium (wide dashed line), and high (narrow dashed line) population density. For details of variables incorporated in the model, see table 1. The high rates of mortality at high population density cause an increase in available vegetation per head, slightly mitigating the rate of weight loss. *B*, Predicted patterns of weight loss in adult females. *C*, Predicted proportions of each class surviving winter plotted in relation to total population. Males are unable to regain body reserves after rutting at high population densities and are then more likely to die than females, while lambs of both sexes have lower body reserves than older animals. The results were obtained by initializing the model to a starting population of 400 sheep, in the ratio 0.5:0.2:1 females and 0.5:0.2:0.2 males and then running the simulation for 100 yr. The model population shows cyclic fluctuations, with crashes occurring about once every 4 yr that reduce the population from more than 1,600 to about 600, approximately the magnitude of mortality in crash years observed on St. Kilda.

TABLE 2
A COMPARISON OF THE MEANS AND VARIANCES IN DEATH DATES OF SOAY SHEEP ON HIRTA, ST. KILDA, AND RED DEER ON RUM

	SOAY SHEEP (HIRTA)			INTERSPECIFIC COMPARISON OF MEANS		INTERSPECIFIC COMPARISON OF VARIANCES		RED DEER (RUM)		
	Mean	SE	CV (%)	<i>n</i>				Mean	SE	CV (%)
Male lambs/calves	2.65 a	.15	55.1 b	101	NS	NS	NS	2.64 b	.09	49.8 a
Male yearlings	3.09 b,c	.12	29.7 a	57	**	**	**	2.89 b	.18	49.2 a
Male adults	3.13 b,c,d	.19	41.5 b	46	***	***	***	3.99 c	.26	86.2 b
Female lambs/calves	2.86 a,b	.15	58.1 b	124	**	NS	NS	2.33 a,b	.12	61.9 a
Female yearlings	3.39 c,d	.11	21.2 a	46	***	***	***	2.31 a,b	.23	69.1 a
Female adults	3.49 d	.13	38.4 b	111	***	***	***	2.18 a	.16	106.9 c

NOTE.—Means refer to mean month of death, starting with October, month -2; November, -1; December, 0; January, 1; and so on. Within species, means and variances with shared letters do not significantly differ from each other at the 5% level. For interspecific comparisons, means are compared by two-sample *t*-tests and variances by variance-ratio tests. NS = $P > .05$.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

bear twins (see Clutton-Brock et al. 1991). Second, there is no decline in fecundity until the year *after* female numbers in summer have reached 170 and mortality has been high (fig. 2D, E). As a result, changes in fecundity delay population recovery but have no effect on the magnitude of the die-off. Finally, neonatal survival is high, in contrast to most wild ungulate populations with natural predators.

The dynamics of red deer on Rum differ in two important ways from those of Soay sheep. First, the potential rate of population increase is low in red deer because hinds do not breed until they are 3 or 4 yr old, twins virtually never occur, and a substantial proportion of individuals skip opportunities to breed (Clutton-Brock and Albon 1989). As a result, numbers can rise by no more than 20% during the course of a single breeding season compared with more than 50% in Soay sheep. Second, fecundity and juvenile survival show an approximately linear decrease with rising density so that recruitment rates start to fall as soon as the population begins to rise (fig. 4D, E). As a result of these two differences, red deer populations are unable to overshoot winter carrying capacity to the same extent as the sheep. Minor "overshoots" may occur from time to time, generating unusually high overwinter mortality, but their consequences are small enough to be masked by the effects of density-independent fluctuations in climate and food availability.

Why Is Fecundity Density Dependent in Red Deer but Not in Soay Sheep?

The absence of any decline in fecundity with initial changes in density in the sheep contrasts with the changes observed in red deer (Clutton-Brock and Albon 1989) and is probably related to the timing of reproduction and the duration of parental investment. The sheep conceive their lambs in November (Grubb 1974) and bear them in April, shortly before the onset of rapid plant growth. Within a few days of birth, the lambs begin to graze independently, and the frequency of suckling begins to fall when they are between 2 and 3 wk old (Robertson et al. 1992). By the beginning of June, suckling frequency and duration are low, and demands on the mother are probably slight, though lambs will suck occasionally until the autumn. As a result, energetic demands on the mother arising from lactation decline during the midsummer months when food is still plentiful and mothers can regain body condition.

Estimates of seasonal changes in body fat generated by our energetic model suggest that ewes breeding in all years of the cycle are capable of regaining peak body condition by August, 2 mo before the November rut, though they are likely to regain condition rather more slowly in years when summer population density is high (fig. 6). This prediction is confirmed by empirical evidence that, by August, ewes on St. Kilda that have raised single or twin lambs do not differ in weight from those that have failed to rear a lamb and have consequently not suffered the costs of lactation (fig. 7A).

The stronger response of adult fecundity to rising population density in the red deer is probably caused by their slower rate of maturation. Red deer in the Scottish Highlands mostly conceive in October. Calves are born in June and continue

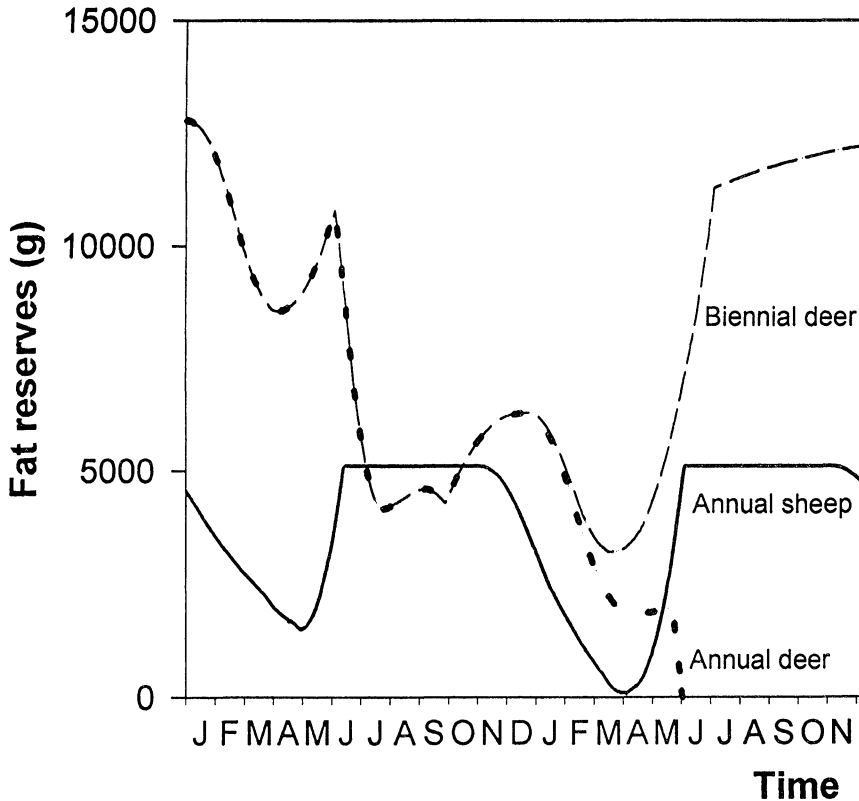


FIG. 6.—Predicted changes in body fat in adult female sheep and deer. A negative energy balance can be seen in the loss of fat during late pregnancy (January–April in sheep; February–June in deer) and especially in the ensuing lactation. For details of variables incorporated in this model, see table 1.

to suck regularly throughout the summer so that energetic demands on the mother persist until the autumn or early winter (Clutton-Brock et al. 1982; Loudon et al. 1983). Adaptation of our energetic model to Highland red deer predicts that hinds that have successfully raised calves will usually be unable to regain body condition before the autumn rut since they have heavier and longer lactations, which prevents the recovery of body reserves over late summer. Predicted values for annually and biennially breeding red deer (fig. 6) were obtained by adjusting the animal description in the energetic model (including body size, duration, and reproductive expenditure and incorporating seasonal grass growth rates appropriate for Rum *Agrostis/Festuca* grassland from Job and Taylor 1978). Animals attempting to breed in two adjacent years ("annual deer") would die following the loss of all their body reserves during the subsequent pregnancy and lactation (months 16–18, April–June), while biennial reproduction allows body reserves to recover by the following year. Empirical studies confirm that, in contrast to Soay

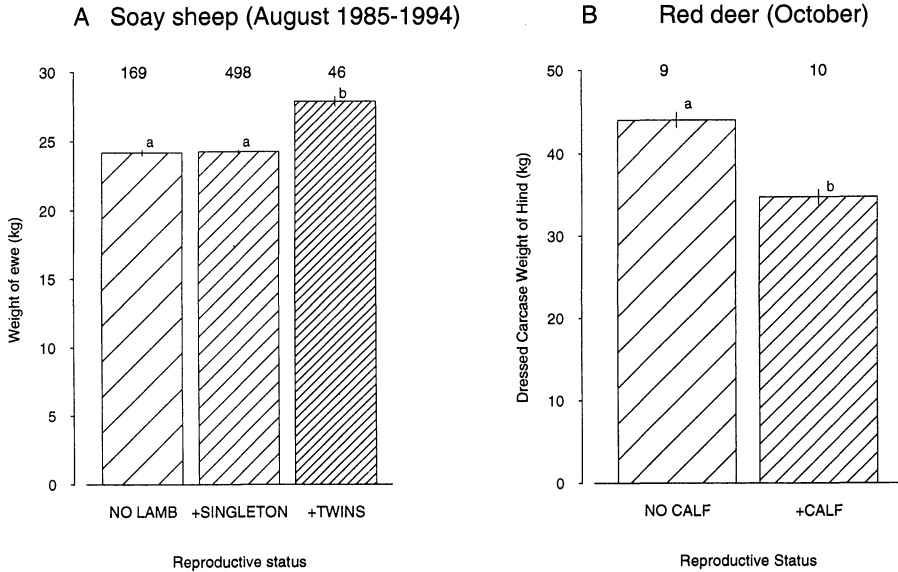


FIG. 7.—Body weight in August in (A) Soay ewes ≥ 2 yr old that have failed to breed, raised a single lamb, or raised twins (ANOVA, $F = 44.72$, $df = 2, 709$, $P < .001$). B, Red deer hinds that have failed to breed or have raised a single calf ($t = 7.307$, $df = 17$, $P < .001$). Means that differ significantly at the 5% level are indicated by different superscripts (Soay ewes: T. H. Clutton-Brock, S. D. Albon, and J. Pemberton, unpublished data; red deer: calculated from Mitchell et al. 1976 from data collected from a culled red deer population in Glen Feshie, Central Highlands).

sheep on St. Kilda, female red deer that have successfully raised calves are usually unable to regain body weight by late summer (see fig. 7) and commonly fail to conceive as a result (Albon et al. 1983a).

Another contrast occurs in the relation between population density, birth weight, and neonatal survival in the two populations. In the sheep, birth weight and neonatal survival fall after years when summer numbers and winter mortality have been high (Grubb 1974; Clutton-Brock et al. 1992). In contrast, neither birth weight nor neonatal survival is consistently related to density in the deer, but both parameters are closely related to variation in weather conditions in spring and early summer (Albon et al. 1983b; Clutton-Brock and Albon 1989). This difference also is probably a consequence of the timing of reproduction. In both species, neonatal survival is strongly affected by birth weight (Guinness et al. 1978; Clutton-Brock et al. 1987, 1992), which is, in turn, affected by food availability during the last 2 mo of gestation when fetal weight increases rapidly, imposing considerable energetic demands on the mother (Robbins 1983). In the sheep, these demands occur in February and March, preceding the onset of plant growth, when standing crop is negatively related to population density ($r = -0.659$, $n = 5$, $P = .054$). Pregnant females draw on their own body resources (which are also likely to be influenced by population density) to meet these costs, with the result that lamb birth weights are closely related to autumn density. In

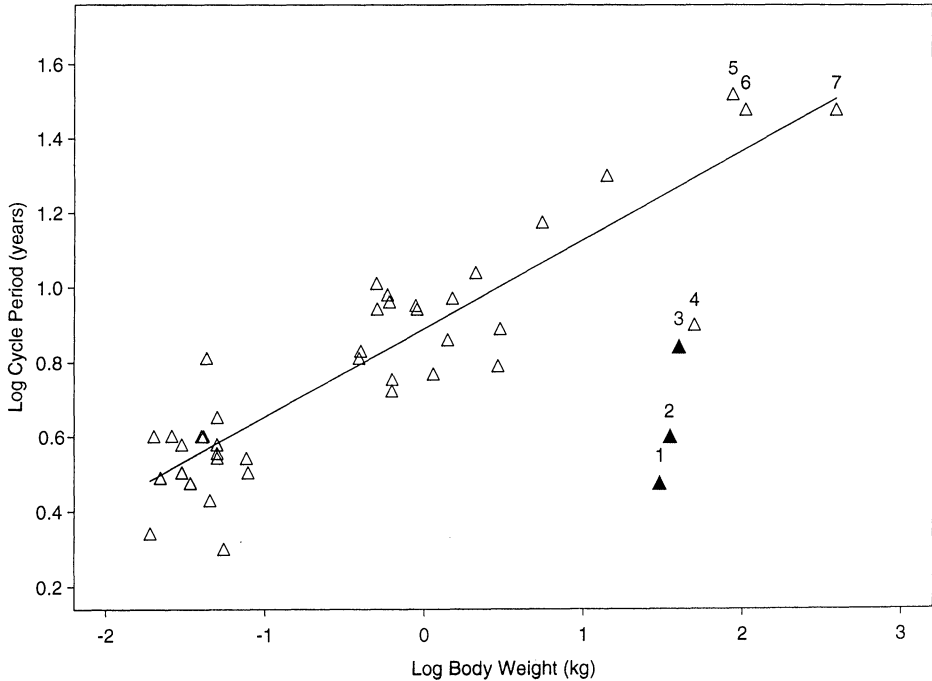


FIG. 8.—Population cycle periods as a function of body mass for 40 species of birds and mammals (based on Peterson et al. 1984). Points 5, 6, and 7 show the three ungulates included by Peterson et al.: *Odocoileus hemionus*, *Rangifer tarandus*, and *Alces alces*. Points 1–3 show values for Soay sheep (this study), mouflon (Boussès et al. 1992), and feral goats (Boyd 1981), respectively. Point 4 shows the duration of a single oscillation in Dall sheep (Hoefs and Bayer 1983). Feral species are indicated by closed symbols. The equation for the regression line (excluding the feral populations) is \log_{10} cycle period = $0.8920 + 0.2373$ (log body weight); $r^2 = 0.81$, $P < .001$. The slopes of the regression lines, with and without the feral species, are significantly different ($t = 2.237$, $df = 87$, $P = .028$).

the deer, peak costs of gestation occur in April and May, coinciding with the onset of plant growth (Albon et al. 1992). Climatic conditions (and, consequently, food availability) in April vary considerably between years, which generates substantial density-independent variation in calf birth weights.

DISCUSSION

The Soay sheep study shows that persistent oscillations are not confined to herbivorous rodents (e.g., Finnerty 1980; Cockburn 1988; Hanski et al. 1993; Boonstra 1994). In the past, a number of authors have suggested that populations of large herbivores may show regular or semiregular population cycles but that their periodicity may be so long that their existence has not been noticed (see Calder 1983). For example, Peterson et al. (1984) demonstrated a significant correlation between body weight and the periodicity of population cycles across a sample of 40 birds and mammals ranging from wood mice (*Apodemus sylvaticus*) to moose (*Alces alces*) (fig. 8). They used the allometric slope from this analysis

to predict cycle periodicities of 46 ± 15 yr for humans and 71 ± 21 yr for elephants (Peterson et al. 1984; though see also Krukonis and Schaffer 1991). However, the three ungulate studies listed by Peterson et al. cover (at most) the course of a single oscillation, and (as Peterson et al. noted), in two cases, estimates of periodicity were based on single irruptions following introduction or release from predation. The results of the Soay sheep study (Clutton-Brock et al. 1991) and research on other populations of feral sheep and goats (Boussès et al. 1992; Boyd 1981) show that the periodicity of ungulate population oscillations can be substantially shorter than would be predicted from Peterson's allometric plot (see fig. 8).

Comparison of the dynamics of Soay sheep with red deer suggest that relatively minor differences in life-history parameters can generate contrasting population dynamics in long-lived organisms. The St. Kilda sheep population oscillates because of a lack, at low to medium population densities, of density-dependent constraints on fecundity, combined with a relatively high recruitment rate. This permits autumn numbers to exceed the winter carrying capacity of the environment, leading to rapid weight loss and high mortality during the winter. In contrast, the fecundity of red deer is lower and declines as soon as population size increases (see fig. 3). Fecundity is probably more sensitive to population density in red deer because lactation imposes a substantial energetic burden on females throughout the summer, with the result that a significant proportion fail to regain the body weight necessary to conceive before the October rut (see Albon et al. 1983*a*). Because of the slower maturation rate of deer calves, the energetic costs of lactation decline more slowly than they do in the sheep (Loudon et al. 1983; Robertson et al. 1992), which prevents females that have raised calves from regaining body condition during summer, when primary production is high and food is probably superabundant (see fig. 7).

Our energetic model also emphasizes the role that variance in autumn condition may have in affecting population stability. In populations in which body condition is highly variable, some categories of animals will die relatively early in the winter, thus reducing the subsequent demand on resources and increasing the chances of survival in the remaining animals. Conversely, in populations in which autumn reserves and subsequent metabolic requirements are relatively uniform, little mortality may occur until a substantial proportion of the population has reached a point where it is susceptible to starvation, intermittently generating high mortality. Factors that increase differences in body condition or resource access in winter (including variation in dominance rank, group size, home range quality, or parasite load) can be expected to reduce the risk or extent of overcompensatory mortality. Differences of this kind are probably greater in the deer than the sheep, partly because of their slower growth rates and partly because the division of the population into matrilineal groups with distinct (though overlapping) ranges contributes to variation in resource access and condition in the population (Clutton-Brock et al. 1982). As a result, mortality in the deer is less synchronized than that in the sheep (table 1). The characteristics distinguishing red deer from Soay sheep (relatively slow development, prolonged parental investment, and long-lasting social ties) are found in many other large mammals

(Western 1979). As a result, the timing of mortality is likely to be more variable than that in smaller species, enhancing population stability (see van Sickle 1990). Where cycles do occur in larger herbivores, they are likely to be of smaller amplitude, which increases the chance that they will be obscured by environmental stochasticity so that only deep crashes are distinguishable from background noise.

Finally, our analysis suggests why short-term fluctuations in population size may be commoner in feral ungulates than in wild ones. As a result of artificial selection, feral animals typically show more rapid development and higher fecundity than related wild species of similar body size (Clutton-Brock 1981). They are typically found in environments from which predators have been removed, and they are often released on islands, from which emigration is impossible. However, it is unlikely that cyclicity will prove to be restricted to feral animals. Some wild ungulates, such as saiga antelope (*Saiga tatarica*), have life histories similar to those of feral sheep (Heptner et al. 1988), and an increasing number of ungulate populations are confined to areas from which predators have been removed. Further cases of persistent instability over relatively short time spans can be expected in other ungulates with high reproductive potential.

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APPENDIX

MODIFIED LESLIE MATRIX MODELS

Predicted numbers of animals in different age and sex categories (see fig. 2) were generated by deterministic age- and sex-structured Leslie matrix models of this general form:

$$n_{t+1} = M_t n_t,$$

where n_t and n_{t+1} are age- and sex-structural vectors of population abundance in the subscripted years and M_t is the transition matrix, expressing the operation of survival and fecundity in year t . In both models, survival and fecundity are represented by density-dependent functions of female population size (yearlings and adults, as explained in the text) and were seeded with the observed population estimates for the starting year (1985 and 1971, respectively). In both models, survival and fecundity were described by density-dependent functions. In the case of the sheep, they were of the following general form:

$$S = d/[1 + (aN_t)^b]$$

TABLE A1
PARAMETER VALUES USED IN LESLIE MATRIX MODELS FOR SOAY SHEEP AND RED DEER

	MALES*			FEMALES		
	<i>a</i>	<i>b</i>	<i>d</i>	<i>a</i>	<i>b</i>	<i>d</i>
Soay sheep parameters:						
Fertility:						
Lambs	.00599	26.09	.205	.00634	17.58	.284
Yearlings	.00574	16.00	.422	.00557	23.46	.352
2-yr-olds	.00541	10.58	.288	.00560	2.50	.510
3-yr-olds	.00530	11.57	.376	.00522	10.47	.573
4-yr-olds	.00522	9.27	.385	.00541	2.01	.623
5-yr-olds +	.00494	8.56	.475	.00541	9.10	.623
Survival:						
Lambs	.00565	41.08	.955	.00552	18.22	.869
Yearlings	.00539	20.33	.882	.00483	9.99	.938
2-yr-olds	.00552	23.49	.954	.00430	7.00	.990
3-yr-olds	.00520	11.00	1.000	.00435	9.62	.952
4-yr-olds	.00520	11.00	1.000	.00435	9.62	.952
5-yr-olds +	.00489	11.49	.974	.00483	11.24	.940
Red deer parameters:						
Fertility:						
Calves	.0000	.0000000000	.000000	...
Yearlings	.0000	.0000000000	.000000	...
2-yr-olds	1.6222	.034991	...	-.1037	.019378	...
3-yr-olds	-.2525	.004654	...	-1.0947	.000286	...
4-yr-olds	.0349	.005897	...	-1.5066	.000892	...
5-yr-olds +	.0784	.006944	...	-.2947	-.005169	...
Survival:						
Calves	2.8120	.016373	...	4.2815	.023175	...
Yearlings	5.8184	.032348	...	4.9737	.022891	...
2-yr-olds	2.1925	.003663	...	4.4483	.012748	...
3-yr-olds	2.1925	.003663	...	9.0694	.040957	...
4-yr-olds	2.2599	.002189	...	4.9612	.006739	...
5-yr-olds +	1.9035	.002855	...	4.6295	.017776	...

NOTE.—For Soay sheep, the survival function is $S = d/(1 + [aN]^b)$. For red deer, the survival function is $S = e^{(a-bN)}/(1 + e^{(a-bN)})$. See the text for details of the models.

* For fertility, males refers to the sex of the offspring produced.

(Maynard-Smith and Slatkin 1973), and estimates of parameters d (density-independent mortality), a (the reciprocal of the threshold density above which density-dependent mortality occurs), and b (the level of density-dependent mortality) were estimated by binomial maximum-likelihood methods. In the case of the red deer model, density dependence was described by

$$S = \frac{e^{(a-bN)}}{1 + e^{(a-bN)}}$$

where a and b are constants, again estimated by binomial maximum-likelihood methods. In both models, there were two sex classes and six age classes (see table A1). Systematic deviations from the predictions of the red deer model in the early 1980s are associated with density-independent weather effects (Clutton-Brock and Albon 1989), not with any density-dependent factor.

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