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Definitive case studies

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Certain long-term studies on large herbivore populations have made especially influential contributions to current understanding of population dynamics. They are outstanding either for the detailed understanding that they have provided based on individually recognizable animals, or for the windows opened into particular processes from the prolonged study duration, or both. This chapter provides a summary outline of the findings that have emerged from these studies, and thus of the particular ways in which studies of large herbivores have advanced our understanding of population processes. It provides the empirical context for the reassessment of theoretical models that is the theme running through the book.

The eight studies assembled all extended over one or more decades. Two have been especially eminent for the wealth of publications produced, including two books: the study of red deer on the Isle of Rum, and of Soay sheep on the Isle of Hirta, both situated off the west coast of Scotland. Two further investigations based likewise on individually identifiable animals have recently become prominent in the literature, focused on roe deer in two regions of France, and bighorn sheep in two localities in Canada. Among African ungulates, a study on greater kudu employing individually recognizable animals was conducted in two regions of South Africa's Kruger National Park over a decade, and extended through a broader spatial and temporal context by park-wide censuses. Another exceptionally long-term

Scientific names of species referred to in the text are given in the index.

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2 Chapter 1

study used repeated aerial censuses supported by ground surveys to follow the long-term dynamics of the migratory wildebeest population within the Serengeti ecosystem in Tanzania. Two further studies in North America employing aerial surveys within an ecosystem context documented the long-term dynamics of moose in Isle Royale National Park, and elk in Yellowstone National Park.

Some of the theoretical issues to be borne in mind when evaluating these studies, anticipating the models to be assessed in later chapters, are listed below:

- 1 How stable, or unstable, have the dynamics of these populations been, as indicated by temporal variation in abundance?
- 2 How have island restrictions on movements affected population dynamics?
- 3 How has density dependence been manifested?
- 4 What climatic influences on abundance have been apparent?
- 5 What distinctions in demographic responses to these factors are evident?
- 6 How has predation, or hunting, modified population dynamics?
- 7 Has vegetation degradation been apparent at high herbivore density?

1.1 Red deer on Rum

This detailed study of red deer (Fig. 1.1) commenced in 1971 in a 12 km² section of the North Block of the Isle of Rum (Clutton-Brock et al. 1982). Culling was suspended within the study area the following year, but continued on the remainder of the island. Although the study population was open to movements, females and their offspring generally remained resident, while males frequently dispersed beyond the study area (Coulson et al. 2004). Predators were absent, apart from golden eagles, and there was little grazing competition from the cattle and goats found elsewhere on the island. Individual deer were identified from natural markings or body shape features, plus collars or ear tags placed on a large proportion of calves soon after birth. Many adult animals were also marked with collars to reduce the likelihood that they would be shot when they moved out of the study area. Censuses of the deer population within the study area were carried out several times each month on foot, facilitated by the prevalently open heathland vegetation.

The number of animals over 1 year in age in the study population grew from about 160 initially to fluctuate between 230 and 370 animals after 1986 (Coulson et al. 2004, Fig. 1.2). The population increase was greater among females than among males, and correspondingly the adult sex ratio



Figure 1.1 Red deer hind on Rum, Scotland (photo: N. Owen-Smith).

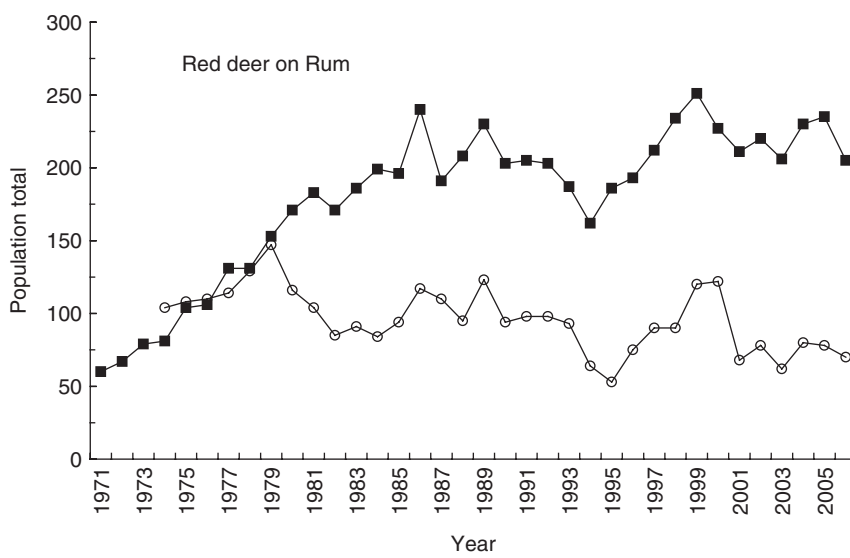


Figure 1.2 Changes in adult red deer population in the North Block of Rum (females: filled squares; males: open circles).

shifted from 0.5 females per male initially to 1.7 later (Clutton-Brock et al. 1997). The widening skew in the sex ratio was due to greater emigration by locally born males plus reduced immigration by new males. At peak abundance, the deer density in the North Block was 30 animals over 1 year in age per km².

The 2.5-fold increase in abundance of the female segment was associated with a decline in fecundity among both young and old females: the proportion of 3-year-old females giving birth dropped from 80% to 5–30%, whilst the annual proportion of females over 9 years in age producing offspring decreased from 95% to 65–80% (Clutton-Brock et al. 1982, Coulson et al. 2004). Calf mortality during summer showed little change, whereas calf mortality during winter rose from initially under 5% (Guinness et al. 1978, Clutton-Brock et al. 1985) to around 40% (annual range 10–80%) (Albon et al. 2000, Coulson et al. 2004). As a result, the ratio of juveniles to adult females the following spring decreased from 48 to 28% (Clutton-Brock et al. 1985). Overwinter mortality among adult females doubled, from 4% per year during the increase phase prior to 1980 to 8.5% per year over the subsequent period of stabilization (Albon et al. 2000). Two severe winters associated with mortality greater than 20% contributed to this elevation in mortality. Mortality among adult males differed similarly between these periods (Kruuk et al. 1999).

Weather conditions affected juvenile mass at birth, with warmer springs promoting heavier calves (Albon et al. 1987). Individuals that weighed more at birth showed higher reproductive success as adults. The proportion of 3-year-old females giving birth was negatively related to precipitation during the preceding late summer, as well as being influenced by winter temperature conditions and the number of days with snow cover (Albon and Clutton-Brock 1988, Langvatn et al. 1996). Conditions in the year of birth also affected the subsequent survival and reproductive success of males (Rose et al. 1998).

Annual variance in the population growth rate was low during the early increase phase, affected mainly by the pregnancy rate among adults (Albon et al. 2000, Coulson and Hudson 2003, Coulson et al. 2004). Only about 80% of females older than 3 years produced offspring each year during this period (Clutton-Brock et al. 1982). After peak abundance had been attained, the annual growth rate fluctuated more widely, with annual variation in adult survival becoming the main contributor, reinforced by strong covariation in overwinter survival of juveniles. This was partly a result of the increased proportion of individuals older than 8 years in the adult segment. Yearling survival also varied widely between years. Conditions experienced in the year of birth affected birth mass, early growth, subsequent survival and reproductive performance as adults (Albon et al. 1987).

Male survival was more variable than that of females at all stages, from birth through adulthood.

The reduction in birth mass associated with rising density indicated food limitation. However, grazing and browsing impacts on the vegetation were not apparent. Females with young concentrated their grazing especially on patches of *Agrostis/Festuca* grassland offering highest quality forage while sufficient amounts remained, and spread into the extensive *Calluna* heathland and patches of *Molinia* grassland during winter (Clutton-Brock et al. 1982). Contesting for food was evident during summer when grazing was locally concentrated, but access to food took the form of a scramble in winter when the deer were more widely dispersed (Coulson et al. 1997). Lags related to instability in the age structure of the population persisted for almost two decades through the period of population stabilization, somewhat beyond the generation time of 8 years. A two-fold difference in contributions by the most and least successful cohorts to population dynamics was evident (Coulson et al. 2004).

This red deer population reached its asymptotic density without much overshoot or vegetation degradation. The oceanic climate with high precipitation but relatively light snow cover helped maintain food availability through winter.

1.2 Soay sheep on Hirta

Soay sheep (Fig. 1.3) are feral survivors of primitive domesticated sheep introduced into the St. Kilda archipelago 2000–3000 years ago. The Hirta



Figure 1.3 Soay sheep ewe on Hirta (photo: T. Coulson).

population was established in the 1930s when humans moved out and sheep were moved across from the nearby Island of Soay. The first studies began in 1955 (Jewell et al. 1974), while more detailed investigations were initiated in 1985, concentrated in the Village Bay region (2.3 km²) of the 6.4-km² island (Clutton-Brock and Pemberton 2004). Annual censuses covering the whole island have been conducted each summer, supported by more frequent counts within the Village Bay area. In the latter area, over 95% of lambs born were caught, weighed, and marked with ear tags during the first month after birth, adding to tags placed earlier, so that the precise age of most animals was known (Clutton-Brock et al. 1991). The total Soay sheep population on Hirta has fluctuated between lows of around 600 and peaks sometimes exceeding 2000 individuals, with the oscillation period typically 3–4 years (Fig. 1.4; Clutton-Brock et al. 1991, Grenfell et al. 1992). The effective population density is extremely high (100–330 sheep per km²), facilitated by high rainfall supporting lush meadows on volcanic soils fertilized by sheep manure, and enriched in sodium by sea spray (Jewell et al. 1974).

The repetitive oscillations in abundance shown by these sheep have been related to the early timing of births relative to the seasonal cycle in food abundance, plus the early age at first parturition (Clutton-Brock et al. 1991, 1992, 1997, Clutton-Brock and Coulson 2002). Lambs are born

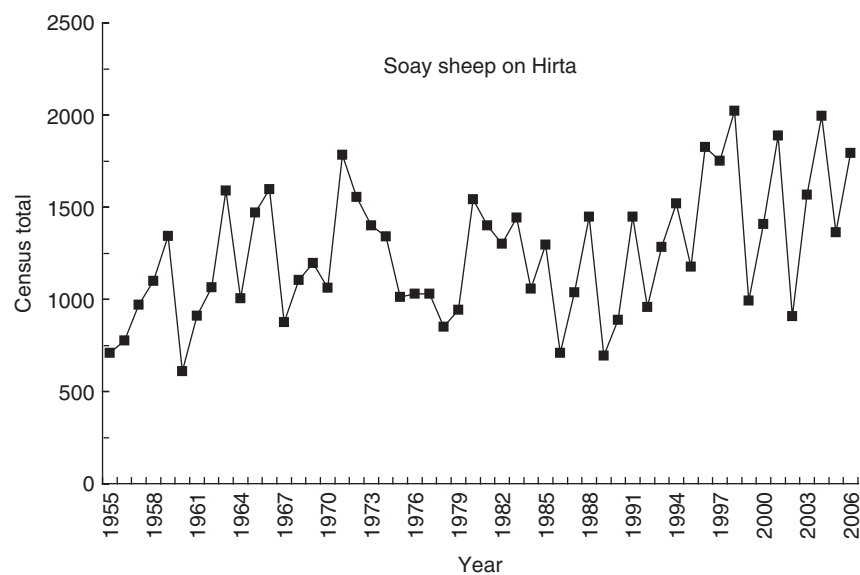


Figure 1.4 Changes in the Soay sheep population on Hirta.

in March preceding the spring growth of grasses, and weaned early in summer, enabling mothers to recover before the food restrictions of winter. First conception generally occurs at 7–8 months, so that most females produce their first offspring by 1 year of age. About 15% of adults produce twin offspring. This high reproductive potential has enabled the population to increase numerically by as much as 50% during the course of summer. The rapid rise in abundance led to depletion of most food by the following winter, with grass biomass dropping to as low as 5–10 g/m² (Milner and Gwynne 1974). Severe mortality followed when adverse weather conditions occurred towards the end of winter.

Wet and windy weather through February–March, associated with high values of the North Atlantic oscillation (NAO) index, amplified mortality to varying degrees among different population segments after high abundance had been attained (Clutton-Brock et al. 1991, Milner et al. 1999, Catchpole et al. 2000). Population density rather than weather was the overriding influence on the survival of lambs and adult males. Juvenile recruitment at 6 months of age declined from up to 0.45 per adult female at low density to about 0.25 at high density (Clutton-Brock et al. 2004). Survival among adult females was affected by adverse weather but not by density. The proportion of yearling females producing lambs was lower when the autumn density was high. About 80% of adult females gave birth each year irrespective of the population size, but the twinning rate declined with increasing density. The decline in body mass of the sheep during winter was greater in crash years than in other years, indicating food limitation, although nematode parasite loads may have contributed to the mass loss. Wet, stormy weather during the preceding winter as well as high density resulted in a reduction of the birth mass of lambs, and hence reduced survival. In some years, more than 80% of lambs, yearlings, and adult males, more than 50% of yearling females, and up to 45% of adult females of all ages, died during a single winter. Because of this differential mortality, the overall magnitude of the population crash depended on the prior population structure (Catchpole et al. 2000, Coulson et al. 2001). Adverse weather had little impact on mortality in years when the population density remained low following a crash.

Following population crashes, the survivors consisted mainly of prime-aged females. Fecundity remained low in the year after a population crash. Annual mortality among adult females averaged 7.5%, including 45% mortality in 1 crash year (Milner et al. 1999). Cohorts of sheep born after adverse winters, or following winters of high population density, were not only lighter at birth, but reached reproductive maturity at an older age, gave birth at a later date, and were less likely to produce twins than sheep born in other years (Forchhammer et al. 2001).

The synchronizing effect of regional weather was evident from the spatially correlated dynamics of Soay sheep populations on neighboring islands in the St. Kilda group (Grenfell et al. 1998). Long-term effects of the severe grazing pressure on the capacity of the vegetation to support the sheep were not evident. Milder winters may have contributed to the elevated peak densities attained in recent years (Berryman and Lima 2006).

1.3 Roe deer in France

The roe deer (Fig. 1.5) study took place in two forest areas (Gaillard et al. 1993a, 1997). Trois Fontaines (13.6 km²) in eastern France represented a continental climate with relatively severe winters, but otherwise good quality habitat. Chizé (26.6 km²) in western France has an oceanic climate with relatively mild winters, but habitat conditions are less favorable due to infertile soils and frequent droughts. There was no predation on adult roe deer, although foxes killed some fawns. Because fences precluded emigration, roe deer numbers within both areas were controlled by annual removals. The density of roe deer at Trois Fontaines was maintained at 15–18 animals per km² until 2001, after which the population was



Figure 1.5 Roe deer female in France (photo: B. Hamann).

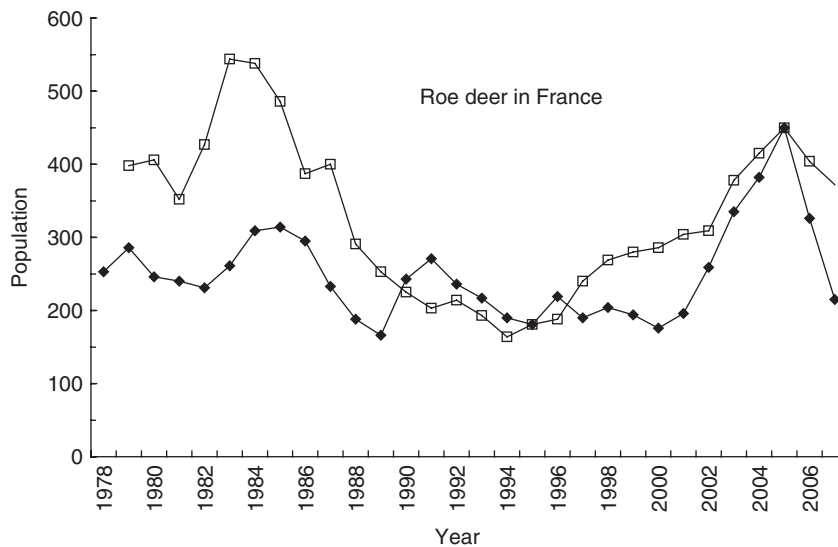


Figure 1.6 Changes in adult roe deer populations in two study areas in France (Trois Fontaine: *filled squares*; Chizé: *open squares*).

allowed to grow towards a peak of around 25 animals per km² (Fig. 1.6). At Chizé the density increased from 13 to 21 animals per km² between 1979 and 1983, then was reduced to around 8 per km², but allowed to rise after 2000 towards the earlier density level. To overcome the difficulty in observing the deer in their dense woodland habitat, population dynamics and demography were followed by marking and recapturing animals, commencing in 1976 at Trois Fontaines and in 1978 at Chizé. About half of the marked animals still alive were recaptured annually. From 1985 onward, many neonates were caught and marked within a few days of birth in both sites.

At Trois Fontaines, almost all females aged 2 years or more gave birth each May, producing on average 1.64 fawns per reproductive female (Gaillard et al. 1992, 1997). At Chizé, the proportion of 2-year-old females producing offspring varied among years depending on the population density, and the number of fawn produced per female declined from 1.6 in 1979 to 1.3 in 1985. Early survival through the summer was affected by the population density at Chizé (Gaillard et al. 1997), and at Trois Fontaines after 2001 (Gaillard et al. unpublished data). In both sites, early survival increased with increasing rainfall during spring and early summer (Gaillard et al. 1997). However, heavy rain in April–May during late gestation and cooler summers had a negative influence on the mass of

fawns during winter at Chizé (Gaillard et al. 1996). Low fawn survival was associated with reduced birth mass and/or retarded early growth (Gaillard et al. 1993b). However, at Trois Fontaines, fawns born during unfavorable springs were able to compensate for reduced early growth by exploiting the high availability of forage through late summer and early autumn (Gaillard et al. 1993c). Fawns surviving at the end of winter tended to be heavier at Trois Fontaines than at Chizé (Gaillard et al. 1996), and fawn survival was generally lower at Chizé than at Trois Fontaines. Differences in the birth mass and subsequent growth rate gave rise to cohort differences expressed through effects on subsequent survival and reproduction at Chizé (Gaillard et al. 1997).

Adult survival rates were higher for females (93%) than for males (85%) in both study areas (Gaillard et al. 1993a). Adult survival rates decreased beyond 7 years of age more strongly among males than among females, associated with more pronounced tooth wear. Survival between the juvenile and yearling stages (i.e. from 8 to 20 mo of age) was lower than adult survival at Chizé but not at Trois Fontaines, with growth also slower in the former study area. Juvenile survival to 6 months of age averaged 50% at Chizé compared with 63% at Trois Fontaines, with the annual range of variation being 39–91% (Gaillard et al. 1997). Adult survival was reduced in years with severe winters at Trois Fontaines in both sexes. Cohort effects on the body mass attained and consequent reproductive success were long-lasting among animals born under high-density conditions (Pettorelli et al. 2002, Gaillard et al. 2003). Adult survival rates within the prime age range (2–8 yr) appeared insensitive to both changing density and climate, so that variation in juvenile survival through summer was mostly responsible for the annual changes in population abundance, after discounting the effect of culling (Gaillard et al. 1993a, 2000).

1.4 Bighorn sheep in Alberta

The bighorn sheep (Fig. 1.7) study was conducted in two study areas 160 km apart in the eastern ranges of the Rocky Mountains in Alberta, Canada. Observations at Ram Mountain (38 km²) commenced in 1971, and those at Sheep River (60 km²) in 1981 (Festa-Bianchet et al. 1997, Jorgenson et al. 1997). The isolated Ram Mountain population was maintained at about 100 animals until 1981 by annual removals. Thereafter it was allowed to grow to a peak of 210 individuals in 1992, following which numbers declined due to density feedbacks plus predation (Fig. 1.8). The study animals at Sheep River represented a segment of a wider metapopulation. Sheep numbers there fluctuated around 150 animals until reduced



Figure 1.7 Bighorn sheep ewe with lamb in Rocky Mountains (photo: F. Pelletier).

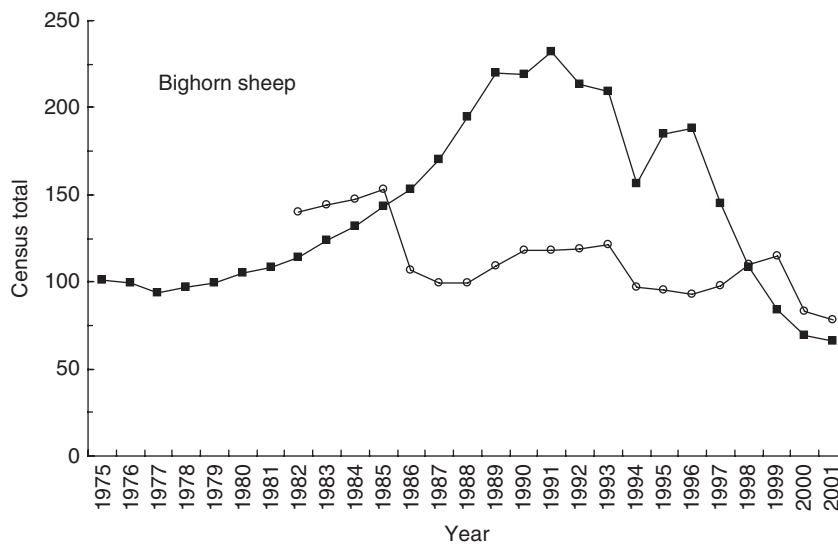


Figure 1.8 Changes in bighorn sheep populations in two study areas in Canada (Ram Mountain: *solid squares*; Sheep River: *open circles*).

by a pneumonia outbreak in 1986. Both study areas were unfenced and open to predation by wolves, cougars, black bears, and coyotes, as well as being subject to trophy hunting of males (Festa-Bianchet et al. 2006). Over 90% of the sheep at Ram Mountain, and up to 94% of those at Sheep River, were marked with ear tags for individual identification. Population

surveys took place several times monthly through summer in both study areas until 1987, then four times annually through 1988–93, with survival estimated using capture–recapture methods. At Ram Mountain, sheep were trapped repeatedly in a corral for weighing, while only chest girth measurements on lambs were obtained at Sheep River.

At Ram Mountain, the proportion of lactating 2-year-old females declined shortly after the population began increasing, following the suspension of removals (Festa-Bianchet et al. 1995). A density influence on the overwinter survival of juveniles was apparent in both study areas (Jorgenson et al. 1993, Portier et al. 1998). Mortality among yearling females varied widely between years, and at Ram Mountain was related to population density (Jorgenson et al. 1997), apparently through effects on body mass (Festa-Bianchet et al. 1997). Density effects on adult survival were not detected. Survival rates among prime adult females averaged 94% at Ram Mountain and 92% at Sheep River, in the absence of predation (Festa-Bianchet et al. 2006). Adult survival rates declined beyond 7 years of age more strongly among males than females. Differences in body mass and chest girth at weaning influenced the survival of juvenile sheep (Festa-Bianchet et al. 1997), which was higher on average at Ram Mountain (53%) than at Sheep River (41%). Female longevity was related to their body mass while young, affecting lifetime reproductive success (Bérubé et al. 1999).

At Ram Mountain, warm springs improved the survival of juvenile sheep through summer and over the following winter, but only when population density was high (Portier et al. 1998). Winter temperature also had a positive influence on first-year survival under high-density conditions. High precipitation during spring improved juvenile survival, in this case, independently of density. However, the growth rate of juveniles was lower following springs with a rapid green-up in forage (Pettorelli et al. 2007). Slower snowmelt led to small-scale variability in snow disappearance and hence greater variability in forage green-up and quality among patches. Winter weather did not affect survival beyond the juvenile stage (Jorgenson et al. 1997).

Surges in predation were recorded as a result of the targeting of bighorn sheep by individual cougars causing declines in both sheep populations, at Ram Mountain by two-thirds over 5 years (Festa-Bianchet et al. 2006). The increase in annual mortality among prime-aged females due to predation was from 6 to 10% at Ram Mountain, and from 8 to 20% at Sheep River, with impacts on other demographic segments somewhat greater. Juvenile mortality rose from 47 to 80% at Ram Mountain, and from 59 to 79% at Sheep River.



Figure 1.9 Greater kudu female in Kruger (photo: N. Owen-Smith).

1.5 Kudu in Kruger

The detailed study on greater kudu (Fig. 1.9) was carried out in two areas 70 km apart in the southern part of Kruger National Park, each about 60 km² in extent, over a 10-year period (1974–84). Observations covered the growth of these subpopulations towards peak abundance, followed by a drop in numbers associated with a severe drought, then a rebound (Fig. 1.10). All animals in both study areas were individually recognizable from natural markings, documented photographically. Females could be aged to the year of birth from relative body size up to 2 years of age, and males up to 5 years of age from horn shape. The age of an increasing proportion of the study populations became known from photographs of individual animals taken in or shortly after the year of their birth. The annual survival of females plus young was recorded by registering the individuals present in discrete social units during the late dry season, 7–9 months after calves were born. Annual sample sizes were 31–135 in one study area and 62–135 in the other study area, representing about half of the total number of animals on file in these groups within each area. Age-related changes in male survival beyond 2 years of age were estimated from the age structure of the male segment over the study period, corrected for cohort variation and emigration. The maximum density levels attained amounted to almost four animals per km² in one study area and around three animals per km² in the other. Records of changes in kudu

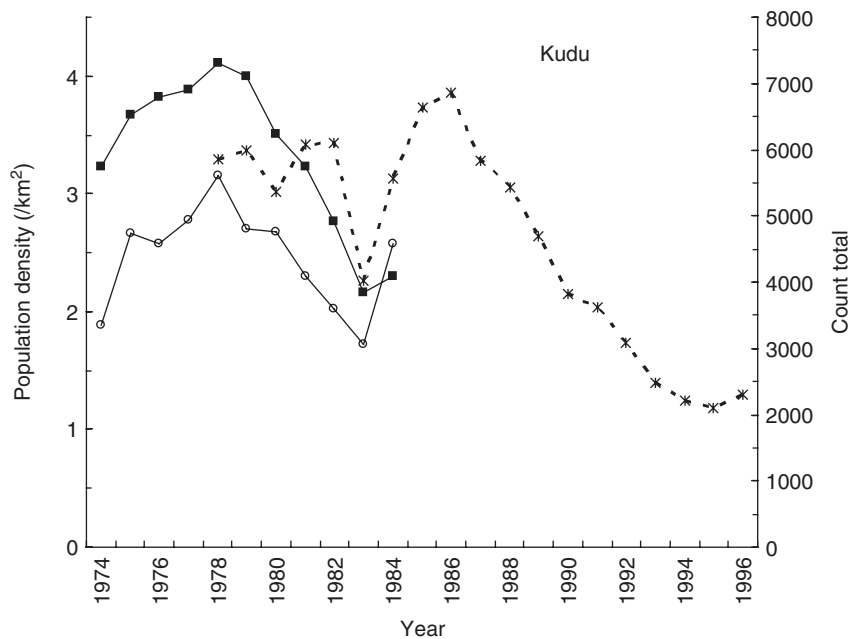


Figure 1.10 Changes in kudu population density in Pretorius Kop (solid squares) and Tshokwane (open circles) study areas, plus change in kudu population counted in southern half of Kruger National Park (stars and dotted line).

abundance were extended by aerial censuses covering almost the entire 19,500 km² extent of Kruger Park in most years between 1977 and 1996, supported by ground surveys of population structure between 1983 and 1996 (Fig. 1.10).

Annual rainfall variation strongly influenced age-class-specific survival rates (Owen-Smith 1990). Juvenile recruitment represented by the mother : offspring ratio varied annually from between 10 and 80%, with a mean of 45%. Most of the calf losses occurred before the dry season, indicating that rainfall influences on food availability during the wet season affected offspring survival, presumably via the nutritional status of the mother. The prior annual rainfall also influenced survival into the yearling stage (mean 85%) as well as that of females older than 6 years of age (mean 80%). Survival among prime-aged females (2–6 yr) varied little between years, averaging 92% per year. Virtually all mortality was as a result of predation, amounting to 8% per year for females through the prime age range, and 13% for the adult female segment as a whole. Mortality among males was substantially greater than that of females beyond 3 years of

age (Owen-Smith 1993). No male survived longer than 10 years, while the oldest female reached 15 years of age. Cold stress evidently reduced the survival of all age classes in a year when exceptionally cold and wet conditions occurred at the end of the dry season (Owen-Smith 2000).

Density effects on survival were revealed only after controlling for rainfall variation (Owen-Smith 1990). While rainfall had the greatest influence on juvenile survival, density effects appeared relatively stronger for older age classes, and were evident even among prime-aged females (Owen-Smith 2006).

Park-wide censuses indicated that kudu numbers in southern Kruger Park rebounded after the 1982–3 drought to reach a peak in 1986, followed by a progressive decline to 20% of the peak abundance several years later (Ogutu and Owen-Smith 2003; Fig. 1.10). Neither annual rainfall nor cold weather explained this trend (Owen-Smith 2000), and there was no density compensation. The declining trend was associated with an elevation in mortality within the adult female segment from 12 to 27% per year, estimated by reconciling the population change with annual juvenile recruitment. Juvenile recruitment estimated from the mother : offspring ratio in ground surveys showed only a minor reduction from 50 to 37% (Owen-Smith and Mason 2005). Enhanced predation was implicated as the most likely cause, both through an increase in the prey base supporting lions (Owen-Smith et al. 2005, Owen-Smith and Mills 2006), and through a shift in prey selection by lions towards alternative prey species including kudu (Owen-Smith and Mills 2008).

1.6 Wildebeest in Serengeti

This study monitored changes in the vast population of migratory wildebeest (Fig. 1.11) moving seasonally between the Serengeti plains in Tanzania and the Mara region of southern Kenya, over a linear distance of 180 km (Boone et al. 2006, Holdo et al. 2009). Starting in 1961, wildebeest aggregations were photographed from the air, and the animals were counted later from the photographs (Campbell and Borner 1995). Recent surveys have been sample-area counts recording other species as well as wildebeest over the full 27,000 km² extent of the ecosystem, with sampling intensity increased where wildebeest aggregations were found (Sinclair 1979). Surveys were not undertaken in every year, with a gap of 5 years between 1972 and 1977, and only one count between 1991 and 1999.

Wildebeest numbers increased from an estimated 250,000 in 1961 to reach a peak of about 1.4 million by 1979 (Fig. 1.12). Following a severe drought in 1993, the population decreased to 0.9 million, but



Figure 1.11 Wildebeest aggregation in Serengeti (photo: N. Owen-Smith).

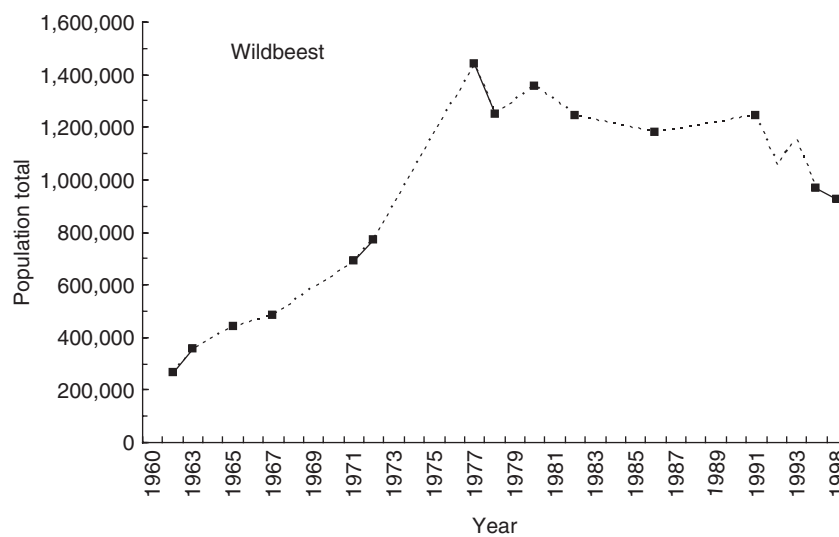


Figure 1.12 Changes in migratory wildebeest population in Serengeti (count totals: *solid squares*; linear interpolation between count totals: *dotted lines*).

thereafter regained its peak abundance, equivalent to a regional density of over 50 animals per km². Population structure was assessed from the aerial photographs, distinguishing calves from older animals, plus supporting ground surveys in some years, most comprehensively between 1992 and 1994. Survival rates of juveniles and yearlings were estimated

from changes in the ratios of young animals to adult females (>2 yr). Pregnancy rates were estimated from autopsy samples in earlier years, and from radioimmunoassay of fecal samples over 1992–4. Mortality rates of adults were estimated from fresh wildebeest carcasses found during ground surveys, aided by the presence of predators or scavengers on these carcasses as well as the open visibility of the landscape. The number of animals dying each day was expressed as a proportion of the population of live animals in the vicinity.

With rising abundance, the proportion of 2-year-old females producing calves decreased substantially from over 80 to 20%, while pregnancy rates among adult females declined from 95 to 84% (Mduma et al. 1999). Juvenile recruitment averaged 0.27 calves per female at the end of the dry season, which allowing for pregnancy indicates a survival rate of around 40%. Juvenile recruitment fell as low as 0.10 during the 1993 drought, but showed no significant trend with density alone (Owen-Smith 2006). Estimated annual survival among adults averaged 0.91, with a low of 0.75 associated with the severe 1993 drought. Adult mortality rose with increasing density beyond a threshold level. The proportion of adult deaths constituted by older animals increased between 1970 and 1990, but the majority of the dying adult wildebeest remained prime-aged animals. However, the proportion of animals dying that were in poor condition, as revealed by low fat content in bone marrow, increased with density. Wildebeest killed by lions tended to be in better condition, as revealed by bone marrow fat, than those found dead of other causes (Sinclair and Arcese 1995).

The continued population growth of the wildebeest during the 1970s was associated with an increase in amount of rainfall received during the normally dry season months (Pascual and Hilborn 1995). While calf recruitment appeared related to the amount of rainfall received during the dry season months relative to the population density (Mduma et al. 1999), the statistical significance came largely from the low calf survival recorded in the severe drought year (Owen-Smith 2006).

Migration has enabled the wildebeest population to grow to a level where food rather than predation limits its abundance (Fryxell et al. 1988). Illegal harvests by humans, occurring when the animals move outside park boundaries during their migratory circuit, have amounted to around 40,000–50,000 wildebeest annually, equivalent to 3–5% of the population (Mduma et al. 1998). The fairly abrupt increase in adult mortality towards high density may reflect the rapid rise in this source of mortality during the 1980s when anti-poaching efforts were lax. The recent recovery by the population from the post-drought low occurred after better control over the illegal harvests had been achieved by park managers.

Despite the extremely high abundance attained by the wildebeest, there has been no apparent reduction in the productive potential of the grassland. A thickening in density of woody plants, which commonly follows as a result of reduced fire intensity caused by high grazing pressure in savanna ecosystems, appears limited in its extent.

1.7 Moose on Isle Royale

This study has been focused on the interactive dynamics of wolves and moose (Fig. 1.13) in Isle Royale, located in Lake Superior near the United States–Canada border. The 544 km² island is managed as a national park with minimal intervention. Observations began in 1958, after a wolf population had become established following earlier colonization of the island by moose (Mech 1966). Moose population estimates for 1959–93 were derived from recoveries of dead moose, while subsequent estimates were obtained from aerial counts conducted during winter when moose were readily visible against the snow. The moose population grew towards a projected peak of around 1500 animals by 1972, then declined in association with a growing wolf population (Fig. 1.14). Following a crash in wolf numbers from 50 to 14 animals by 1981 caused by viral infection, the moose population increased to a high of almost 2500 animals by 1995.



Figure 1.13 Moose female on Isle Royale (photo: J. Vucetich).

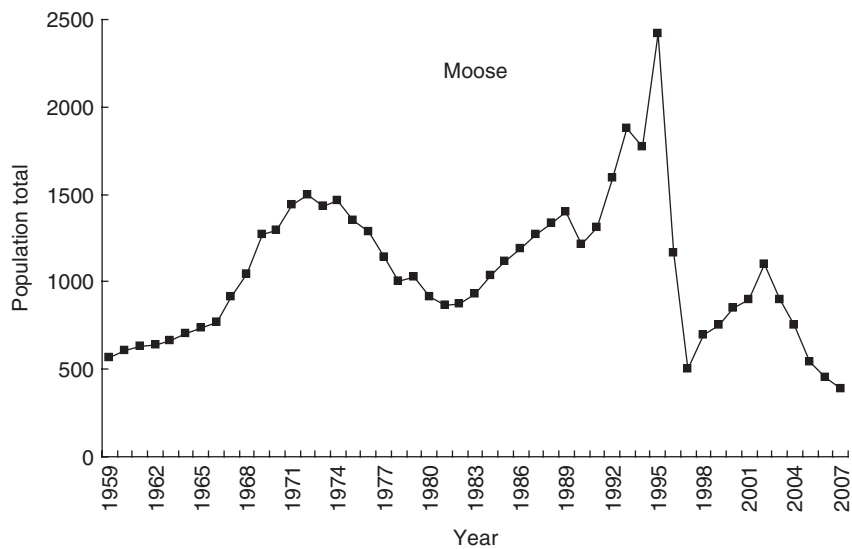


Figure 1.14 Changes in moose population in Isle Royale National Park.

Severe mortality over two successive winters then reduced the moose population by 80% (Peterson 1995, Smith et al. 2003). Recovery from this low point has since been suppressed by a combination of hot summers, abundant ticks, and elevated wolf predation, associated with a persistently low calf proportion.

Early observations suggested that top-down control through the lagged numerical response of the wolves had restricted the irruptive potential of the moose population (Mech 1966). Wolf abundance responded largely to changes in the number of moose over 9 years of age, together with the availability of moose calves, since success in killing prime-aged moose in good condition was low. Snow depth additionally affected the susceptibility of moose to predation, and had persistent effects on twinning, birth mass, and calf survival (Mech et al. 1987, Messier 1991). Calf : adult female ratios in summer varied between extremes of 18 and 58%. Snow conditions were in turn a consequence of broadscale weather patterns associated with the NAO (Post and Stenseth 1998). Severe winters had a negative effect on population growth in the same year, but a positive response the subsequent year due to the benefits of improved food availability in summer on reproductive success. Reductions in survival rates among juvenile or adult moose in response to increasing density were either lacking or insufficient to dampen the sustained growth of the moose population when wolf numbers were low (Peterson 1999). The eventual crash in

moose abundance through 1995–6 was associated with extreme weather conditions, exacerbated by an outbreak of ticks (DelGiudice et al. 1997).

Short-term oscillations in moose abundance appear to be related mainly to the availability of winter food (Vucetich and Peterson 2004), with the predator–prey interaction being influential over a longer period. The growth of the moose population has had a substantial negative impact on the abundance of balsam fir (*Abies balsamea*), a major winter food source for the moose (McLaren and Peterson 1994, Post et al. 1999). The proportional representation of balsam fir in the forest canopy declined from 46% around 1850, before the moose arrived, to under 5% (McLaren and Peterson 1994). Nevertheless, abundant regeneration of these firs is evident in the eastern section of the island.

1.8 Elk in North Yellowstone

In the late 1960s, the management policy of the US National Parks Service for Yellowstone National Park shifted towards allowing natural regulatory mechanisms to operate. The largest elk (Fig. 1.15) subpopulation in the north of the park had previously been restricted to around 6000 animals by culling (Houston 1982, Coughenour and Singer 1996, Wagner 2006, Eberhardt et al. 2007). These elk continued to be exposed to hunting during winter when they moved beyond the boundaries of the park, with the offtake increasing to around 25% of the female segment outside the



Figure 1.15 Elk hind in Rocky Mountain National Park (photo: D. Lutsey).

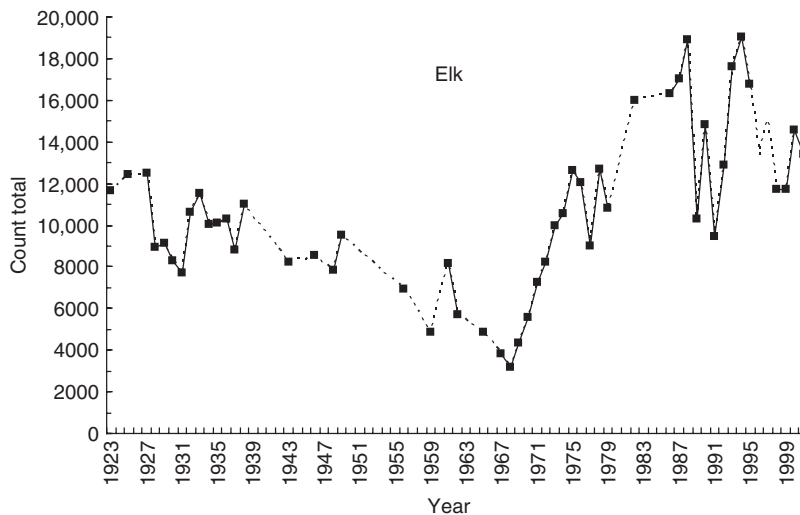


Figure 1.16 Changes in elk population in North Yellowstone (count totals: *solid squares*; interpolation between counts: *dotted lines*).

park between 1976 and 2004. Aerial counts of the winter range accounted for about 75% of the total population. Population classifications made from the helicopter or the ground distinguished calves and yearlings from older animals. The elk reached a peak abundance of 23,000 in 1988, but declined progressively after the reintroduction of wolves into the park in 1995 to 12,000 by 2004 (Fig. 1.16). The summer range occupied by the northern elk subpopulation exceeds 5000 km², so that the peak population density amounted to a little over four animals per km². During winter, these animals concentrate within a reduced range of 1520 km² at an effective density of up to 15 animals per km², thereby greatly increasing the browsing pressure in these bottomlands.

Density-related feedbacks on population growth became apparent as the elk population increased towards its peak abundance (Houston 1982). Pregnancy rate among adult females dropped from 87 to 61% (Coughenour and Singer 1996, Singer et al. 1997), and calf survival decreased both through summer and over the following winter, associated with a lowered birth mass. Predation accounted for over 40% of the calf losses. A density feedback on the survival of the adult segment became apparent only towards higher density levels.

Precipitation in the form of rain, especially during spring, positively influenced calf survival during summer as well as survival among both juveniles and adults through the following winter (Coughenour and Singer 1996),

and consequently also overall population growth (Taper and Gogan 2002). Juvenile recruitment, indexed by the calf : cow ratio after the birth pulse, depended on precipitation 2 years earlier. Severe winter weather was associated with elevated mortality in late winter, particularly when ice crusts formed on deep snow (Singer et al. 1997, Smith et al. 2003, Evans et al. 2006). Exceptionally severe conditions experienced in the winter of 1996 resulted in the death of most calves and reduced survival among females older than 10 years (Garrott et al. 2003).

Predation losses to coyotes, grizzly and black bears were concentrated especially on light and late-born juveniles (Singer et al. 1997). Wolves targeted mainly young animals and old females (Evans et al. 2006, Wright et al. 2006). The mean age of the adult female elk killed by wolves was almost 14 years, compared with 6.5 years for those shot by human hunters. Models incorporating these patterns suggested that wolf predation was largely compensatory, and that human harvests coupled with adverse climatic conditions were mostly responsible for the elk decline after 1995 (Vucetich et al. 2005). However, indirect consequences of the risk of predation on habitat use and activity could have effects on the elk population not accounted for in this model (Creel et al. 2007, Kauffmann et al. 2007). The annual survival rate of adult female elk fell from 92% prior to 1994, when mortality was largely due to hunting, to 82% after 2000, following the introduction of wolves (Coughenour and Singer 1996, White and Garrott 2005, Evans et al. 2006). Juvenile recruitment estimated by the number of calves per adult female towards the end of winter declined from a mean of 0.27 prior to 1994 to 0.17 after 2000, despite the reduction in population density (Barber-Meyer et al. 2008). Survival rates would be about 10% higher, allowing for pregnancy rates which remained unchanged. However, extremely dry conditions in recent years probably contributed to the elevated mortality rates.

Vegetation in northern Yellowstone has been drastically altered by the browsing effects of elk (Wagner 2006). Aspen, sagebrush, and willow, which were abundant at the turn of the century and contributed substantially to the winter forage of the elk, have been greatly depressed through heavy browsing (Romme et al. 1995, Kay 1997, Ripple and Larsen 2000, Zeigenfuss et al. 2002). Consequences for the capacity of the vegetation to support the elk population have not been assessed.

1.9 Overview

The set of eight studies encompass a wide range of ungulate species, feeding types, and body sizes, but is weighted strongly towards north temperate

environments (Table 1.1). Study areas varied vastly in their extent, with those based on individual recognition tending to be in restricted areas and those with the widest spatial coverage tending to show the greatest temporal duration. The two most intensive studies, on red deer and Soay sheep respectively, were conducted in island situations precluding dispersal, although in the case of red deer, animals were able to move out of the study area into other parts of the island. Predation was also lacking in these islands, although management culling restricted red deer numbers outside the study area. Maximum population biomass levels varied over an order of magnitude, from under 5 kg ha^{-1} to over 50 kg ha^{-1} . All studies spanned at least twofold variation in population density levels.

Two of the populations studied have manifested repeated oscillations in abundance, with the attainment of peak numbers being followed by severe mortality, generally in association with adverse weather conditions. The period between successive peaks has been 3–4 years for Soay sheep, but 25 years or more for moose. Both populations exist on islands, but of vastly differing area. The population crashes by moose have been associated with progressive reduction in the browse resource upon which they depend, while the extreme peak biomass levels attained by the Soay sheep have not led to any apparent reduction in the productive potential of their grass forage. In contrast, the red deer population studied, also within an island context, has stabilized in abundance with only minor fluctuations around the asymptotic density. Substantial reductions in pregnancy rates, as well as in both juvenile and adult survival, have contributed towards suppressing the population growth of these deer. The Soay sheep intrinsically have a much higher population growth potential than red deer. Females can produce their first offspring at 1 year of age, while 20% of adults give birth to twins, enabling the population to increase by 50% during the course of a year under ideal conditions. Accordingly, the population level attained by the end of summer may be much greater than what food resources can support through winter, especially when adverse weather intervenes (Clutton-Brock et al. 1997, Clutton-Brock and Coulson 2002). However, moose show irruptive dynamics on Isle Royale despite much slower growth towards reproductive maturity, although a proportion of females do similarly produce twins. The roe deer populations studied also occupy effective islands without predators because of fence restrictions on dispersal from the forest patches, but management culling has restricted the density levels attained.

The kudu population in Kruger Park has shown wide fluctuations in abundance almost equal to the range shown by the Soay sheep, but in this case the declines were associated with perturbations related to rainfall variation, and more recently to an elevation in predation pressure. Rather than

Table 1.1 Summary information for the set of studies

Species	Body mass ¹ area (kg)	Study	Extent (km ²)	Duration (yrs)	Density (/km ²)	Peak biomass ² (kg/ha)	Indiv. recog.	Dis-persal	Pre-dation	Hunt/cull	Survival rates		Density feedback		Weather influence		Veget. degrad.	
											AdF	Juv	AdF	Juv	AdF	Precip.		Temp.
Red deer	65	Rum	12	37+	15-33	15	X	(0)	0	(0)	0.96-0.915 (→-0.79)	0.75 (→0.3)	X	X	X	-ve	+ve	0
Soay sheep	24	Hirta	6.4	50/23+	100-330	55	X	0	0	0	0.925 (→-0.55)	0.45→ 0.2	0	X	X	-ve	+ve	0
Roe deer	30	France	14+26	32+	8-25	5.5	X	0	0	X	0.93 (0.4-0.9)	0.56 0.47	0	X	X	+ve	-ve	0
Bighorn sheep	72	Canada	38+60	38+	2-5	2.8	X	X	X	X	0.93	0.47	0	X		+ve	+ve	0
Kudu	180	Kruger Park	60+60	10/22	2-4	5.4	X	X	X	0	0.92/0.87 (→-0.73)	0.55 (0.1-0.8)	X	X		+ve	+ve	0
Wild-beest	160	Serengeti	27,000	47+	10-52	62	0	X	X	(X)	0.91 (→-0.75)	0.40 (→0.1)	X	0	X	+ve		0
Moose	400	Isle Royale	544	50+	1-4	12	0	0	0	X	0					-ve		X
Elk	250	Yellowstone	5,200	85+	1-4	7.5	0	X	X	X	0.92 (→-0.80)	0.30 (→0.19)	X	X	X	+/-	+ve	X

X = presence of factor or effect, 0 = absent or no effect, - = no information, +ve = positive influence, -ve = negative influence, brackets indicate equivocal assignments.
¹ mean adult female mass, ² assumes mean individual mass = three-quarters of adult female mass, AdF = adult female.

being stable in abundance, this population appears resilient through showing fairly rapid recovery from these disturbances. The elk population in northern Yellowstone has also shown widely variable abundance, but mostly related to recovery from the low level previously maintained by management culling. It is uncertain where the recent downward trend following the introduction of a major predator will lead. Contributing to the uncertainty are indications that the adverse vegetation changes induced by elk browsing are being reversed in the presence of the predator. In contrast, the wildebeest population in Serengeti increased from relatively low density to stabilize with only minor fluctuations around its enormous biomass density, despite a huge abundance and diversity of predators. However, its wide migratory movements have evidently enabled it to escape predator limitation. Adverse vegetation changes have not resulted from the huge grazing pressure, perhaps because of the migratory rotation. Predation also emerged as a disrupting influence on both study populations of bighorn sheep, when a specific predator started targeting this prey species.

Red deer on Rum, and wildebeest in Serengeti increased from relatively low density to stabilize with minor fluctuations around an upper abundance asymptote. The trend shown by elk in Yellowstone resembles this pattern, but it remains unclear whether an upper abundance level is being maintained, or a predator-related decline being initiated. For both kudu in Kruger and bighorn sheep in Alberta, equilibration around a maximum abundance level was disrupted by elevated predation losses. Soay sheep on Hirta have exhibited persistent oscillations in abundance over a three-fold range, with a period between peaks of only 3–4 years. Moose on Isle Royale have increased to high abundance followed by population crashes at intervals of 25 or more years, with the most recent case being the most extreme. For roe deer in France, the suspension of removals has been too recent to reveal the intrinsic population trend.

Density feedbacks counteracting population growth were detected in all populations, except for moose, where there has been no critical assessment. Fecundity declined with increasing density, most commonly through a delay in the age at first parturition, although pregnancy rates among adult females were also lowered for red deer, elk, and wildebeest. Juvenile survival was also negatively influenced by rising density, except for wildebeest where a density influence could not be detected when the direct effects of changing food availability were taken into account. Only some of these populations showed reduced survival among adult females, generally in interaction with extreme weather after high-density levels had been attained. Adult males seemed more sensitive to extreme density or weather conditions than females, in those cases where information was available. Density effects

were associated with reductions in birth mass and subsequent growth, indicating malnutrition as the underlying cause. However, the density feedback became apparent at widely differing biomass density levels among these populations (Table 1.1).

Warmer temperatures generally had a positive influence on juvenile survival and hence population growth, except for roe deer where cooler summers led to reduced body mass and hence survival among fawns. Effects of lower winter temperatures on northern ungulates were generally not clearly separated from those of snow cover. Kudus showed reduced survival during unusually cold and wet weather at the end of dry season at temperature levels that would be benign for northern ungulates. Increased precipitation in the form of rain during summer generally had a positive influence on calf survival, although not for red deer on Rum. For wildebeest, rain received during the normally dry season was most influential. Greater snowfall during winter negatively affected moose and elk populations occupying regions where snow depth restricted movements. A combination of extreme weather and density conditions in the year of birth had long-lasting influences on the subsequent fecundity of red deer, Soay sheep, and roe deer females.

Mean mortality rates among adult females varied within a surprisingly narrow range of 6–8% per annum, excluding the early growth phase of the red deer population (Table 1.1). However, comparisons are affected by whether survival was estimated across all adult females, including mortality due to senescence, or only through the prime age range. Mortality among adult females in worst years increased to over 20%, but in the case of Soay sheep to as much as 45%. Juvenile mortality prior to weaning appeared somewhat more variable over a range of 44–70%, increasing to as much as 90% under worst conditions. In this case, comparisons are blurred by the stage at which survival was measured and by whether pregnancy rates were taken into account when estimating survival from mother : offspring ratios. Studies following recognizable individuals recorded reduction in survival rates of females beyond some prime age range, with lowered fecundity also evident among old red deer females.

Rather than controlling population growth via a density-related feedback, changes in predation pressure had a disruptive influence on the dynamics of moose, bighorn sheep, and kudu populations. The ungulate populations exposed to substantial predation did not show lower survival rates than those lacking predation, except for Yellowstone elk where mortality among both adults and calves rose substantially following the introduction of wolves. However, for these elk, an additional influence from adverse weather on survival rates cannot be discounted. Culling conducted by the management authority controlled the size of the roe deer population,

and perhaps contributed to the stabilization of the red deer subpopulation in the study area through the removal of animals from elsewhere on the island. Controlled hunting had no obvious effect on the dynamics of bighorn sheep, while hunting (now curtailed) probably contributed to the initial decline of elk in Yellowstone following the introduction of wolves. Illegal killing of wildebeest moving outside park boundaries during their mass migration may have contributed to the stabilization of this population.

The growth of the elk population in Yellowstone has clearly had a massive influence on woody plant populations, but with no obvious consequences for the dynamics of the elk. The increase of moose in Isle Royale has also substantially influenced woody vegetation composition, but with no apparent influence on the dynamics of the moose population. Despite the extremely high biomass levels attained by wildebeest in Serengeti, Soay sheep on Hirta, and red deer on Rum, the productive potential of the grass layer upon which they depend does not seem to have been adversely affected.

The attainment of high, relatively stable, abundance levels by wildebeest in Serengeti and red deer on Rum represents the ideal situation that managers desire, but for red deer there was some assistance from management removals, and for wildebeest via illegal hunting. The pattern shown by Soay sheep on Hirta and moose on Isle Royale is what managers fear, i.e. growth to extremely high density levels curtailed by starvation-related die-offs. This is the justification for the removals by live capture or hunting carried out for roe deer and red deer outside the intensive study area. However, while damage to woody vegetation was a worry for Isle Royale, this was not a concern for the lush meadows grazed by the sheep on their wet and fertile island. The fluctuating abundance shown by kudu in Kruger in response to both weather and predation did not warrant any intervention. How managers should respond to the widely variable abundance of elk in Yellowstone, with both predation and weather involved, is currently highly contentious (White and Garrott 2005, Wagner 2006).

The empirical data documented in this chapter provide the basis for models to project the variable influences of weather, population density, predation, and human interventions on the dynamics of large herbivore populations in changing environments. Several of these studies have been especially revealing of the demographic mechanisms underlying population changes, manifested through the responses of particular population segments to these conditions. Subsequent chapters will assess the extent to which the patterns revealed by these case studies can be generalized. However, the immediate need is to assess the modeling concepts and theory that have been developed for the interpretation of these population dynamics, which is the topic of the next chapter.

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