12 Controls on the Population Dynamics of Invading Mammals

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12.1 Introduction

This chapter outlines the development of concepts (models) of controls on the population dynamics of invading large mammalian herbivores in New Zealand. The primary aim is to reconcile models with available data. The focus is on models appropriate to the New Zealand context. These models are all based on the assumption that, in the absence of predators, food determines the abundance of large herbivores. A secondary aim is to suggest directions for further work.

12.2 Models of Invading Large Herbivore–Plant Dynamics

12.2.1 Eruptive

Holloway (1950) gave the first description of a sequence of concomitant changes in the density (number per unit area) of invading large mammalian herbivores (red deer *Cervus elaphus scoticus*) and their food supply (forests in western Southland) in New Zealand. Holloway proposed that the forest initially provides a maximum amount of browse, such that the herbivore population increases most rapidly. The deer feed selectively, such that preferred plants are removed first. The population increases and eventually “overtakes … available food supply”. Animals begin to starve and population density declines. The deer population eventually achieves a static (“equilibrium”) density dependent upon the renewal rate of food plants. Holloway recognized that changes in the abundance of the food supply were not uniform, but rather varied according to the palatability of the plant species to deer. He postulated

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that the most palatable species could become locally extinct, and that unpalatable species would increase in abundance.

Subsequent workers (Howard 1964a, b; Riney 1964; Caughley 1970; Challies 1985, 1990) have elaborated upon this model by subdividing it into four stages, but their stage definitions differ. The stages of Howard (1964a, b) and Riney (1964) were based upon attributes of the herbivore and the food supply. Caughley (1970) noted that these were "not congruent", and based his "hypothetical" stages only on attributes of the herbivore's population (Fig. 12.1). The "initial increase" represents the period between establishment and the initial population peak. The "initial stabilization" lasts from the population peak until the start of the decline. The "decline" continues until the population's rate of increase changes from negative to zero. The "postdecline" is characterized by small fluctuations around an equilibrium density. Riney (1964) suggested that the postdecline density is lower than the initial peak because the availability of forage has been modified.

Because herbivore density is postulated to undergo a large increase followed by a decline, this conceptual framework has become known as the eruptive (or irruptive) model. Caughley's (1970) major insight was realizing that changes in rate of increase (from positive to zero to negative to zero) defined the eruptive model. Challies (1985, 1990) confused the issue by attempting to link stages in the eruptive model with the food supply. For example, the zero rate of increase postulated for the initial stabilization was "when deer are temporarily in balance with their habitat" (Challies 1990, p. 448).

The eruptive model has become the paradigm for understanding the population dynamics of introduced ungulates in New Zealand. For example, Challies (1990, p. 448) claimed "many of the local red deer populations have passed through a classic population irruption". The eruptive model has also been an influential concept in North America (review in McCullough 1997).

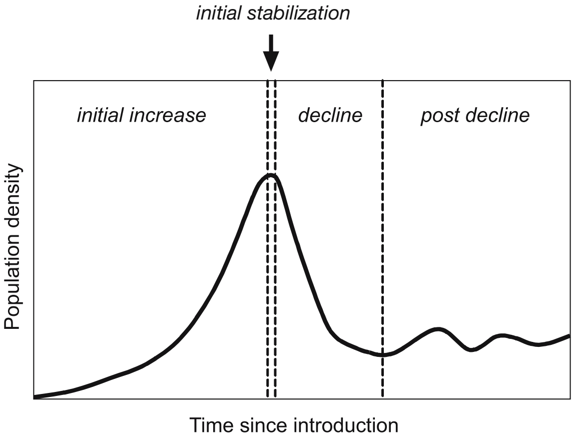

Fig. 12.1 Representation of the eruptive model showing the four stages defined by Caughley (1970)

Forsyth and Caley (2006) recently developed single-species mathematical models that can generate the eruptive dynamics described above.

12.2.2 Logistic

The simplest class of herbivore population model is the θ-logistic (Gilpin and Ayala 1973), which can be written as:

$$N_{t+1} = N_t \exp\left[r_m \left(1 - \left(\frac{N_t}{K} \right)^{\theta} \right) \right] \tag{12.1}$$

where N is the population size in year t, r_{m} the intrinsic rate of increase, K the carrying capacity, and θ represents the form of density dependence (Fig. 12.2a, c). A number of variants on this model are available (see Barlow

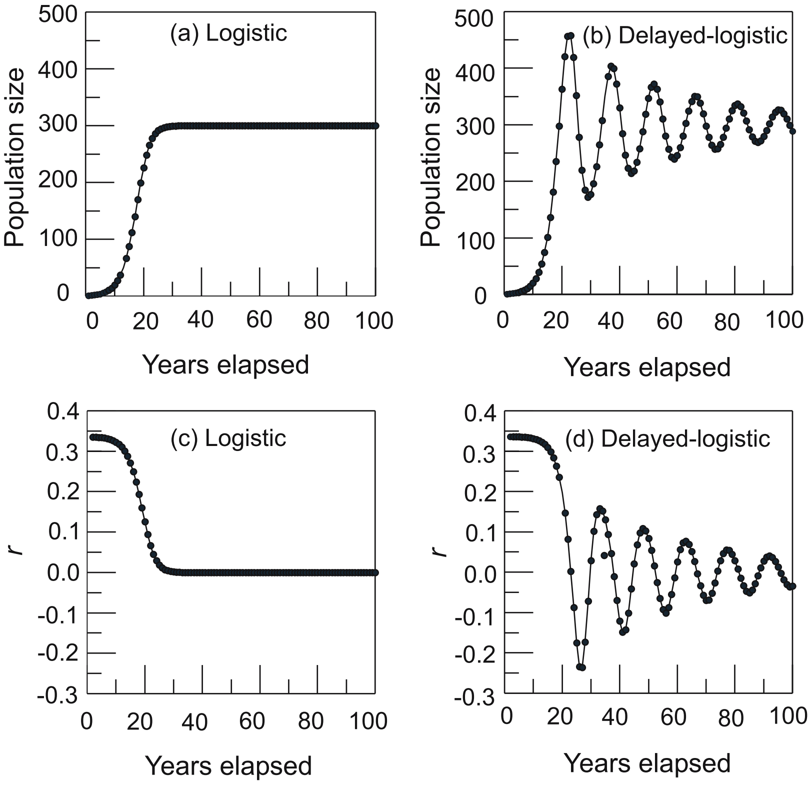

Fig. 12.2a–d Comparison of the θ-logistic (θ=1) and delayed-logistic models (T=3). r_{m} and K were arbitrarily set at 0.4 and 300, respectively, for both models. **a** and **b** show changes in herbivore population size with time; **c** and **d** show changes in the annual exponential rate of increase (r) with time

and Clout 1983). The intrinsic rate of increase is the maximum increase in population size possible from t to $t+1$ (review in Sibly and Hone 2002).

In the θ-logistic, the population's exponential rate of increase (r) is greatest at lowest densities. However, unlike the eruptive model, the θ-logistic population does not undergo any oscillation, instead increasing to equilibrium. The logistic model assumes that the rate of renewal of the food supply is constant, and not influenced by the number of animals using it or by its initial biomass (Caughley 1976).

May and Oster (1976) showed how the θ-logistic model can generate complicated dynamics, ranging from a stable cycle to chaos, when $r_{\mathrm{m}}>2$ (see also May 1976). Hence, it can be difficult to distinguish data generated by these deterministic models from stochastic variation and sampling and/or measurement error.

The θ-logistic model has been widely used to model changes in the abundance of possums (*Trichosurus vulpecula*) in New Zealand (e.g., Barlow and Clout 1983; Barlow 1991) because of "its simplicity and tractability" (Barlow and Clout 1983, p. 256). Barlow and Clout (1983) argued that the two most-likely forms of population regulation in possums – competition for refuges and competition for food – both give growth curves peaked to the right (i.e., $\theta>1$).

Hutchinson (1948) modified the logistic model to include the assumption of a delay between changes in resource availability and changes in the rate of increase. The delayed-logistic,

$$N_{t+1} = N_t \exp\left[r_m\left(1-\frac{N_{t-T}}{K}\right)\right] \qquad (12.2)$$

has the population changing as a function of *lagged* density (T). Although the delayed-logistic model still assumes that the rate of food renewal is constant and independent of N, it may be useful because the lag time could (fortuitously) describe the generation time of vegetation (May 1973). The delayed-logistic therefore appears to better represent the dynamics of the eruptive model than does the θ-logistic (Fig. 12.2b, d).

12.2.3 Interactive

Caughley (1976) considered that the logistic models described above did not adequately represent the food dynamics of the system. He therefore modified the Lotka-Volterra equations into an *interactive* model that related the dynamics of the herbivore to the dynamics of the food resource. Based on May (1973), Caughley's interactive model included one equation for the change in vegetation biomass (V) as a consequence of what is present, potential maximum (K), minus the amount removed by herbivores:

$$V_{t+1} = V_t + a_1 V_t \left(1 - \frac{V_t}{K}\right) - c_1 N_t \left(1 - \mathrm{e}^{-d_1 V_t}\right) \tag{12.3a}$$

The first two components are described in the θ-logistic model, with a_1 the maximum rate at which vegetation biomass increases. The last component describes how much a single herbivore would eat given that biomass was present (i.e., the functional response), multiplied by the number of herbivores present (N). d_1 is the rate at which intake changes as V increases, and c_1 the rate at which vegetation growth is slowed by animals eating it. The change in the number of herbivores was also modeled using the functional response:

$$N_{t+1} = N_t + N_t \left[-a_2 + c_2 \left(1 - \mathrm{e}^{-d_2 V_t}\right)\right] \tag{12.3b}$$

where a_2 is the rate at which the herbivore population will decline when V=0, c_2 the rate at which the population increases when animals can eat unconstrained, and d_2 determines the rate at which c_2 declines as vegetation biomass is consumed.

With this model, Caughley (1976) captured what he considered to be the dynamics of the eruptive model for a hypothetical introduction of white-tailed deer into a mosaic of grassland and forest (Fig. 12.3). He used parame-

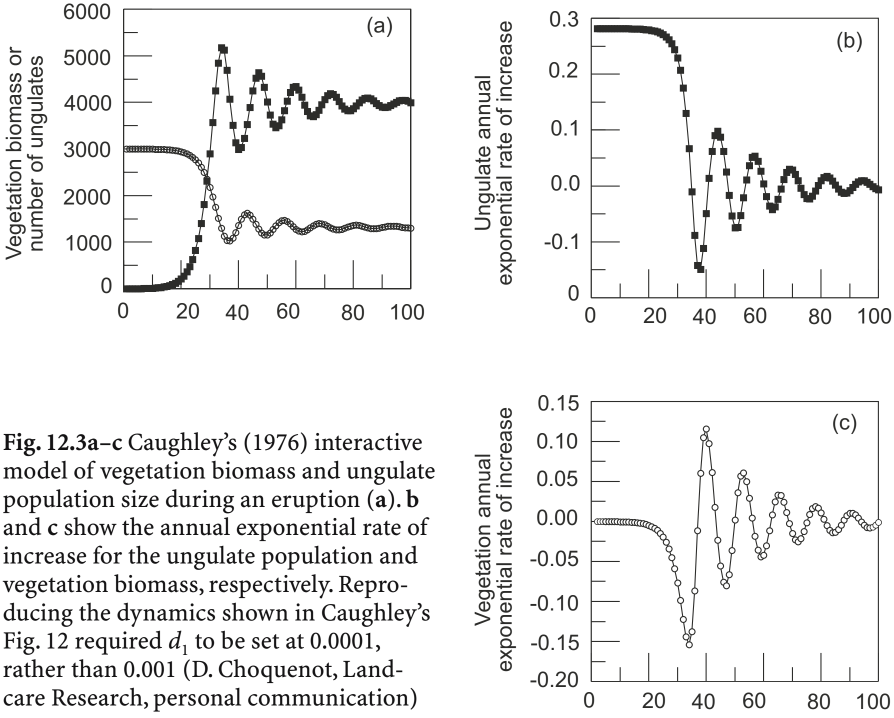

Fig. 12.3a–c Caughley's (1976) interactive model of vegetation biomass and ungulate population size during an eruption (**a**). **b** and **c** show the annual exponential rate of increase for the ungulate population and vegetation biomass, respectively. Reproducing the dynamics shown in Caughley's Fig. 12 required d_1 to be set at 0.0001, rather than 0.001 (D. Choquenot, Landcare Research, personal communication)

ter values that “might be expected”, and considered that his *interactive* model was a more informative simulation of ungulate population dynamics than either the logistic or delayed-logistic models. Owen-Smith (2002) elaborated Caughley’s (1976) model to include density-dependent interference in herbivore feeding, and several mechanisms of vegetation change.

12.3 Reconciling Models with Data

12.3.1 Ungulates in New Zealand

The deterministic models above assume that, following arrival into suitable habitat, populations will grow following the same trajectory. However, there is a strong theoretical basis for expecting that the number of individuals involved (“propagule size”) will be an important determinant of subsequent dynamics. The likelihood of a propagule becoming extinct is inversely related to propagule size because of the combined effects of demographic and environmental stochasticity, and random catastrophes (Dennis 2002). Of the 14 ungulate (order: Artiodactyla) species released into New Zealand, 11 were judged by Forsyth and Duncan (2001) to have established. Across species, there was a threshold introduction size of about six individuals, below which ungulate releases in New Zealand were likely to fail, and above which they were likely to succeed (Forsyth and Duncan 2001). A similar relationship was found for the 16 introductions of six ungulate species into Victoria, Australia, with introductions involving four or fewer individuals going extinct, whereas those introductions involving seven or more individuals established (Forsyth et al. 2004). Hence, there appears to be a strong stochastic component to the establishment of introduced mammal populations.

Caughley (1970) tested the eruptive model using Himalayan tahr (*Hemitragus jemlahicus*), a mountain ungulate that had established near Mt. Cook and subsequently expanded its range north and south along the Southern Alps. Caughley assumed that the four stages of the eruption (Fig. 12.1) would be represented by tahr at different locations along the gradient of colonization, with those in the most recently colonized areas being in the initial increase stage, and those in the longest-colonized areas being in the postdecline stage. His sampling sites were hypothesized to represent the four stages of the eruptive model. Tahr were shot, sexed and aged. Life-tables for female tahr supported parts of the eruptive model, the rate of increase being high (r=0.13) at the site predicted to be in the initial increase stage, and close to zero (r=0.01) at the site predicted to be in the initial stabilization stage. However, because data were not available for the decline stage, these results also support a θ-logistic model. Only long-term monitoring of density can discriminate between the postdecline stage of the eruptive model and *K* in the logistic model. Caughley observed that rate of increase was determined mainly by variation in survival rates, rather than by reproductive rates.

As well as noting the relationship between changes in *r* and stages of the eruptive model, Caughley (1970) predicted a relationship between *r* (a parameter of the population) and body condition (a parameter of the individual). Adult female kidney fat index (an index of body condition) of tahr supported these predictions – highest during the initial increase stage (when *r* is largest), lowest during the decline ($r<0$), but slightly higher in the postdecline ($r=0$), although sample sizes were small (≤27) for the latter two stages. These predictions were supported by analysis of kidney fat data from a much larger sample ($n=4,789$) of tahr shot during May–September 1972–1976, and with many "replicates" of colonization history (Forsyth et al. 2005).

Challies (1978, 1985, 1990) further explored the link between time since establishment, demography and body condition. He estimated carcass parameters from hunted populations of red deer established for different periods of time. The carcass weight of both 2-year-old males and females was highest in the most recently established population (sampled ca. 10 years after colonization), but declined thereafter. A similar pattern was observed for the proportion of lactating 2- and 3-year-old females (Challies 1978, 1985, 1990). Following the advent of intensive commercial hunting, which reduced deer densities >90 % in 15 years (Challies 1977), carcass weight subsequently increased, presumably due to increased per capita food availability.

12.3.2 Possums in New Zealand

Patterns in annual kill-trapping of possums in a southern North Island catchment during 1945–1989 were reported as being consistent with "irruptive fluctuation" (Thomas et al. 1993). Possums colonized the catchment in ca. 1920, and kill-trapping was conducted along the same lines in 1945, 1951, and annually from 1964 onward. There appeared to be a large decrease in the abundance of possums from 1945 to 1965, and a further decline in 1977. Possums subsequently increased, such that by 1989 the numbers trapped were comparable with those reported for the period 1965–1976. Although the eruptive model was originally developed for "large herbivores", possums have many of the demographic characteristics of ungulates (Thomas et al. 1993). Hence, the eruptive model could reasonably be expected to apply to possums, too.

A mark-recapture study of possums on a 15-ha grid in mixed lowland podocarp-broadleaved forest in the Orongorongo Valley, North Island, during 1967–1997 provides strong evidence for an "equilibrium" (Efford 2000). The population has fluctuated between 5.5 and 13.3 possums ha^{-1} for 30 years, and shows a return tendency (sensu Murdoch 1994). The Orongorongo possum population was more stable (i.e., the fluctuations around a long-term mean were lower) than most other mammals that have been studied (Efford 2000). However, the equilibrium is consistent with both the "postdecline" of the eruptive model and *K* in the logistic models.

12.3.3 International Studies

Two long-term studies of the abundance of invading large herbivores are summarized in Fig. 12.4. Sæther et al. (2002) reported annual counts of a population of ibex (*Capra ibex*) derived from seven animals introduced into the Swiss National Park in 1920. The population increased to a peak of 280 animals in 1963, then declined to a low of 128 in 1970, before increasing again (Fig. 12.4a, d). Scheffer (1951) reported the number of reindeer (*Rangifer tarandus*) counted annually on St. Paul and St. George islands, Pribilof Group, USA, following their introduction in 1911 (Fig. 12.4b, c, e, f). Both populations

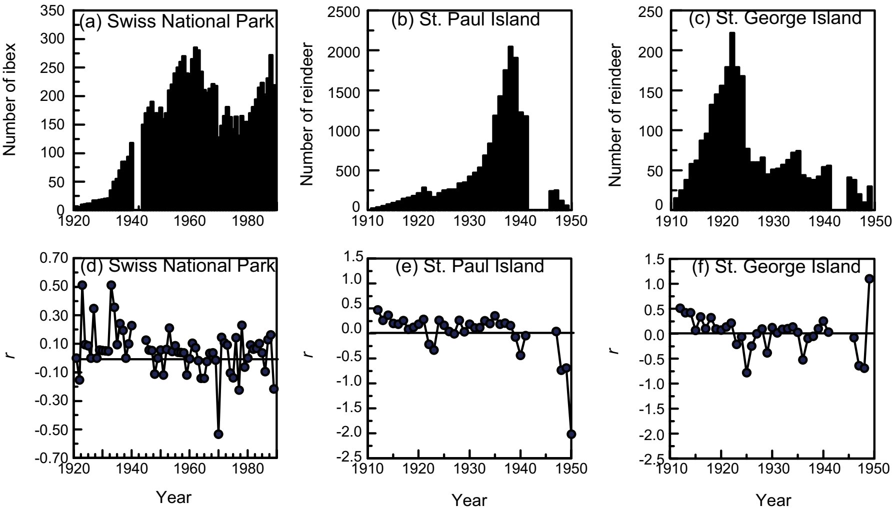

Fig. 12.4a Number of ibex counted annually in the Swiss National Park following their introduction in 1920. Note that no counts were conducted during 1941–1943. **b, c** Number of reindeer counted annually on St. Paul Island and St. George Island, Pribilof Group, USA, following their introduction in 1911 (data from Scheffer 1951). No counts were conducted during 1942–1945 on St. Paul, and during 1942–1944 and in 1950 on St. George. On St. Paul, harvests were nil or <9 %, except in 1941 and 1942 when 21 and 27 % of animals were killed, respectively. On St. George, harvests were negligible, except during 1918–1926, when 10–22 % of the annual count were killed (see Scheffer 1951). **d–f** Respective annual exponential rates of increase (*r*) of ibex and reindeer calculated from those data

increased substantially before declining to very low numbers. The population on St. George appeared to fluctuate around some postdecline equilibrium predicted by the eruptive model, although it was close to extinction in 1949 (eight animals). Insufficient data prevent assessment of the postdecline stage on St. Paul. Forsyth and Caley (2006) showed that the dynamics of these three populations, plus three of four other populations either introduced to new range or released from harvesting, were best described by eruptive models (of which the delayed logistic was one model): only one of the seven populations did not display the predicted eruptive dynamic (i.e., was best described by the θ-logistic model).

To my knowledge, only one other study has attempted to compare which of the θ- and delayed-logistic models best describes the dynamics of invading mammals. Maas (1997) experimentally reduced the abundance of a population of feral goats (*Capra hircus*) in the semi-arid rangelands of New South Wales, Australia, and compared its subsequent dynamics (abundance estimated quarterly) with a nearby population that was not manipulated. Both the θ- and delayed-logistic models fitted the data poorly. This may have been because the density of goats was not sufficiently reduced to detect either form of logistic growth with the monitoring used, even if logistic growth was the true model (Maas 1997). Maas concluded "the dynamics could not be represented by single species models … probably due to the stochastic environment in which they lived".

12.4 Environmental Variation and the Dynamics of Invading Mammals

Sæther (1997) concluded that stable equilibria in large ungulate populations and their environment were unlikely because of the effects of both environmental variation and population density on demography. Environmental variation can vary the food supply available to herbivores (Caughley et al. 1987), and McLeod (1997) argued that the notion of a relatively constant carrying capacity (K) is inappropriate in variable environments. Bayliss and Choquenot (2002) illustrate how even small stochastic variation in K (5 % year-to-year) can mask θ-logistic growth. These studies suggest that variation in food supply caused by the environment independent of the herbivore will be an important determinant of the dynamics of invading herbivores. Such variation, at least in some circumstances, may be extreme (Caughley et al. 1987).

If it is assumed that the abundance of large herbivores, in the absence of predators, is determined by food availability, then two sources of variation in food availability and quality could affect the dynamics of animal populations

(Andrewartha and Birch 1954). *Intrinsic* variation arises from the effect of animals consuming their own food resources; *extrinsic* variation arises from the effects of factors independent of the animals' foraging. Choquenot (1998) evaluated the relative influence of intrinsic and extrinsic variation in food availability on the rate of increase of feral pig (*Sus scrofa*) populations in New South Wales, Australia. In a large-scale field experiment, neither pasture biomass nor *r* declined with increasing pig density, suggesting that food availability was dominated by extrinsic factors. Modeling indicated that such a result was likely because pigs, relative to other herbivores present, were inefficient grazers and occurred at low densities.

A continuum of disturbance exists, from frequent but small-scale gap formation, through to infrequent but large-scale catastrophes such as fires, floods, hurricanes, and earthquakes. In Westland, New Zealand, there is evidence of three massive earthquakes within the last 650 years, with a large proportion of the forest cover comprising a cohort of trees established after the most recent disturbance (Wells et al. 2001).

One difference between grasslands and forests is that in the former ungulates have virtually constant access to all of their food supply, whereas in forests these animals can access forage only within the browse tier (e.g., assumed to be 2 m for red deer; Nugent et al. 2001a). The amount of food available in a forest is dependent on tree demographics, which can be unrelated to deer (see Coomes et al. 2003). Ungulates can therefore remove only a small proportion of foliage from most canopy trees, and are unlikely to affect the mortality of mature trees. However, there may be a lack of regeneration, because saplings and seedlings are killed faster than they are replaced. Litterfall is an important component of the diet of deer in some New Zealand forests (Nugent et al. 2001a).

Choquenot (1998) proposed a continuum between grazing systems dominated by intrinsic and extrinsic sources of variation in food availability. Increasing environmental stochasticity and declining efficiency of the vegetation–herbivore feedback loop means that food availability would be of an increasingly extrinsic origin. Feral pigs in the rangelands of New South Wales are at the extrinsic end of the continuum (Choquenot 1998). New Zealand forests, in which the *supply* of a major food of deer (litterfall) is independent of the density of deer, will be at the extrinsic end of the continuum (D. Choquenot, Landcare Research, personal communication). However, litterfall could also be a consequence of deer historically altering canopy composition. Decreasing environmental stochasticity and increasing efficiency of the vegetation–herbivore feedback means that food shortages would be increasingly intrinsic in origin.

Temperature-driven synchrony in fruiting by masting species may link simultaneous fluctuations in animal condition and breeding in New Zealand (see Chap. 16). At four long-term study sites spanning 120 km in lower North Island, possum breeding was much reduced in one year (1996) at all sites

(28 % of adult females bred, compared to >80 % in other years; Ramsey et al. 2002). The probability of adult females breeding declined as body condition fell below average. Hinau (*Elaeocarpus dentatus*) is a masting tree species (Schauber et al. 2002), and possums eat its fruit. An index of hinau fruiting plus possum population density in the preceding year were the most important predictors of both body condition and breeding rate (Ramsey et al. 2002). Data from two of the sites (ca. 50 km apart) suggested a delayed density-dependent effect on breeding, through competition for highly nutritious components of the diet reducing body condition.

12.5 Harvesting and the Dynamics of Invading Mammals

Harvesting can be an important driver of the dynamics of some populations. Forsyth et al. (2003) used a θ-logistic model to investigate how the form and size of the harvest relative to recruitment can regulate a population already at K. Three outcomes are possible for a harvested population: eradication, regulation at low density, and regulation at high density. There are well-documented examples of feral goats being eradicated from offshore islands (e.g., Raoul Island; Parkes 1984). Red deer appear to be regulated at low density by helicopter-based commercial hunting, at least in areas with a large proportion of open habitat (e.g., Fiordland; Nugent et al. 1987). Helicopter-based commercial hunting reduced the density of Himalayan tahr in Carneys Creek by >90 % (Tustin and Challies 1978), enabling recreational hunters to subsequently regulate this population at low density (Forsyth 1999).

12.6 Interspecific Competition and the Dynamics of Invading Mammals

Smaller ungulates may have the potential to out-compete larger species by depressing vegetation biomass below that required to meet the greater absolute requirements of the latter (review in Owen-Smith 2002). The decline and possible extinction of moose (*Alces alces*) in Fiordland, New Zealand, has been attributed to the reduced availability of food caused by the arrival and subsequent eruption of the smaller red deer (Nugent et al. 2001b). Sika deer (*Cervus nippon*) have apparently out-competed the larger red deer in central North Island (Davidson and Fraser 1991). Red deer have failed to expand their range into the Greenstone and Caples valleys (Otago), which were first colonized by fallow deer (*Dama dama*). Red deer also have a limited distribution on Stewart Island, where the smaller white-tailed deer is widespread and abundant (Challies 1990). However, a counter-example is the observation that increasing densities of Himalayan tahr are associated with declining densities of the smaller chamois (*Rupicapra rupicapra*) in the eastern Southern Alps (Forsyth and Hickling 1998). Both species overlap in diet (Parkes and Thomson 1995) and habitat selection (Forsyth 2000), so scramble competition for food may be important. An alternative mechanism is that chamois avoid the more social tahr (Forsyth and Clarke 2001).

12.7 Synthesis and Directions for Further Work

How can the sources of variation described above be incorporated into models of the dynamics of invading mammals? Some interactive models can capture components of variation affecting the food supply (review in Bayliss and Choquenot 2002), and may be appropriate for systems in which the herbivore has access to all of a homogenous food resource (e.g., feral pigs and pasture; Choquenot 1998). However, when dealing with multi-species forest communities, where turnover may take hundreds of years, these models appear simplistic.

Mechanistic and spatial simulation models appear to have the greatest potential to extrapolate from short-term and small-scale field measurements to long-term and large-scale dynamics of mixed forests, and to incorporate disturbances (i.e., model the food supply). One of these models (SORTIE: Pacala et al. 1996) is being parameterized for the forests of eastern Fiordland (Coomes et al. 2003). The challenge is to link the foraging and energetics of the herbivore (Moen et al. 1997) to the recruitment, growth and mortality of the forest species at the appropriate scales. The energetic intake of the herbivore should predict age-specific changes in body mass and body condition (see Illius and Gordon 1999), the determinants of survival, and reproduction. In an important recent advance, Owen-Smith (2002) describes methods for scaling ungulate foraging across spatial and temporal scales, and for linking intake to nutritional gain and then individual growth, storage, reproduction, and survival. Since the latter two life-history variables are determinants of *r* (Sibly and Hone 2002), the dynamics of both the invading herbivore and vegetation could be simulated under various scenarios. Owen-Smith (2002) proposes that the apparent complexity of ungulates foraging on potentially many species can be reduced to a manageable level by classifying plant species into classes based on the likelihood that they will be consumed when encountered by a foraging herbivore (see also Forsyth et al. 2002).

This approach could therefore capture the dynamics described for both the herbivore (changes in: herbivore foraging behavior, body mass and condition, age-specific fecundity and survival, *r*, and abundance) and plants (changes in: growth, survival, demographics, dispersal, recruitment, and abundance) during the invasion of New Zealand habitats by large herbivores.

Such models could be modified to include the effects of harvesting (predation) risk and interspecific competition outlined above (see Owen-Smith 2002). Parallel to model development should be the collection of independent data by which to test and refine the model.

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