

IN FOCUS

On being the right size: food-limited feedback on optimal body size



Left: Two male white-tailed deer *Odocoileus virginianus* on Anticosti Island, Québec, Canada in early autumn (Photo credit: A. Simard). Right: A 0.09-ha enclosure dominated by white birch *Betula papyrifera* and balsam fir *Abies balsamea* within an area cleared in 1983 on Anticosti Island (Photo credit: S. Côté). Browsing by deer outside of the enclosure reduces total food availability for the island's population.

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An insular population of white-tailed deer *Odocoileus virginianus* introduced in 1896 to predator-free Anticosti Island, Quebec, has caused long-term changes in the plant community. Food quality declined as did body weight. Although different parameters of reproduction changed, overall reproductive rates remained similar, thus maintaining deer density and promoting further change in habitat. These results show (i) long-term feedbacks on carrying capacity, (ii) the mechanism for reduction of body mass, and (iii) the lack of strong reduction in reproductive rates to regulate the population at high density, a feature of Eutherians. They are relevant to mechanisms determining the evolution of vertebrate body sizes.

There has long been an unanswered question as to the nature of 'carrying capacity'. In the short term the answer appears obvious – it is the amount of food resources that induce density-dependent demographic responses such that the population is regulated. There is now much evidence in support of this. Far less clear is whether the population induces a long-term change in carrying capacity itself. Aldo Leopold (1943) hypothesized a long-term change in carrying capacity in his studies of deer in Wisconsin, as did Caughley (1970) in his model of erupting ungulates in New Zealand, but empirical evidence is scarce (Myserud 2006). Simard *et al.* (2008) have documented an unusually clear example of the change in habitat on Anticosti Island in the Gulf of St. Lawrence, Canada, caused by white tail deer *Odocoileus virginianus* browsing. Since deer were introduced to the predator-free island in 1896, numbers increased to a peak in the 1930s with concomitant browsing impacts. As a result of persistent high levels of herbivory, the forest has lost much of its deciduous tree diversity and has become

dominated by unpalatable white spruce *Picea glauca* – first to go were white birch *Betula papyrifera*, trembling aspen *Populus tremuloides* and several shrub species, and later balsam fir *Abies balsamea*. Deer numbers have remained unchanged since the 1930s, and the population structure is currently stationary. Such high densities arise through the prevention of emigration off the island creating the well-known *Krebs fence effect*, namely the change in vegetation due to extreme depletion of food supplies (Krebs *et al.* 1969).

Early models of carrying capacity made no predictions on changes in body size of herbivores. In his classic book *On Growth and Form* written in 1917, D'Arcy Thompson (1942) emphasized that body shape and size were adaptations to the physical forces of nature. He noted that although smaller animals needed less *absolute* amount of food, their *relative* requirements (per unit of body mass) were higher than larger animals due to the changes in surface area to volume ratio. This allometric relationship results in metabolic rates scaling to a power function of 2/3, first noted by Max Rubner in 1880 (quoted in White & Seymour 2003). The second important result of Simard *et al.* is that they show the consequences of

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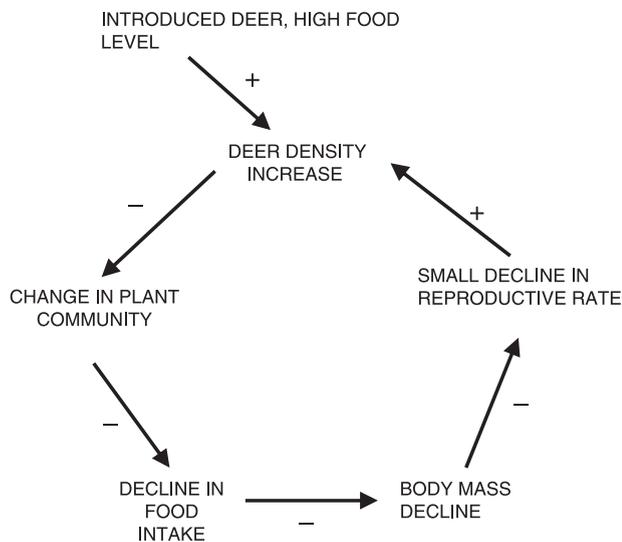


Fig. 1. Positive feedback of white-tail deer causing plant community change. Although there is a decline in nutrition and body weight as quality of food supply declines, reproduction compensates so that deer numbers remain high, producing further change in the plant community.

reduced food availability on body size and throw some light on the dichotomy of absolute vs. relative needs.

As habitat deteriorated on Anticosti Island, nitrogen intake declined some 22% over the 25 years from 1977 to 2003. In turn, body mass has diminished, with the large males declining more than the smaller females. The 25-year study showed that body mass declined but not size itself. However, size has declined on the island since the deer were first released – they are now some 50% smaller than the source population on the mainland (Boucher *et al.* 2004). This reduction is still partly a phenotypic effect, because they increase in size when fed well (S. Côté, pers. com.). Similar changes in body size were related to per capita food availability during the irruption of wild red deer *Cervus elaphus* in New Zealand (Nugent & Fraser 2005). However, the implication is that nutritional limitation, and intraspecific competition, provide the selection pressure for the evolution of small size observed elsewhere on islands.

Life history theory (Eberhardt 2002) predicts that populations under nutritional stress should first respond by changes to juvenile survival, then by increasing age of maturity, and finally through depressing adult female reproductive rates. The third important aspect of the Simard *et al.* study is that their results do not conform to these predictions: juvenile survival did not decline and females adjusted their reproductive rates by lowering litter size, thereby conserving energy, and so improving their annual pregnancy rate. The consequence is that numbers have remained high, so producing further changes in vegetation – negative feedbacks to stabilize the system are not yet evident (Fig. 1). This important result confirms previous work (e.g. Clutton-Brock *et al.* 1983; Gaillard *et al.* 2000) that reproduction, although declining under nutritional stress at high population density, particularly through delayed maturity, does not change sufficiently to

regulate the population. This implies that mortality must be creating negative feedbacks when they occur.

What is important in this study is that it highlights the mechanism between food availability, intake rate, intraspecific competition, and life history consequences, resulting in lower body mass (Fig. 1). Allometric relationships make two opposing predictions: lower nutrient intake rate would favour small size because of smaller absolute needs; but lower nutrient intake would also favour large size because the large body can assimilate lower-quality diets due to lower relative needs. Simard *et al.* show empirically that the former prediction may prevail with these large mammals.

This result raises an interesting conundrum first discussed by van Valen (1965): large mammals on islands tend to become smaller whereas small mammals, birds and reptiles become larger. This dichotomy is known as the *island rule*. Striking examples of dwarfism have been documented: a pygmy elephant *Elephas falconeri*, only 0.90 m tall, once occurred on Sicily, and pygmy deer *Candiacervus ropalophorus* on Crete reached only 0.40 m in height. Small forms of red deer have been described for Corsica and Jersey Islands (Lister 1989; Balouet *et al.* 1990). There were also miniature mammoths on islands (Lister 1993). An extinct dwarf hominid was recently discovered on Flores Island, Indonesia (Culotta 2006). In general, ungulates, carnivores and lagomorphs tend to become smaller (Foster 1964; Case 1978; Lomolino 1985), although not all species conform to the same rule – brown bears on Kodiak Island are the largest known.

There is now extensive information on the increasing size of small mammals on islands (Foster 1964; Alder & Levins 1994). House mice *Mus musculus*, normally around 12–25 g on mainlands, are on average 34 g on Gough Island, South Atlantic, and have become predators of nesting seabird chicks: this change must have occurred since 1810 when they were introduced (Rowe-Rowe & Crafford 1992). Similar changes are reported for passerine birds (Clegg & Owens 2002; Scott *et al.* 2003): for example, in white-eyes *Zosterops*, where there have been more than one invasion of an island, such as Lord Howe, the earliest forms are larger (Hutton *et al.* 2007). For reptiles, giant tortoises have evolved at least twice from smaller mainland forms – on Indian Ocean and Galapagos islands. Giant geckos *Hoplodactylus* sp. occur on New Caledonia (Case 1978); one species, 0.60 m long, may have occurred in New Zealand.

Models of optimum body size for efficient use of energy in warm-blooded vertebrates range from 100 g (Brown *et al.* 1993) to 1 kg (Damuth 1993), and both predict that under conditions of chronic food shortage species sizes tend towards these values (small become larger and vice versa). Case (1978) proposed that for large mammals when food is in short supply on islands, intraspecific competition is high, and so body size should decrease. If other constraints on the mainland are more important, such as interspecific competition or predation, then release from these on islands will promote increases in size. Several more specific hypotheses have been proposed in recent years that address the Case (1978) dichotomy (Robinson-Wolrath & Owens 2003; Scott

et al. 2003). For example, in small animals that are territorial, large dominant individuals have higher fitness under high competition than smaller ones, thus promoting larger size (the dominance hypothesis). The jury is still out on which of these processes are prevailing in small animals (Scott *et al.* 2003).

In general, the intensification of intraspecific competition for food is a consistent feature of these ideas for both small and large mammals. Simard *et al.*'s long-term study provides empirical evidence for food shortage and high intraspecific competition. Whether there will be a future density-dependent decline in deer numbers as habitat continues to deteriorate remains to be seen.

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