
Abstracts of symposium presentations

Native insects as targets and non-target species of biological control

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The use of population models for predicting desirable and undesirable outcomes of biological control are described using three case studies from New Zealand. The first reviews the models of Barlow and colleagues used to understand and improve the control of native grass grub *Costelytra zealandica* populations by augmentative application of pathogenic *Serratia entomophila* bacteria. A variety of modelling approaches have been used to predict grass grub outbreaks and thus the cost-effectiveness of applying bacteria. Models have also been developed to understand the competitive interactions between pathogenic and non-pathogenic forms of the bacteria. The other two case studies show how retrospective modelling has been used to quantify the non-target impact of introduced biological control agents. The parasitoid *Microctonus aethiopoidea* was introduced to control the lucerne pest *Sitona discoideus*, but was found to disperse outside of the target habitat and attack several native weevil species in the Entiminae family. Retrospective modelling suggests that, given average parasitism levels of 15%, native *Irenimus* spp. and *Nicaeana* spp. weevil populations are likely to have been reduced by 8% due to non-target parasitism. Similarly, population models have shown that native red admiral butterfly (*Bassaris gonerilla*) populations are likely to have been reduced by 5% due to non-target parasitism by *Pteromalus puparum*, which was introduced to New Zealand for the control of the cabbage white butterfly (*Pieris rapae*).

The importance of environmental spatial heterogeneity and host social structure in disease transmission

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The spatial structure of a host population determines the spatial probability distribution of interaction between individuals, and therefore influences the spatio-temporal dynamics of disease transmission within the host population (Keeling, 1999; Gudelj and White, 2004). Nigel Barlow recognised this and included non-linear transmission in his later models (Barlow, 1991), simulating the result of spatial heterogeneity of risk in susceptible hosts. These models produced behaviour that could not be found in models with homogeneously mixed host populations: more rapid disease dynamics and a greater robustness of disease to control measures. However, in this model there was no causal mechanism driving the initial spatial heterogeneity of risk in host individuals.

Environmental heterogeneity is likely to be a key factor in determining the spatial distribution of host individuals (Cronin and Reeve, 2005). We attempted to explore how environmental heterogeneity may affect disease dynamics via its influence on the spatial distribution of host individuals. We developed a spatially explicit stochastic model that incorporated spatially variable host density distributions, primarily driven by environmental heterogeneity.

In the model, space was represented by a contiguous toroidal grid of hexagonal cells. These cells represented an area which would contain host individuals that could be regarded as a group; a group being a collection of individuals whose population and disease dynamics were closely interlinked with each other, although not necessarily operating as a single social unit. Each cell also had a carrying capacity associated with it which remained constant through

time. The link to population dynamics was through rates of mortality for a group of host individuals being density-dependent, determined by the ratio of group size to carrying capacity in that area.

Different levels of environmental heterogeneity could be simulated through the use of different patterns of carrying capacities over the toroidal area. For simplicity the environment was composed of two habitat types, one favourable and one less favourable (i.e. relatively high and low carrying capacities respectively). Half of the total grid area was assigned to each habitat quality. Changes in regular spatial patterns of fragmentation of favourable habitat gave five levels of environmental heterogeneity, which increased with larger numbers of smaller favourable habitat patches.

Adult individuals had a constant probability of movement away from their current group, with an exponentially declining probability function associated with distance of movement, up to a set maximum. By varying the probability of an adult moving and the maximum distance that could be moved in parallel, we were able to simulate different levels of spatial rigidity in the host population. A zero probability of moving produced a totally rigid spatial structure, whereas a probability of 1 in conjunction with a maximum movement distance of half the grid size produced a highly fluid host spatial structure.

The simulation was discrete, stepping through four seasons in a year, and running through 38 years. There were two disease states, susceptible and infectious. A single infectious male was added to each group at the start, data being collected from the simulation only after an initial settling period of 12 years.

We found that habitat heterogeneity had a marked effect on disease dynamics, but the nature of this effect was determined by its interaction with the level of rigidity in the host's spatial structure. Disease prevalence levels declined sharply with increasing habitat heterogeneity. At low and intermediate levels of habitat heterogeneity, for a given probability of movement, short movement distances generated the highest prevalence levels. However, as habitat heterogeneity increased, the smaller movement distances became less effective relative to the longer movement distances at maintaining prevalence levels. At all levels of habitat heterogeneity, peak prevalence occurred at low to intermediate probabilities of movement.

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Body size and resource partitioning in ladybirds

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Resource utilisation is usually viewed in terms of food species size (Schoener, 1974) with each species in a predator guild adapted to exploit a particular-sized species of prey. Large species of predators exploit large species of prey and vice versa. That is, each species in a guild is able to displace other species from a particular portion of the resource space by virtue of it being better adapted to exploit that particular species of prey in that resource space.

Aphidophagous insects all exploit aphids as food but there appears to be no association between the size of aphidophagous predators and that of the species or age structure of the aphid colonies they exploit. Aphid colonies generally increase, peak and decline in abundance, and are exploited by a sequence of predators that is consistent from year to year. The objective of this study was to determine the rules underlying this temporal pattern.

For example, aphid colonies in the field are often attacked first by a small and then by a larger species of ladybird. Theory based on the geometry of ladybirds predicts that the quantity of food required for oviposition and the area searched per unit time should scale with body weight with exponents of 1 and 0.66, respectively. An analysis of empirical data supports these predictions. Thus, in relative terms a 30-mg ladybird requires 1.5 times more aphids per unit area for oviposition than a 10-mg ladybird. That is, the temporal pattern in oviposition is possibly mainly determined by geometrical constraints associated with body size with small species of ladybird able to lay eggs at lower aphid population densities than large species. Cannibalism is thought to be the mechanism by which these predators are able to coexist.

Reference

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Historical factors mediate the effects of interspecific competition

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Biotic interactions, such as interspecific competition, are potentially important in determining whether introduced species succeed or fail to establish wild populations. Such effects may be difficult to detect, however, because the outcome of interspecific competition may depend on historical and largely unpredictable circumstances such as the timing of introductions and the number of individuals of each species introduced. I used a stochastic birth-death model to explore the effects of interspecific competition, the timing of introductions and the numbers of individuals of each species introduced, on invasion success in a two-species competitive system. I then compared the model predictions with actual data on establishment outcomes for passerine birds introduced to New Zealand, for which we have data on the timing of introductions, the size of release populations, and a measure of the strength of per capita competition (the degree of morphological similarity among species). The model and data agree well, suggesting that interspecific competition was an important determinant of invasion success in this assemblage, but that the outcome of competition depended critically on circumstances such as the timing of introductions and number of individuals released. Hence, while there is a deterministic component to invasion success in this assemblage (morphologically similar species are less likely to establish), historical circumstances played a critical role in mediating the outcomes.

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Seasonally pulsed resources and non-interactive plant-herbivore models

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A strong argument for consumer-resource models over single-species population models is that they are consistent with actual ecological processes, and that this mechanistic realism leads to greater predictive power. These benefits depend wholly on the accuracy with which a model captures the dynamics of the resource. We review the key food resources used by brushtail possums in New Zealand and find that their dynamics are poorly represented in "interactive" models of the dynamics of possums and their plant foods. More realistic models that we develop lead to direct density dependence of approximately δ -logistic form (Barlow and Clout, 1983), where δ depends on observable characteristics of the system.

Standard consumer-resource models for plant-herbivore systems assume that plants grow continuously according to some multiplicative law (e.g. logistic). In temperate systems, many foods of browsing herbivores have instead a pulsed seasonal phenology. Seasonal food pulses deviate from the logistic model in two important respects. Firstly, the palatable plant parts (e.g. young leaves or flowers) appear each year by outgrowth from a long-lived woody stock, rather than by multiplicative growth of the previous cohort. Lack of self-regeneration in the edible fraction of plant biomass substantially reduces the possibility for a classic plant-herbivore interaction. Secondly, pulsed foods carry a natural "expiry" date; unbrowsed plant parts automatically senesce, or mature into a different and possibly less palatable form.

We develop an alternative plant-herbivore model for pulsed systems. In the model, herbivore dynamics are assumed to be "reactive" (rate of increase is a function of the amplitude of an annual pulse of highly nutritious food, without a reciprocal feedback). Per capita consumption varies with density because of within-year depletion. The duration of the unbrowsed food pulse and the herbivore λ jointly determine the shape of this relationship, and hence δ . We further explore these ideas with examples from field studies of brushtail possums, and suggest observations that may test their relevance. More data are needed on the numerical response of possums to varying food intake.

Reference

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Seasonal population dynamics of ticks, and their influence on infection transmission: a semi-discrete approach

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A semi-discrete model for tick population dynamics is presented, whereby tick feeding is assumed to occur only during summers of each year. Conditions for existence, uniqueness, and stability of a positive equilibrium were found; the system was then studied numerically using parameter estimates calibrated for the tick *Ixodes ricinus* in Trentino, Italy, and the sensitivity to parameters was examined. This model was then extended to consider tick-transmitted infection of one species of hosts, while other hosts are incompetent to the infection. Assuming, for simplicity, that the infection is not affecting the total number of either hosts or ticks, a threshold condition for infection persistence was obtained. The dependence of the equilibrium infection prevalence on parameters was studied numerically; in particular, we considered how infection prevalence depends on host densities. This analysis reveals that a dilution effect occurs both for competent and for incompetent hosts. This means that, besides a lower threshold for host densities for infection to persist, there also exists an upper threshold: if host densities were higher than the upper threshold, the infection would go to extinction. Numerically, it was found that the upper threshold was not much higher than observed densities for realistic parameter values.

Microbes, models and management of the New Zealand grass grub, *Costelytra zealandica*.

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Improved grasslands pose particular problems in pest management. The areas are extensive and the returns per hectare from grassland agriculture are much less than those from intensive cropping or horticulture, but pastures are usually sown to last for a number of years and have a much more stable ecology than in cropping or horticulture. For these reasons, biological controls and plant resistance have long been the preferred options for managing pasture pests. Within this context, the role of diseases in pasture pest population dynamics has received increasing attention, especially their ability to control pest outbreaks. Diseases are common within

our major pasture pest species but their role in population regulation is often difficult to define. One of New Zealand's major pasture pest species, the grass grub *Costelytra zealandica*, is widespread and often damaging throughout the country. The insect is an endemic species that has adapted to an introduced pasture system, dominated by exotic plant species (*Lolium perenne*/*Trifolium repens*), where it can reach populations ten-fold higher than in its native habitat. Such high densities favour disease transmission and it is not surprising that a wide array of pathogens have been recorded from this insect (Glare *et al.*, 1993). But the insect can still be highly damaging and can cause total loss of sown species within 3–4 years from sowing in grass grub prone regions. Probably the most important of these diseases, found throughout New Zealand, is amber disease caused by strains of the bacteria *Serratia entomophila* and *S. proteamaculans*. This is an unusual disease, controlled by a bacterial plasmid which has only been found in New Zealand bacterial isolates (Jackson *et al.*, 2001). As is common in disease dynamics, amber disease follows a delayed density dependent relationship with its host the grass grub with a cycle of pest outbreak, disease ingression and population collapse taking 5–7 years (Jackson, 1993). This means that damage from the feeding larvae will occur prior to pest population collapse due to disease. However, early modelling by Barlow *et al.* (1985) indicated that natural occurrence of the bacteria was maintaining the insect at 50% of its potential density and suggested that manipulation of disease could prevent damage. The grass grub/disease interaction has been further elucidated using both discrete-time difference equation models and Markov models (Barlow, 1999; Barlow and Jackson, 1993, 1998) which were used to examine tactics of application and estimate the benefits of disease application for grass grub control. In order to gain these postulated advantages for farmers we have carried out a programme of biopesticide development with the disease-causing microbe. The bacterium *S. entomophila* has now been bulk-produced through fermentation and produced as the liquid product Invade™ and currently in the granular formulation Bioshield™ for control of grass grub in pasture. The bacterial products can be applied to consistently cause disease outbreaks in the target population but, as pointed out by Barlow (1998), microbes must be applied at the right time within the pest population cycle to obtain optimal economic benefits from disease application. This leads directly to the need for effective prediction systems for pest outbreaks. The potential for grass grub outbreaks is generally set by climatic factors such as rainfall during the flight season or summer temperatures (Jackson *et al.*, 1999) but the interaction of climatic factors and disease and the potential for disease to prevent pest

outbreaks through enzootic activity requires further study. The arena for these actions, the pasture soil, has long been regarded as a "black box", too difficult to unravel. But preliminary steps in modelling the ecology of insect pathogens within the soil microbial reservoir are leading to an improved understanding of soil microbial dynamics. A modelling evaluation by Godfray *et al.* (1999) demonstrated the importance of a free-living, saprophytic phase of growth in the soil. The modelling approach has been incorporated into soil ecology studies leading to further understanding of the bacterial dynamics in the soil (O'Callaghan *et al.*, 1999). Thus modelling has had an important role in assisting conceptualisation and analysis of this disease/host reaction despite the complex interactions involved and has made an important contribution to the effective use of microbes in management of grass grub in New Zealand pasture soils.

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Wasp dynamics: A colony model

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Social wasps are significant pests in many parts of the world, constituting a threat to human health and indigenous fauna as well as a commercial cost to industries such as beekeeping. In New Zealand *Vespa vulgaris* and *V. germanica* are significant environmental pests in large areas of native forest and, while limited chemical control is possible, for many areas there is no practical control option available. As part of a larger-scale ecological investigation into wasp biology and control, a within-colony model has been developed. The model is a simulation of intermediate complexity for which the driving relationships are drawn from an extensive field data set and published information. Although the model is conceptually similar to previous models and yields similar parameter values and output, it is mechanistically different. In particular, two new mechanistic relationships are derived: (1) the rate at which workers build cells is related to the larva:worker ratio; and (2) the rate at which the queen lays eggs is related to the number of worker-sealed brood present in the colony. Sensitivity analysis supports a possible role for queen quality in colony dynamics although other factors may also be involved. Also, sensitivity analysis results in model behaviour that is different to previous models; a result of its more mechanistic relationships. The model is intended as a tool to improve our understanding of wasp ecology and help develop effective strategies for wasp control.

Modelling biosecurity change: Ecology, economics, technology and social values

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The threats and responses to biosecurity are constantly changing, creating decision problems for policy makers setting priorities for future biosecurity systems. In the United Kingdom during 2003–04, the Department for Environment, Food and Rural Affairs (DEFRA) commissioned a Horizon Scanning project to predict the future (20–30 years) of biosecurity needs in the United Kingdom. This project created an integrated model of key ecological, economic and technological processes involved in the development and control of invasive species, across a range of taxa, and also sought views on social values that could limit response options and affect the economic and political importance of introduced species. The model demonstrates the ability to make useful probability-based estimates of economic impact given practical assumptions on ecological, economic and technological inputs. Sensitivity analyses show where improved data could reduce uncertainty. The model establishes a framework that has been used to identify major drivers of biosecurity change affecting the next generation: increased and more diverse trade and travel increasing the entry of new species; climate change affecting establishment and spread of pests introduced from new zones that could approximate Britain's climate; social values affecting attitudes to control measures such as animal culling and greater concern for environmental and amenity resources rather than agriculture; and technological improvements in pest detection. An important economic issue affecting the value of the impact caused by invasions is the time scale over which the impact is felt, ranging from immediate in the case of many livestock diseases through to the long-delayed recognition of loss of environmental quality from competition or diseases affecting native plants. New pest detection technology offers substantial opportunity to improve eradication of introduced species and could affect the prevention versus cure paradigm for many species for which general exclusion systems are presently adopted. An integrated modelling framework allows some quantification of these drivers and offers a tool to guide biosecurity planning.

Software identification tools for biodiversity and biosecurity monitoring

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The taxonomic crisis, associated with declining taxonomic expertise and resources, poses serious problems for biodiversity and biosecurity monitoring and management. While there has been a dramatic increase in the amount of taxonomic information available on the Web, resulting from such global initiatives as Species 2000, All Species and the Global Biodiversity Information Facility (GBIF), the lack of identification services has meant this information is often not accessible to many potential users. Apart from the immediate problems raised by the inability of ecologists, conservation managers, plant health inspectors and other practitioners to identify specimens of concern, this in turn means they are also unable to access the increasing wealth of information about particular organisms that is potentially available to them.

Computer-based identification keys provide one means of addressing this issue and the Centre for Biological Information Technology at The University of Queensland develops, distributes and supports two identification systems that enable taxonomists and other biologists to create and edit multi-media identification keys for distribution to end-users via CD or free-to-air across the Internet.

Lucid Phoenix (www.lucidcentral.org/phoenix) is a cross-platform dichotomous key system (released earlier this year) that allows key developers to scan and easily transform printed dichotomous keys into Phoenix web-based keys.

Lucid3 (www.lucidcentral.org/lucid3), the latest release of the Lucid Professional matrix key system, is cross platform and has an applet player that provides more convenient access to Lucid keys across the Web.

Examples are provided of how these tools have been used for developing keys for quarantine and biodiversity purposes worldwide, and plans for greater international collaboration in key development are discussed. The experience obtained in developing and implementing this identification software is used to make some generalisations about important issues of relevance, cost-effectiveness and sustainability that face most software projects aiming to provide practical tools for applied biology.

Persistence of Tb in possums: Insights from a spatially explicit, stochastic model

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The majority of models for predicting the dynamics of bovine Tb in brushtail possums in New Zealand owe much to the pioneering work of the late Nigel Barlow. These non-spatial, deterministic models subsumed local disease dynamics by using a heterogeneous mixing term that assumed Tb was confined to a fraction of the population (in patches). However, the underlying mechanism(s) that could result in this heterogeneity of infection risk were obscure. We present a new individual-based, spatial, stochastic simulation model of Tb in possums that provides an explicit mechanism for simulating heterogeneous risk of infection based on a model of individual home range utilisation and disease susceptibility. The manipulation of parameters governing individual utilisation of space also means that processes such as non-linear contact structure can be handled naturally. We use the model to predict the persistence of Tb in possums under scenarios currently implemented for the management of bovine Tb in wildlife and determine conditions under which Tb might be predicted to persist despite control efforts.

The koala-forest-management interactive game: are there lessons in modelling a complex system?

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Koalas are considered to be overabundant in some areas of their natural range. This is the case at Mount Eccles National Park, Victoria, Australia. The concern at Mount Eccles National Park is that an overabundant koala population will have deleterious impacts on the unique forest community as well as leading to a koala population collapse. Due to social and political constraints, the only available management technique is to sterilise adult female koalas. Two questions of interest to management are: (1) Can sterilisation reduce

the likelihood of both a decline in the forest community and a severe collapse in the koala population? (2) Can management sterilise enough koalas such that the likelihood is sufficiently reduced?

As part of a program for the adaptive management of koalas at Mount Eccles National Park, we have constructed a koala-forest-management interactive model to examine sterilisation options available to management. The model consists of three basic components, where each component interacts with at least one other component: (1) forest dynamics; (2) koala dynamics; and (3) koala management. We use the model to investigate the likely outcomes of the intended management at Mount Eccles National Park. Sterilising 2000 koalas per annum appreciably reduces the likelihood of the koala population collapsing to very low densities and leads to improved forest condition after some years. Subsequent monitoring and research will remove some of the uncertainties that exist in our current understanding of the system, and consequently presenting opportunities to update the model with new information and allow more targeted management questions to be developed.

Population dynamics of size-structured populations

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Dedicated to the memory of Nigel Barlow with whom I have often discussed this.

Many population cohorts are structured by different attributes: space and age are the most common of these. For many applications this structure is just as important as the temporal evolution with discrete or continuous time. For these applications modellers have to cope with this greatly increased complexity and cannot afford to neglect it. Different modellers proceed in a variety of ways to suit the circumstances and tools available. Nigel Barlow introduced me (in 1988) to the idea of using a limited number of spatial or age compartments, each of which was structurally uniform with well-defined interactive links between compartments. His view, if I interpret it correctly, was that this enabled us to avoid the technically difficult partial differential equation analysis. Of course, there are a wide variety of opinions about this, but I have recently used this approach in an analysis of a plankton-nutrient model, where Nigel was clearly right. We would have never succeeded in using the lovely path-following (in parameter space) computer algorithms

had we not adopted Nigel's approach.

This paper addresses a situation where compartments were not, in fact, sufficient: where the population is structured by size or DNA content. Data sets of plant-root-cells, plankton, muscle cells, and cancer cells, often show a steady (in time) size distribution that appears asymptotically and structurally stable. ("Steady-size" means it is constant in shape as time changes.) About the same time as Nigel and I began (in Palmerston North around 1988) looking at a spatially compartmentalised model for tuberculosis in possums, another biologist, Dr Paul Gandar, asked whether we could explain this with a relatively simple model which, when validated and embedded in the cell physiological context, could have the capability of making robust predictions.

Here I outline a simplified model that does just that. It has all phases of the cell-cycle lumped together, and admits steady-size distributions (SSDs) that match the data sets remarkably well, and requires a minimum of parameters to be determined empirically away from the physiological context. The mathematics involved is simple and known to most undergraduate students in mathematics. It has led to a rather simple explanation to the SSDs observed in practice, the data for which match the model very well. This has provided a greater understanding of cell population dynamics. It is currently being used to underpin decision-support of cancer treatment.

Postscript

During the symposium when building dynamical system models, which are structured in size, space or even age, it was often observed that "to obtain structured solutions, this has to be explicitly inserted into the equation system". This is not the case and it is quite possible, at least in continuous models, to obtain structured solutions from autonomous systems, that is, when the coupling terms in the biomass-balance equations are just dependent on the constituent biomasses (populations) only. There are many ecological systems where as a parameter is varied, a structurally uniform solution will at a given value become unstable and the system will beyond that value be attracted to a preferred (asymptotically stable) solution. This occurred in the spatially structured model constructed for the interaction (competition) between the grey (introduced) and red (indigenous) squirrels in the United Kingdom. This model and its behaviour were explained in Norbury and Wake (1993).

This outcome is fairly common and serves to underline the message: **Spatially-structured solutions can occur without being forced explicitly in the model.** Similarly a system can have periodic solutions naturally without periodic forcing, as evidenced by the simplest of systems, the predator (P1) – prey (P2)

model:

$$dP_1/dt = kP_2$$

$$dP_2/dt = -kP_1$$

for which all solutions, other than the extinction solution, are periodically oscillating with period $2\pi/k$ units of time. Non-linear systems of this kind frequently have similar thresholds in parameter space, where the attractors change from steady equilibria to oscillatory ones. Again these thresholds are ecologically very important and are usually the points at which experimental work should be carried out in the first instance.

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The importance of inverse density dependence in population viability analysis: an example using threatened woodland caribou in Canada

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Population viability analysis (PVA) refers to a group of analytical and modelling approaches for assessing the risk of population extinction. PVA is commonly used to estimate absolute time to extinction or probability of persistence under either current or novel conditions. However, the amount of information of species specific biology as well as the dynamics of small populations needed to confidently estimate population persistence is high, a fact often overlooked in the light of increasing availability of easy-to-use software packages.

For example, reliable estimates of future population projections are dependent on an understanding of how demographic parameters change with population density. Our understanding of such density-dependent processes in large herbivores is predominantly based on results from large, viable populations where the per capita growth rate usually decreases with increasing population density (i.e. density dependence). Oppositely, at very small population sizes, the per capita growth rate may decrease with decreasing population densities (i.e. inverse density dependence or Allee effect). However, because empirical evidence of inverse density dependence remains rare, resource

managers frequently ignore the potential importance of negative changes in demographic parameters with declining population density when attempting to predict population persistence.

The decline of woodland caribou (*Rangifer tarandus caribou*) in the interior of British Columbia, Canada, is inversely density-dependent caused by higher per capita predation of adult female caribou at low population densities. To demonstrate the effect of inverse density dependence in PVA, we initialised stochastic population projection models based on demographic information sampled from >350 collared caribou. Our results suggest that caribou populations are declining towards extinction. When the observation that survival of adult females decreases with decreasing population densities was included in the model, estimated persistence times decreased by an additional 21%. Thus, neglecting inverse density dependence where it occurs will lead to a significant underestimation of time to extinction, and recovery efforts of these woodland caribou will require an appreciation of the influence of inverse density dependence on population trajectories.

