

Rats dying for mice: Modelling the competitor release effect

STÉPHANE CAUT,¹ JORGE G. CASANOVAS,^{2†} EMILIO VIRGOS,³ JORGE LOZANO,³ GARY W. WITMER⁴ AND FRANCK COURCHAMP^{1*}

¹*Ecologie, Systématique & Evolution, UMR CNRS 8079, Bat 362, Univ Paris-Sud, 91405 Orsay Cedex, France (Email: franck.courchamp@u-psud.fr);* ²*Dynamical Systems Group, Depto. Ecología. Fac. Biological Sciences, Universidad Complutense de Madrid,* ³*Dpto. Matemáticas, Física Aplicada y Ciencias de la Naturaleza, ESCET, Universidad Rey Juan Carlos. C/Tulipán s/n, Móstoles, Spain; and* ⁴*USA Department of Agriculture, APHIS, Wildlife Services, National Wildlife Research Center, Fort Collins, Colombia, USA*

Abstract Introduced vertebrate predators are one of the most important threats to endemic species throughout a range of ecosystems, in particular on islands in biodiversity hot spots. Consequently, the reduction of predator numbers is considered a key conservation action in the management of many native vertebrates vulnerable to predators. It is now established that control attempts may affect non-target species through trophic interactions, but little is known concerning their consequences on competitive relationships. We study a mathematical model mimicking the effects of controlling introduced species in the presence of their competitors. We used two competing rodents to illustrate our study: black rats, *Rattus rattus*, and mice, *Mus musculus*. Analyses of the model show that control of only one introduced species logically results in the dramatic increase of the overlooked competitor. We present empirical data that confirm our theoretical predictions. Less intuitively, this process, which we term ‘the competitor release effect’, may also occur when both introduced competitors are simultaneously controlled. In our setting, controlling both predators can promote their coexistence. This occurs as soon as the inferior competitor benefits from the differential effect of the simultaneous control of both competitors, that is, when the indirect positive effect of control (the removal of their competitors) exceeds its direct negative effect (their own removal). Both control levels and target specificity have a direct influence on the extent of this process: counter-intuitively, the stronger and more specific the control, the greater the effect. The theoretical validation of the competitor release effect has important implications in conservation, especially for control management.

Key words: alien predator control, biological invasion, competing rodent, control strategy, introduced mammal.

INTRODUCTION

Predation and competition may interact to structure communities. This concept is now well adopted by fundamental ecologists (e.g. Kotler & Holt 1989; Holt & Lawton 1994; Chase *et al.* 2002; Caro & Stoner 2003), but still needs greater attention from applied conservationists. In their race against biodiversity erosion, conservation managers are often faced with dilemmas and the resulting choices often translate into a need to give priority to fighting simple direct causes of species loss, leaving little space for interacting processes. In the context of biological invasions, a major cause of population extinctions, this often

amounts to controlling invading predators to protect local animal communities (Diamond & Veitch 1981; Towns & Ballantine 1993; Courchamp *et al.* 2003). Yet, processes that are less obvious than direct predation can operate even in very simple systems such as insular ecosystems (Glen & Dickman 2005), which makes risky the necessary removal of exotic predators. One such process that has been previously described is the mesopredator release (Soulé *et al.* 1988). In that scenario, the sudden removal of a predator revealed the importance of an inconspicuous intermediate predator, which, once released from the predation pressure, rapidly led to the extinction of the shared prey. This case had been encountered in several conservation programmes before it was studied in detail theoretically. It is now widely accepted in management strategies but similar processes are often overlooked in the design of current conservation plans. Even though that first theoretical study aimed to highlight the necessity to study the community in its entirety before

*Corresponding author.

†Present address: Instituto de Investigación en Recursos Cinegéticos (IREC), CSIC-UCLM-JCCLM, Ronda de Toledo s/n. 13071, Ciudad Real, Spain.

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removing a species, the specific example more than the general message seems to have prevailed. In this study, we provide another, more counter-intuitive example of how seemingly straightforward choices of management strategies can lead to opposite results if the conservation design is not envisaged in the context of the ecosystem as a whole (Zavaleta *et al.* 2001; Courchamp & Caut 2005).

Rats are considered as among the most detrimental of invading species (Atkinson 1985; Towns *et al.* 2006). They are present on most islands off New Zealand, Australia, Indonesia, Polynesia, Madagascar, in the subantarctic and other groups of high biodiversity. Currently present in most insular locations, rats are major predators of birds, reptiles and arthropods (Atkinson 1985; Cree *et al.* 1995; Palmer & Pons 1996; Towns *et al.* 1997; Daltry *et al.* 2001; Towns *et al.* 2001; Towns *et al.* 2006). They are omnivorous and eat seeds, stems, fruits and leaves of many plant species (Campbell & Atkinson 1999; Williams *et al.* 2000; Campbell & Atkinson 2002). They therefore not only constitute a threat to those plant species, but are also expected to have a globally greater impact than carnivorous predators, because feeding on two types of resources should allow them to survive at relatively large numbers even when one resource is temporally or spatially depleted. Researchers and managers alike thus generally agree that rapid eradication of introduced rats from islands is necessary. The effects of rats being rather straightforward, rats can be (and effectively are) eradicated with minimal pre-control studies on potential detrimental side effects of such eradication.

Such a removal generally involves trapping and poisoning, both of which lack specificity, especially among rodents (Thorsen *et al.* 2000; Donlan *et al.* 2003). To date, this has not been seen as a problem, because rodents being commensal to humans, it is likely that rodents present on most insular ecosystems have been introduced there, and are a potential threat to the ecosystem. Thus, lack of rodent specificity in invader control programmes may be seen as positive, as it should help incidentally control the population of other introduced rodents.

However, we show in this paper that rodent control in the presence of more than one species of rodent can pose a serious threat to the ecosystem, sometimes leading to damages that exceed the pre-control level. In fact, the mesopredator release effect mentioned earlier can be generalized to other types of natural enemies. Once released from an introduced natural enemy by human control, other introduced populations, initially maintained at low densities by that natural enemy, may suddenly increase to levels such that they constitute a larger threat than the initial population ever did. For example, the eradication of rats from an island could trigger a

demographic explosion of a competing mouse population.

Field specialists seem unanimous in viewing rats as strong competitors of mice, negatively affecting the rate of change in mouse abundance and even excluding them when resources are scarce (Choquenot & Ruscoe 2000; Courchamp *et al.* 2000; Ruscoe 2001). It has been shown already that where populations of mice and ship rats coexist in New Zealand forests, mice are scarcer than rats (King *et al.* 1996). Yet, following the poisoning of a significant number of rats, mouse numbers can increase greatly (Innes *et al.* 1995; Murphy *et al.* 1999). Innes *et al.* (1995) and Miller and Miller (1995) suggest that this could be due to a removal from competition and/or predation pressures. A replicated removal of *R. rattus* was carried out on Santiago Island, Galápagos and the response of *M. musculus* was said to be typical of a liberation from interference competition (D. Harris, pers. comm. 2006). The response was mainly driven by adult immigration but survival was also enhanced. In a study to estimate the relative abundance of rats and mice, Brown *et al.* (1996) detected mice presence significantly more often as ship rats were removed by trapping, even though mice were being removed at the same time. They concluded there was a behavioural response of mice to the removal of rats, indicating the likelihood of interference competition. Consequently, competitive interactions between coexisting populations of introduced rodents may result in small mice populations that can easily be overlooked (Tennyson & Taylor 1999; Weihong *et al.* 1999). Such mouse population might be released from rat competition if the latter is suddenly removed, triggering an explosion of the mouse population. Such a dramatic increase could be disastrous as mice have been shown to be active predators of invertebrates, reptiles and even birds that can be 300 times their weight (Newman 1994; Fitzgerald *et al.* 1996; Campos & Granadeiro 1999; Ruscoe 2001; Le Roux *et al.* 2002; Smith *et al.* 2002; Cuthbert & Hilton 2004; Wanless *et al.* 2007).

Throughout this paper, we will call this effect the competitor release effect. An increase of mice has in fact happened on several islands following the removal of rats: released from their competitors, mice have suddenly shown a dramatic increase in numbers. Recent examples include Saint Paul Island, subantarctic ocean (P. Jouventin, pers. comm. 2001), Rimains Island, Brittany, France (M. Pascal, pers. comm. 2005), Midway Atoll, Hawaii, USA (F. Starr, pers. comm. 2006), Quail Island, New Zealand (M. Bowie, pers. comm. 2006) and Bird Island, Seychelles (Merton *et al.* 2001). There are also cases where mice have been detected only after the introduced rats were eradicated, suggesting that they likely increased in number after a release of competition pressure. Recent

examples include seven New Zealand islands: Te Haupa Island, Hauturu Island, Haulashore Island (J. Russell, pers. comm. 2005), Mokoia Island (R. Griffiths, pers. comm. 2005), and Matakohe Island (R. Parrish, pers. comm. 2005). On Pakihi Island, New Zealand, mice erupted after rat eradication in the early 1990s; then rats reinvaded the islands in the late nineties, and mice dropped back to undetectable levels (J. Russell, pers. comm. 12/05). In this paper, we present data of Buck Island, US Virgin Islands, from which rats were successfully eradicated in 1999 by one of us (GWW). We use the rare occurrence of a subsequent rodent trapping programme to document the competitor release effect: an island-wide dramatic increase of mice caught in the rodent traps was observed, paralleling the decrease of caught rats.

The obvious approach to such situations seems simply to apply a simultaneous control to both competitors, which is the common strategy when dealing with rodents now anyway (Clout & Russell 2006). If interacting rodents are suspected, one strategy could thus be to apply a more intense level of control, in order to remove the two populations simultaneously. The aim of this paper is to demonstrate that such a strategy could also lead to a competitor release effect, even though the two species are being killed, and that simply increasing the intensity of control can be counterproductive in this regard.

As a first step, we illustrate our point by briefly presenting some aspects of the Buck Island rat eradication programme. We then use a classical, two competitors mathematical model to compare the efficiency of different control strategies, in terms of final numbers of the two species of competitors. Lastly, we add a third species to the model to illustrate the different effect this might have on a shared prey. We then focus our discussion on the context of conservation of insular ecosystems.

METHODS

Eradication

Buck Island is part of the Buck Island Reef National Monument in the US Virgin Islands. This is a 80-ha island situated about 2.4 km north-east of the Island of St Croix in the Caribbean Sea. The island has no permanent sources of freshwater and is covered with a dry, tropical deciduous forest. Several species of threatened or endangered flora and fauna occur on Buck Island, together with introduced rats and mice. Additional information on the Island can be found in Witmer *et al.* (1998). An eradication programme of rats was set up on Buck Island in 1999–2000.

We used rodenticide bait blocks containing 0.005% diphacinone as the active ingredient (a first generation anticoagulant). The bait blocks contained paraffin wax to prolong their durability in a wet climate; they also contained flavouring that rodents like (initially used a peanut butter-molasses flavour, then switching to a fish flavour). Bait blocks were put into elevated (25 cm above-ground surface and attached to a steel bar driven into the ground) plastic bait stations (to keep crabs from removing bait); the bait stations were also modified to keep birds out that were taking bait initially; insecticide was applied on the ground around some bait stations when there was a problem with ants swarming and eating the bait. The bait stations were in a 40 × 40 m grid over the entire 80-ha island; in cliff areas where bait stations could not be safely used, we hand-tossed bait blocks. Bait was put out and maintained continually in bait stations for 2 weeks in each of April, May and June of 2000. Additional intensive baiting was done in the picnic area/beach area in October 1999 and September 2000 because that area was very prone to having lots of rats. All bait and bait stations were removed from the island in November 2000. About 546 kg of rodenticide bait was used in total. Rodent monitoring (using rat snap traps mounted on tree boles about 0.5 m off the ground and baited with peanut butter) was conducted twice per year in 2000–2005.

Mathematical model

Because adequate field data are lacking to parameterize a predictive model with real values, and for the sake of generality, we chose to use a mechanistic model, studied both analytically and numerically. For simplicity, we base our study on a classical Lotka–Volterra two-species competition model. We assume that one of the two species is globally a better competitor over the other (either by better exploiting resources or by generally winning interference interactions), and we call this species the superior competitor, the other one being the inferior competitor. The dynamics of two competing populations is described by a set of two coupled differential equations: Equation 1. Similar models have been proposed before in other contexts (Shorrocks & Begon 1975). For the sake of readability, we base our presentation on an example involving two competing rodents: the inferior competitor could be mice and the superior competitor could be rats. Accordingly, we use relevant subscripts referring to the two competitors: m for mice and r for rats. Thus, in Equation 1, M is the number of mice at time t , R the number of rats at time t , and their instantaneous population growth rates depend upon the intrinsic growth rate of mice r_m and rats r_r , their carrying capacity K_m and K_r , the effect of competition

with the other species α_r and α_m and the rate at which they are controlled ω_r and ω_m .

$$\begin{cases} \frac{dM}{dt} = r_m M \left(1 - \frac{M + \alpha_r R}{K_m} \right) - \omega_m M \\ \frac{dR}{dt} = r_r R \left(1 - \frac{R + \alpha_m M}{K_r} \right) - \omega_r R \end{cases} \quad (1)$$

It may rightly be argued that in many cases, having a large population of mice may be preferable than having rats, as the latter may inflict far more damage per individual than mice for some species, such as seabirds for example. To study this specific point, we added a third equation to the model, mimicking the dynamics of a population of a third species, a prey shared by the competing predators. The prey is added by a simple differential equation of the logistic form, with a term of predation by both the rat and the mouse.

The model becomes

$$\begin{cases} \frac{dM}{dt} = r_m M \left(1 - \frac{M + \alpha_r R}{K_m} \right) - \omega_m M \\ \frac{dR}{dt} = r_r R \left(1 - \frac{R + \alpha_m M}{K_r} \right) - \omega_r R \\ \frac{dP}{dt} = r_p P \left(1 - \frac{P}{K_p} \right) - \mu_m PM - \mu_r PR \end{cases} \quad (2)$$

Where P is the prey population, r_p its population growth rate, K_p its carrying capacity, and μ_m and μ_r the mouse and rat predation rates, respectively. As both rodents are omnivore and are known to strive on a great variety of resources, their population dynamics

do not depend solely on that of the prey and can thus be approximated without requiring the use of a classical prey-predator model. The generality of our model also allows it to illustrate prey that are preferred by either predators, be they large seabirds or small invertebrates. For the sake of simplicity, but also to best fit our objective, we have chosen to study this more complex model through numerical simulations rather than analytically.

RESULTS

Eradication

Three surveys of the rat population were conducted during the baiting operation, during which only one rat was captured. Rats were surveyed at 10 different instances since the end of the baiting operation and no rats were captured, nor any sign of them found (gnawing, active burrow, droppings), suggesting that the rat population on Buck Island had been eliminated.

During the post-eradication rodent surveys, hundreds of house mice were captured, first at an increasing rate, then with a decrease and a stabilization. Mice were captured in all snap-trap lines, suggesting an island-wide distribution. Mice had not been captured previously on the island, although an occasional mouse had been observed in past years. Result of the trapping sessions before, during and after the rat eradication are presented in Figure 1. They clearly show that

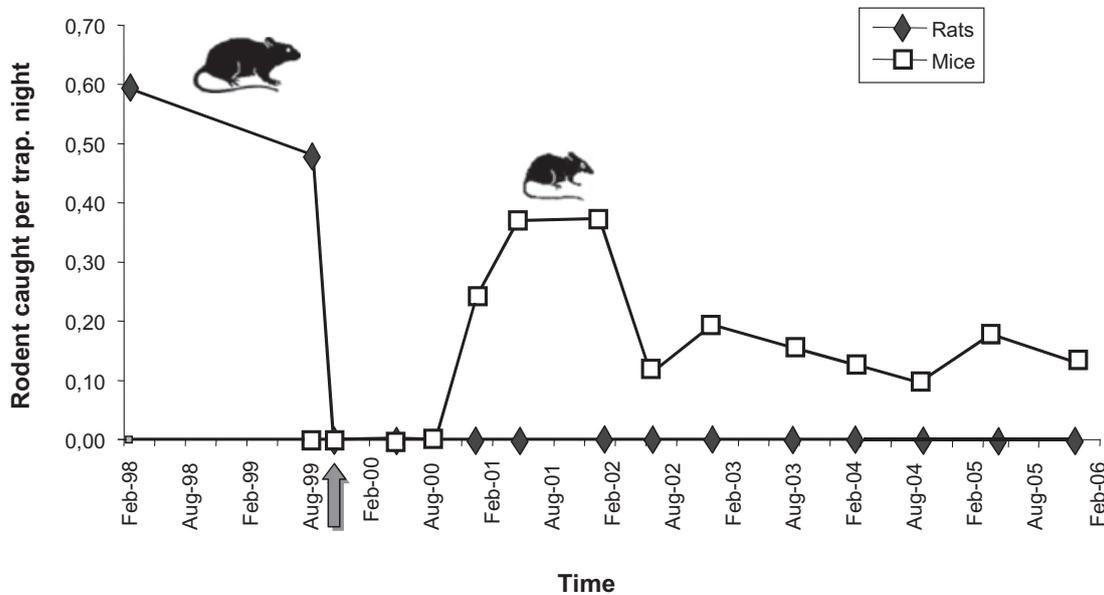


Fig. 1. Numbers of rats (empty squares) and mice (full diamonds) caught in rodent traps on Buck Island, before and after rat eradication (shown by the grey arrow). The release from rat competition allowed mice to increase in numbers, a process we called the competitor release.

rat decrease and disappearance coincided with the appearance and increase of the mouse on the island, suggesting a competitor release.

Mathematical model

The set of Equation 1 leads to four equilibrium points: extinction of both populations [0, 0], of the inferior competitor only [0, $K_r(1 - \omega_r/r_r)$], of the superior competitor only [$K_m(1 - \omega_m/r_m)$, 0] or coexistence of both populations:

$$\left[\frac{r_r K_m (\omega_m - r_m) - \alpha_r r_m K_r (\omega_r - r_r)}{r_m r_r (\alpha_m \alpha_r - 1)}, \frac{r_m K_r (\omega_r - r_r) - \alpha_m r_r K_m (\omega_m - r_m)}{r_m r_r (\alpha_m \alpha_r - 1)} \right].$$

The first point (extinction of both populations) always exists. The control intensity necessary to generate the double eradication is such that the control of both competitors is higher than their own population growth rate: $\omega_r > r_r$ and $\omega_m > r_m$ for rats and mice, respectively. Logically, the extinction of a single competitor occurs only if the rate at which it is controlled is higher than its intrinsic growth rates. The conditions for coexistence are more complex and depend on several parameters of each population, notably on the product of competition rates. The conditions of existence and stability of these points are described in the Appendix. It is interesting to note that because intraspecific density dependence and interspecific density dependence (competition) are linked, adding control to the simple Lotka–Volterra competition model as we did to obtain Equation 1 results in promoting species coexistence in cases where competitive exclusion would have occurred.

Intuitive appreciation of the system suggests that the eradication of one competitor only will trigger the release of the other species, and this is confirmed by the model analysis. The removal of one species, say the rat *R*, systematically yields a system where the other species, the mouse *M*, reaches $K_m(1 - \omega_m/r_m)$. If the mouse is not controlled at the same time, it thus reaches its carrying capacity.

If the rat population is merely controlled instead of eradicated, then the mouse population will reach $\frac{r_m r_r K_m + \alpha_r r_m K_r (\omega_r - r_r)}{r_m r_r (1 - \alpha_m \alpha_r)}$ at equilibrium. Compared to

the equilibrium in the absence of control, this amounts to increasing the mouse population by $\frac{\alpha_r K_r}{1 - \alpha_m \alpha_r} \cdot \frac{\omega_r}{r_r}$,

and thus triggering a competitor release process. This highlights that the strength of the competitor release depends on the population parameters of the controlled population, on the control effort on this popu-

lation and on the competition rates with the released population. This has interesting consequences in terms of conservation strategies (see *Discussion*). As expected, the higher the control, the stronger the competition release effect. Similarly, the higher the competition rate, the stronger this effect.

However, deeper analysis of the model shows that the competitor release process can also be generated in conditions that are more counter-intuitive, for example when both populations are controlled simultaneously.

To study this aspect, we linked the two control terms (but this need not be the case): $\omega_m = \omega_r/\delta$, where δ is a coefficient of control specificity. Simply, a value of, for example, 2 for δ means that superior competitors are controlled twice as well as inferior competitors. Thus, controlling for one competitor only will also incidentally allow some control of the other, albeit to a lesser extent. In addition to being easier to study, this situation is the most realistic in most control situations (see *Discussion*).

In cases where the two competitors are not immediately and simultaneously wiped out by the control, two scenarios may arise. If the control is sufficiently strong to eradicate the superior competitor, then the inferior competitor will suddenly reach a stable population size at $K_m(1 - \omega_m/r_m)$. In this case, the control leads to an increase from $\frac{K_m - \alpha_r K_r}{(1 - \alpha_m \alpha_r)}$ to $K_m(1 - \omega_m/r_m)$

as soon as the mouse control is insufficient (i.e. lower than $\frac{K_m r_m - \alpha_m K_r}{K_m r_m - K_m \alpha_m \alpha_r} - 1$). Unsurprisingly, the

parameters that have the most influence on the final population size of the inferior competitor are the demographic parameters of the superior competitor.

Alternatively, the control will not be sufficient to cause eradication of the superior competitor, and this will be associated with an increase of the inferior competitor population size to $\frac{\alpha_r r_m K_r (\omega_r - r_r) - r_r K_m (\omega_m - r_m)}{r_m r_r (1 - \alpha_m \alpha_r)}$. This formulation of

the final population size of the inferior competitor shows clearly that it is, expectedly, inversely proportional to the strength with which it is controlled (ω_m), but at the same time proportional to the control rate of the superior competitor (ω_r). Thus, unexpectedly, and because both control terms are linked, some combinations of parameters will be such that the stronger the control of the two populations, the more one of them will increase. Figure 2 shows clearly that the competitor release effect will be proportional to the intensity of competition as well as the intensity of the control and its specificity.

Although the simplicity of the model allows its study entirely through analytical methods, a numerical study is more fruitful here in terms of interpretation. It also

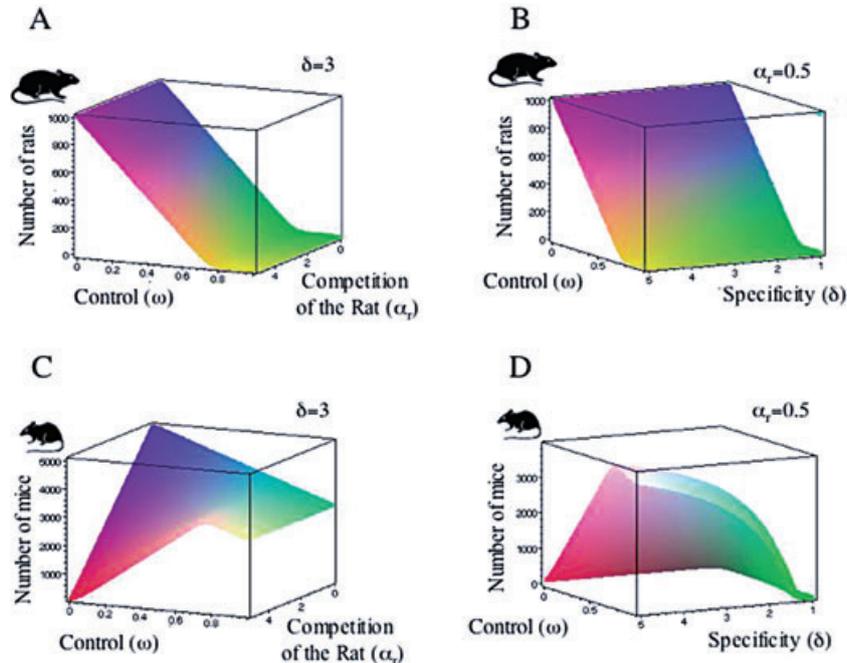


Fig. 2. Control efficiency in presence of two competitors, as a measure of the final population size of the superior competitor (e.g. rats: A, B) and of the inferior competitor (e.g. mice: C, D). This control efficiency is shown as a function of the control strength and either the competition strength (A, C, $\delta = 3$) or the control specificity (B, D, $\alpha_r = 0.5$); other parameters are $r_r = r_m = 0.75$; $K_r = 1000$; $K_m = 5000$. While the superior competitor always decreases proportionately to the control strength, the inferior competitor only do so when competition is very low or when there is no control specificity ($\delta = 1$, i.e. the control is as efficient for both competitors). When either one of these parameters increases, the stronger the control, the more the inferior competitor increases.

has the advantage of emphasizing the limits of analytical results, which must not be taken as guidelines to quantify control intensity. We thus provide simulations for didactic purposes (Fig. 3). This illustrates how some control strategies that would overlook the competitor release effect may fail to restore the ecosystem, through an unexpected increase of the inferior competitor, even if that species is controlled too. When the control specificity is low, a low level of control will lead to a small decrease in the superior competitor population and to a concomitant increase in the inferior competitor population. For higher levels of control, the superior competitor population may be decreased, but the inferior competitor population may explode. In the absence of control, we have chosen parameter values allowing a coexistence of two competitors: the inferior competitor population is low, but stable and the superior competitor reaches its carrying capacity, K_r .

Lastly, our simulations of model (2), with the shared prey, show that different values of the predation rates of the two competitors can render the competitor release more or less destructive for different shared prey (see Fig. 4): for some prey species that are favoured by mice, 'fewer rats' is not more damaging than 'more mice'.

DISCUSSION

The aim of this study was to highlight the potential risks associated with the control of predators in the presence of their competitors. Analyses of a classical model showed that the control of the superior competitor may lead to an increase in the inferior competitor, as pressure from competition is lifted. We called this process the competitor release effect, by analogy to the mesopredator release effect (Soulé *et al.* 1988). We also showed that the more intense the control, the larger the final population of the inferior competitor. This increase may be sudden and dramatic if the superior competitor is eradicated. Outbreaks can be more damaging than simply large populations because for a moment the predator population may exceed the size sustainable by the prey. This dramatic increase may also occur in conditions where the two competitors are controlled simultaneously. In this case, the inferior competitor increases despite it being controlled. The solution in this situation may appear to be intensification of control effort, but this option would only enhance the competitor release effect. Although this process may be less intuitive and therefore less often foreseen, it is *a posteriori* straightforward to

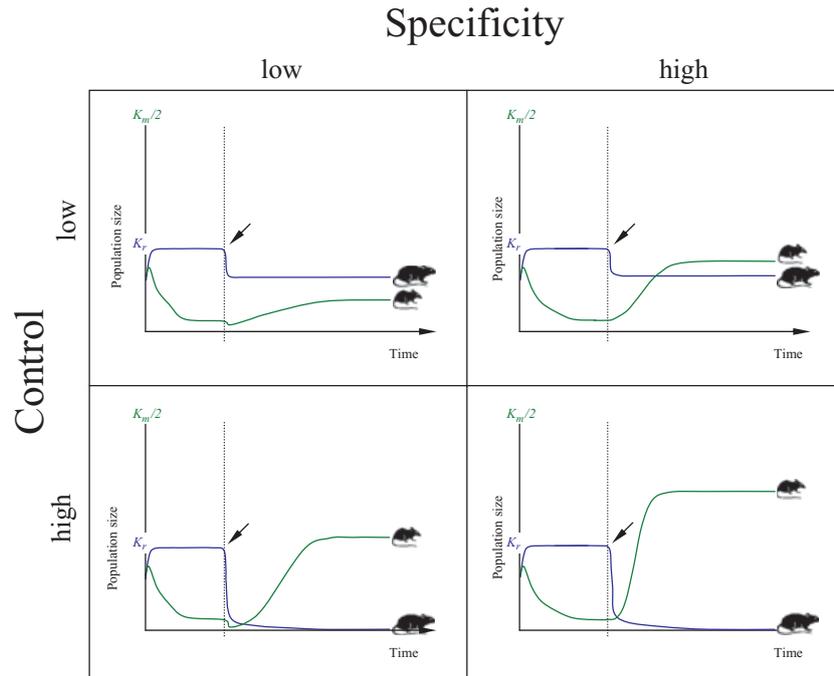


Fig. 3. Effects of different control strategies on the final fate of the two competing populations: with a low ($\omega = 25\%$) or a high ($\omega = 75\%$) control effort and a low ($\delta = 1.3$) or a high ($\delta = 2$) control specificity. Other parameter values do not change: $r_r = r_m = 0.75$; $K_r = 1000$; $K_m = 5000$; $\alpha_r = 0$; $\alpha_m = K_m/K_r$. The control of the competing predators is set so it starts when the populations have reached the control-free equilibrium (dashed line, black arrow). In all cases, the superior competitor population, being the primary target, is more or less reduced (in blue). However, this results in a lowering of the competition pressure on the other population, which may be sufficient to compensate and even overcome the control it is undergoing at the same time. This may result in an increase of the inferior competitor (in green), sometimes dramatically, despite its control.

understand. This is likely to occur as soon as the inferior competitor benefits from the differential effect of the simultaneous control of both competitors: when the indirect, positive effect (that is, the removal of its competitor) exceeds the direct, negative effect (that is, its own removal). These conditions can be caused when the control effort is high and either the control specificity is low or the intensity of competition is high. Because the intensity of the competitor release is directly proportional to the control effort, indiscriminate intensification of the control only leads to exacerbating the process. A competitor release is also shown to be more damaging to prey species which are sensitive to the impact of the inferior competitor.

The Buck Island rat eradication programme provides a clear illustration of such unexpected chain reaction: as rats were eradicated from the island, mice increased, from undetectable to very high numbers. Evidently, such empirical data to demonstrate an unexpected chain reaction are scarce, and experimental approaches are not feasible in the context of conservation biology. During several years, one of us (GWW) monitored a dramatic increase of the mice, followed by a return to lower level, yet still much higher than before the rat eradication. A rodenticide bait efficacy trial showed that the house mice were not

resistant to the anticoagulant (diphacinone) toxicant used, and they might well have died in numbers during the rat eradication. It is thus clear that the increase of mice does not come from a differential mortality to poison. The release cannot be explained by mice behavioural changes either, as the response would have been much more rapid. In this case, partial rat predation on mice cannot be entirely ruled out. However, it is generally admitted that where rats do not out-compete mice, they predate on them, so if rat removal does not trigger a competitor release, it might well trigger a mesopredator release, with similar results (Courchamp *et al.* 1999). These data, quite exceptional in the sense that it is rare to be able (or willing) to collect them, match nicely the prediction of the competitor release model.

In many cases where control of the predator is the advocated option, this cannot be accompanied by a preliminary study of the interspecific relationships within the entire community. As a result, another introduced species that competes with the predator can benefit from the predator control, because usually in these cases the control is rather specific. Recently, specificity has become a key component of pest control. As a consequence of the double need to control unwanted pest populations while limiting

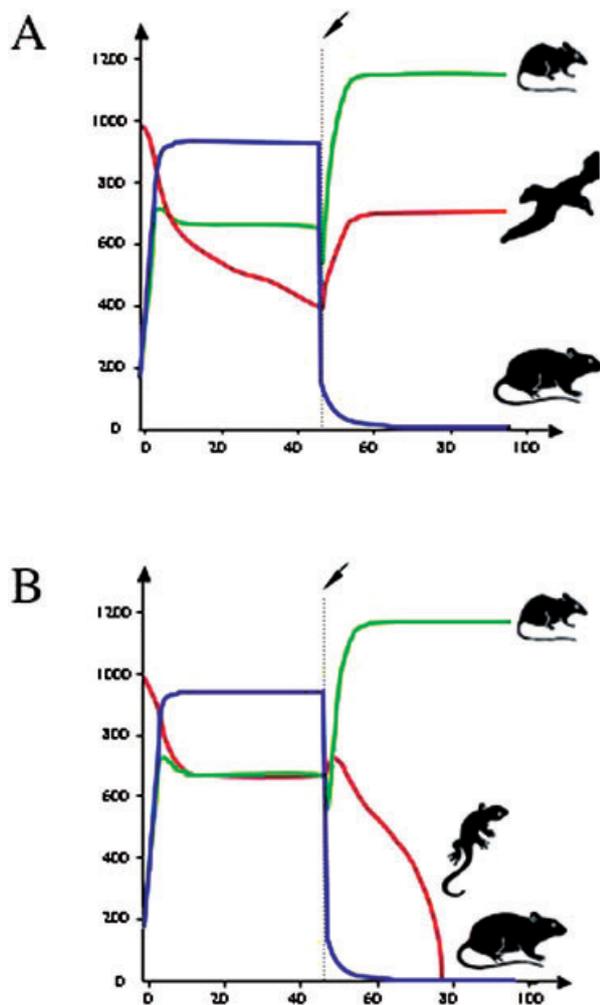


Fig. 4. Impact of the competitor release effect for the population of a prey shared (in red) by the two competitors. In (A), predation is equivalent for both rodents and the prey population avoids extinction but does not recover entirely. In (B), the predation of the mice is much higher than that of the rat and the competitor release causes extinction of the prey (higher in blue, lower in green). Parameter values are the following: $r_r = 0.75$, $r_m = 0.75$, $r_p = 0.5$, $K_r = 1000$, $K_m = 1500$, $K_p = 10000$, $\alpha_r = 0.10$, $\alpha_m = 0.90$, $\delta = 5$, $\omega = 0.85$, and (A): $\mu_r = 0.75$; $\mu_m = 0.9$, (B): $\mu_r = 0.35$; $\mu_m = 1.2$.

non-target mortality, the current tendency is to enhance specificity of control techniques. The problem of accidental by-kills of non-target species is a recurring theme in biological conservation, as exemplified in reviews in quite distinct fields such as risk related to fungi used to control plant diseases (Brimner & Boland 2003), chemical substances against introduced lamprey in American lakes (Sullivan *et al.* 2003), organophosphate spraying to control the red-billed quelea (*Quelea quelea*) in Africa (McWilliam & Cheke 2004), brodifacoum used to control invasive mammal species (Eason & Spurr 1995; Murphy *et al.* 1998), and biological control in general (Simberloff & Stiling 1996).

Increased specificity is achieved either by deterring non-target species (Hickling 1997; Day & Matthews 1999; Hartley *et al.* 2000; Martin *et al.* 2002), by physically preventing them from reaching the lethal device/substance (e.g. McDonald *et al.* 1999; Short & Reynolds 2001; Glen & Dickman 2003; Petel *et al.* 2004), or by increasing bait attractiveness to the target species (e.g. Saunders & Harris 2000; Clapperton *et al.* 1994). In all these cases, current effort is understandably aimed towards increasing efficiency of control through better selectivity by lethal methods.

While this progress has allowed successful control of mammals in conditions with difficulties that were previously judged impossible to overcome, we must underline the potential caveats of using too selective a control method. Our study highlights the role of control specificity with respect to the likelihood of a competitor release effect. As a major outcome from this paper, we stress that although highly specific control is generally seen as a safety for non-target species, it may in some cases become dangerous for them, as the control is more likely to trigger a significant competitor release effect. Obviously, our message is not that no intervention is the suggested solution. On the contrary, we believe the following two steps should be used systematically in the design of predator control: (i) a characterization of the invaded ecosystems as a whole, in order to assess potential competitor release effects (and also similar processes) followed by, if needed, (ii) the use of as many specific methods as there are species to be controlled. Note that some authors (Billing & Harden 2000) have highlighted the increase of mouse population following rat control because mice were feeding on rat baits and not sensitive to its poison (warfarin). This process is not taken into account in our model (it would only exacerbate the process we highlight), but should be accounted for in rodent control programmes.

It is also noteworthy that control efforts are generally linked economically, as resources allocated to controlling one species may reduce resources available to control the other. In this case control terms would be negatively linked, not positively linked as we chose to model. We did not present such a possibility here, but it appears clearly that such change would result in an exacerbation of the competitor release. It would indeed then be very dangerous to use all the resources to control the superior competitor, as this would release the inferior competitor from both competition and control. In this case, it may be better to preferentially allocate resources to controlling the inferior competitor first, so that the combination of control and competition (or predation) eliminates the inferior competitor. Then all resources could be allocated to eliminating the superior competitor without danger of

releasing the (already eliminated) inferior competitor. Of course this would depend on the relative impact of the two species on the local community and, once again, we must call for case-by-case assessments of the optimal strategy (see for example Ramsey & Veltman 2005).

There are several examples of islands where mice outbreaks have followed a rat eradication; we have cited eight such examples in the *Introduction*, and there are probably many others. Yet, competitor release can occur in very different ecological contexts, such as, for example, game management. As for biological invasions, the main goals of the management strategies in areas of game interest or in natural reserves with species that are predation sensitive is to reduce its incidence, through predator control (Harris & Saunders 1993; Reynolds & Tapper 1996; Tapper *et al.* 1996). The techniques used vary greatly in their degree of selectivity or effectiveness with regard to the target species (Calver *et al.* 1989; Windberg & Knowlton 1990; Hein & Andelt 1994). Unfortunately, many of these methods are non-selective, in particular many types of snares, traps and poison.

A recent field study (Virgós & Travaini 2005) illustrates well the present paradoxical findings in the context of game management, with this time four competing predators of hunting interest (the badger, *Meles meles*, the red fox, *Vulpes vulpes*, the genet, *Genetta genetta* and the stone marten, *Martes foina*). They showed that in areas of predator control the target species, the red fox, was paradoxically the only predator remaining in most of the field plots, whereas conservation-concern species had disappeared. The control strategy aimed at fox control resulted there in higher fox abundance and eradication of protected or threatened species, probably through a competitor release effect: the fox obviously benefited more from the release of its controlled competitors than it suffered from its own control. A model similar to the one presented here (Casanovas *et al.*, unpub.) confirms that non-selective control of one predator may lead to the increase of one or several of the other predators even as they are controlled. This ultimately leads to an overall decrease of prey abundance, the exact opposite of the intended management outcome.

The model presented here is simple but proves appealing from an applied perspective, such as for the conservation of species threatened by introduced predators. The optimal control strategy for each case is neither simple to find nor intuitive. Techniques of eradication can play an important role in removal success, but also in the upheaval of trophic relationships (competition and predation). Understanding how horizontal and vertical components of trophic interactions can interact to shape biodiversity is of major interest for fundamental ecologists and of crucial importance for applied conservationists.

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APPENDIX

Four equilibrium points are possible.

1. Both competitors go extinct: $[0,0]$. This point is stable if $r_r < \omega_r$ and $r_m < \omega_m$.
2. Only the inferior competitor disappears: $[0, K_r(1 - \omega_r/r_r)]$. This point exists if $\omega_r < r_r$ and is stable if $\alpha_r < \frac{K_m}{K_r} \times \frac{r_r(r_m - \omega_m)}{r_m(r_r - \omega_r)}$
3. Only the superior competitor disappears: $[K_m(1 - \omega_m/r_m), 0]$. This point exists if $\omega_m < r_m$ and is stable if $\alpha_m < \frac{K_r}{K_m} \times \frac{r_m(r_r - \omega_r)}{r_r(r_m - \omega_r)}$.
4. Both competitors coexist:

$$\begin{cases} M = -\frac{r_m K_m r_r - \alpha_m r_m r_r K_r + \alpha_m r_m \omega_r K_r - \omega_m K_m r_r}{r_m r_r (\alpha_m \alpha_r - 1)} \\ R = -\frac{r_m K_r r_r - \alpha_r r_m r_r K_m + \alpha_m r_r \omega_m K_m - \omega_r K_r r_m}{r_m r_r (\alpha_m \alpha_r - 1)} \end{cases}$$

The condition for existence for this last point is $K_m(1 - \omega_m/r_m) < K_r(1 - \omega_r/r_r)/\alpha_m$ and $K_r(1 - \omega_r/r_r) < K_m(1 - \omega_m/r_m)/\alpha_r$, that is, intraspecific density dependence must be stronger than interspecific density dependence (competition).