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Cats protecting birds: modelling the mesopredator release effect

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Summary

1. Introduced predators account for a large part of the extinction of endemic insular species, which constitutes a major component of the loss of biodiversity among vertebrates. Eradication of alien predators from these ecosystems is often considered the best solution.

2. In some ecosystems, however, it can generate a greater threat for endemic prey through what is called the 'mesopredator release'. This process predicts that, once superpredators are suppressed, a burst of mesopredators may follow which leads their shared prey to extinction.

3. This process is studied through a mathematical model describing a three species system (prey–mesopredator–superpredator). Analysis of the model, with and without control of meso- and superpredators, shows that this process does indeed exist and can drive shared prey to rapid extinction.

4. This work emphasizes that, although counter-intuitive, eradication of introduced superpredators, such as feral domestic cats, is not always the best solution to protect endemic prey when introduced mesopredators, such as rats, are also present.

Key-words: bird conservation, feral cats, introduced mammals, control strategy, rats.

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Introduction

Most contemporary worldwide extinctions have occurred, or are currently occurring in island ecosystems. As an example, of the 30 species of reptiles and amphibians that have gone extinct since 1600, more than 90% are island forms (Honnegger 1981); 93% of 176 species or subspecies of birds (King 1985), and 81% of 65 mammal species extinctions (Ceballos & Brown 1995) that have occurred during this period have occurred on islands.

The introduction of vertebrate species is one of the most important threats to many endemic species in many islands (Moors & Atkinson 1984; Atkinson 1989). Numerous rare or endemic vertebrate species are currently endangered because of predation by introduced invertebrates, reptiles, birds or mammals, or by competition from or habitat destruction by introduced grazers such as rabbits (*Oryctolagus cuniculus*, Lilljeborg) or goats (*Capra hircus*, L.) (Moors & Atkinson 1984; Atkinson 1989; Williamson 1996). According to King (1985), predation by introduced animals has been a major cause of 42% of island bird extinctions in the past, and is a major factor endangering 40% of currently threatened island bird species. In particular, introduced feral cats (*Felis catus*, L.) are known to be a major threat to many island bird species. They are known to have been introduced into at least 65 island groups where they are responsible for the loss of many large land and seabird colonies, populations or even species (e.g. Jouventin *et al.* 1984; Rodriguez-Estrella *et al.* 1991; Monteiro, Ramos & Furness 1996); for example, a few cats (around five) were introduced to the Kerguelen Islands in the mid-century. They are now responsible for the decline or extinction of several bird populations in these islands, killing more than 3 million petrels per year (Chapuis 1995). Cats also constitute a major threat to many endemic reptile species or

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subspecies (e.g. Iverson 1978; Case & Bolger 1991; Arnaud *et al.* 1993) and mammals (Spencer 1991; Mellink 1992). Their impact has also been demonstrated through competition towards endemic mammalian predators such as island foxes (e.g. *Urocyon littoralis dickeyi*, Baird), which they replace when uncontrolled (Steve Kovach, personal communication).

Eradication of those alien cat populations is required in many cases, has often been tried, sometimes achieved (Rauzon 1985; Veitch 1985; Domm & Messersmith 1990; Cooper 1995) and several cat eradication programmes are currently underway. Paradoxically, in some particular situations, the presence of a controlled population of cats might be, at least temporarily, more beneficial to their endemic prey than its eradication. Such is the case on many islands where rodents have also been introduced.

Indeed, it has been shown that the different species of introduced rats (Kiore or Polynesian or Pacific rat *Rattus exulans*, F., Black or Roof or Ship rat, *R. rattus*, F. and Brown or Norwegian rat *R. norvegicus*, F.) have an extremely deleterious effect on numerous species of amphibians (e.g. Thurley & Ben 1994; Towns & Daugherty 1994), reptiles (e.g. MacCallum 1986; Newman & McFadden 1990; Case, Bolger & Richman 1992; Cree, Daugherty & Hay 1995), birds (e.g. Atkinson 1985; Konecny 1987; Bertram & Nagorsen 1995) and even mammals (e.g. Brosset 1963; Bell 1978; Atkinson 1985). This effect can be indirect, such as through competition for shelter, nest-sites (Seto & Conant 1996) or food, as the diet of rats comprises mainly berries, leaves, seeds and invertebrates (Clark 1980, 1981). Rats can also have a direct effect, through predation. Indeed, these three introduced species of rat are known to prey on eggs, chicks, juveniles and even adults of ground-nesting seabirds and land birds (e.g. Kepler 1967; Bertram 1995; Brooke 1995; Lovegrove 1996) and even tree-nesting birds (e.g. Campbell 1991; Seitre & Seitre 1992; Amarasekare 1993). In total, *R. exulans* predation is documented on at least 15 different bird species, *R. rattus* predation on at least 39 bird species, and *R. norvegicus* on at least 53 bird species (for a review, see Atkinson 1985). Not only do rats have a potential impact on numerous species throughout the world (they are known to have colonized at least 82% of the 123 major island groups, Atkinson 1985), but they sometimes cause extremely rapid extinctions on newly colonized islands. A well-known example is the establishment around 1964 of black rats on Big South Cape Island, New Zealand, causing the local loss of three New Zealand endemic birds, and the complete extinction of two more, and of one species of bat, in less than 2 years (Bell 1978). Introduced house mice (*Mus musculus*, L.) also have a potential negative impact on vertebrate species, by competition or direct predation (e.g. Moors & Atkinson 1984; Johnstone 1985; Newman 1994).

The domestic cat is an opportunist predator (Fitzgerald 1988). When both bird and mammal prey are available, it is believed that the domestic cat diet will include mainly mammals (e.g. Konecny 1987; Nogales *et al.* 1992; Nogales & Medina 1996). In some island ecosystems, these cats maintain rodent populations at low levels. Although they also often prey upon endangered species, it is believed that, in some ecosystems at least, the beneficial effects of reducing the rodent population could outweigh the damage done to the endemic prey species (Fitzgerald *et al.* 1991; Tidemann, Yorkston & Russack 1994). The threat posed by introduced cats to the kakapo (*Strigops habroptilus*, Gray) on Stewart Island is a striking example. Here, cats prey lightly on this highly endangered bird species (remains were found in 5·1% of 118 collected scats, Karl & Best 1982), but even low predation pressure may be detrimental for fragile species (Rodriguez-Estrella *et al.* 1991). However, rat remains were found in 93·0% of these 118 scats (Karl & Best 1982), showing the indirect role cats might play in preserving native fauna through reduction of rat predation pressure on the kakapo. Moreover, the elimination of feral cat populations from such ecosystems could lead to a more severe negative impact on the endemic species, as a result of expansion of rodent populations once their predators are removed. Attempted reduction of the cat population of Amsterdam Island is alleged to have caused a compensating rise in the number of rats and mice, and so has been abandoned (Holdgate & Wace 1961). This process, termed 'mesopredator release', had been described in fragmented insular ecosystems (Soulé *et al.* 1988) and applies well to many insular foodwebs (e.g. Schoener & Spiller 1987). Conversely, the eradication of rodents first (which has now proven feasible, even on relatively large islands, Taylor & Thomas 1989, 1993; Towns 1996) might induce cats to switch prey, resulting in a brutal increase in predation pressure on the threatened endemic species, as experienced for stoats and rats in New Zealand (Murphy & Bradfield 1992). Unfortunately (from the theoretical point of view), there is little field evidence from island management either of mesopredator release following superpredator eradication, or of predators switching prey following mesopredator eradication.

As the optimal control strategy is neither simple to find nor intuitive, it is studied through the analysis of a mathematical model which mimics the dynamics of the three species in this system. In the study reported here, the interactions of a prey species, such as a bird species, a threatening alien mesopredator, such as a rat, and an alien superpredator species, such as the feral domestic cat, were examined through their coupled dynamics. Through this model, the theoretical existence of 'mesopredator release' and the effect of the presence of a superpredator on the prey will be investigated. It is assumed that the superpredator preys both upon the prey and the mesopredator. For the sake of simplicity, reference will sometimes be made to them as bird, rat and cat, instead of prey, mesopredator and superpredator, respectively.

The models

THE PRELIMINARY MODELS

For the sake of simplicity, models are first presented taking into account only two species, and only then is the third species added and its implied complications analysed. The construction and analysis of the models are based on previous work (Courchamp & Sugihara 1999), to which the reader can refer for additional details. The first two systems consist of two simple coupled differential equations, each representing the dynamics of one population. Each population is described by a simple logistic equation, modified to take into account its relationship with the other species. The other possible prey species populations are not taken into account; it is assumed that all the prey species form a single 'bird' population, with average characteristics. The realism of these assumptions has been discussed previously (Courchamp & Sugihara 1999). The number of individuals at time *t* in the prey, mesopredator and superpredator populations are *B*, *R* and *C*, respectively. The intrinsic growth rates of the prey, mesopredator and superpredator populations are r_b, r_r and r_c, respectively. The predation rate of the superpredator is μ_b on the prey and μ_r on the mesopredator. The predation rate of the mesopredator is η_b on the prey and η_s on other food items (seeds, leaves, invertebrates). The carrying capacity of the environment for the prey population is K_b. The carrying capacities of the environment for the mesopredator and the superpredator populations are not constants, but depend partially (rats are omnivores) or totally (cats are carnivores) on the number of available individual prey on which their populations can feed at time *t*. For the mesopredator, the carrying capacity of the environment is the number of mesopredators that can live on food other than birds when there is no prey, to which is added the number of mesopredators that can be fed by the total of available prey at time *t*. The carrying capacity is thus the quantity of non-avian food S divided by the consumption rate η_s, plus the number of prey *B* divided by the mesopredator predation rate η_b: $S/\eta_s + B/\eta_b$, that is $(\eta_b S + \eta_s B)/\eta_b\eta_s$. For the sake of simplicity, it is assumed that S is a constant (the carrying capacity in the absence of prey is kept under the form S/η_s instead of a constant, say K_s, to conserve homogeneous notation). Rats are opportunistic predators, and their diet (proportion of avian and non-avian food consumed) depends on relative availability of food items (Clark 1980). Accordingly, instead of $\eta_b R$, the predation rate of rats on birds is: $B\eta_b R/(S+B)$. In the two-species models, the rat/cat system is not presented, because it is the same as the bird/cat system.

The prey/mesopredator (bird/rat) system is given by:

$$\begin{cases} \dfrac{dB}{dt} = r_b B\left(1 - \dfrac{B}{K_b}\right) - \dfrac{B}{S + B}\eta_b R & \text{eqn 1} \\[2ex] \dfrac{dR}{dt} = r_r R\left(1 - \dfrac{\eta_b\eta_s R}{\eta_b S + \eta_s B}\right) & \text{eqn 2} \end{cases}$$

There are several equilibrium points. The first two equilibrium states, extinction of both populations [0, 0] and extinction of the rat only [K_b, 0] are always unstable. The third state, extinction of the bird only, (0, S/η_s) is globally asymptotically stable if and only if $r_b \leqslant \eta_b/\eta_s$. These three points always exist. When both populations coexist, the system reaches (B^*, $S/\eta_s + B^*/\eta_b$). B^* is given in the Appendix with the analysis of the system.

The prey/superpredator (bird/cat) system is given by:

$$\begin{cases} \dfrac{dB}{dt} = r_b B\left(1 - \dfrac{B}{K_b}\right) - \mu_b C & \text{eqn 3} \\[2ex] \dfrac{dC}{dt} = r_c C\left(1 - \dfrac{\mu_b C}{B}\right) & \text{eqn 4} \end{cases}$$

It is the same for the mesopredator/superpredator (rat/cat) system (*B* is replaced by *R* and $_b$ indices are replaced by $_r$ indices). They have three stable equilibrium points only, as the predator cannot survive alone: [0, 0], [K_b, 0] and [$K_b(1 - 1/r_b)$, $K_b(1 - 1/r_b)/\mu_b$].

THE COMPLETE MODEL

To take the three species into account simultaneously, one needs to make further assumptions. First of all, like the rat, the domestic cat is an opportunist predator, which switches prey species according to their availability (Fitzgerald 1988). Accordingly, the number of birds and rats preyed upon by cats will depend on their respective numbers. Instead of $\mu_b C$ and $\mu_r C$, one will find: $\mu_b BC/(B+R)$ and $\mu_r RC/(B+R)$ for the bird and the rat populations, respectively. Potential preferences of the cat for the indigenous prey over the introduced predator are not taken into account (see Courchamp, Langlais & Sugihara, in press). The cat carrying capacity is: $B/\mu_b + R/\mu_r$. The compartmental representation of the model is given in Fig. 1.

One has the following system:

$$\begin{cases} \dfrac{dB}{dt} = r_b B\left(1 - \dfrac{B}{K_b}\right) - \dfrac{B}{S + B}\eta_b R - \dfrac{B}{B + R}\mu_b C & \text{eqn 5} \\[2ex] \dfrac{dR}{dt} = r_r R\left(1 - \dfrac{\eta_b\eta_s R}{\eta_b S + \eta_s B}\right) - \dfrac{R}{B + R}\mu_r C & \text{eqn 6} \\[2ex] \dfrac{dC}{dt} = r_c C\left(1 - \dfrac{\mu_b\mu_r C}{\mu_r B + \mu_b R}\right) & \text{eqn 7} \end{cases}$$

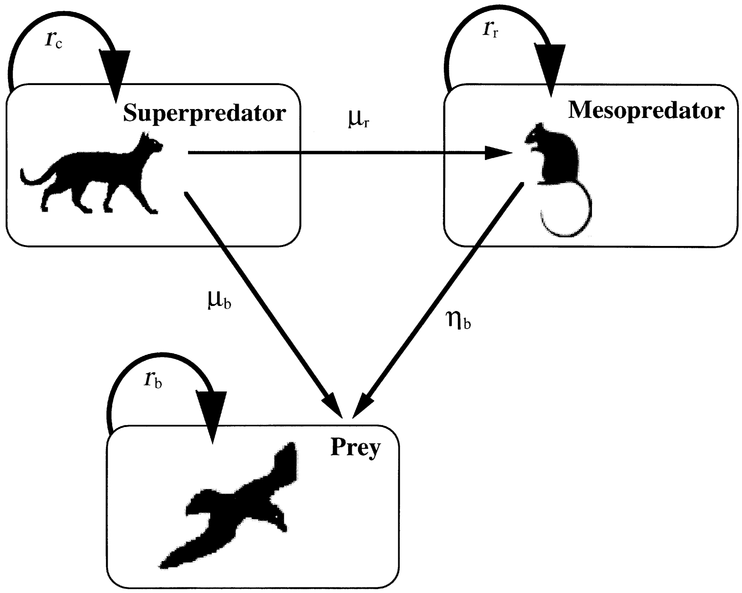

Fig. 1. Compartmental representation of the mathematical model with three species (eqns 7, 8, 9). Each box represents one population, symbolized by a letter and an animal: superpredator (C, cats), mesopredator (R, rats) and prey (B, birds). The arrows represent the flux within and are between compartments: curved arrows are intrinsic growth rates; straight arrows are predation rates. The intrinsic growth rates of the superpredator, the mesopredator and the prey are r_c, r_r and r_b, respectively. The predation rates of the superpredator on the mesopredator and on the prey are μ_r and μ_b, respectively; the predation rate of the mesopredator on the prey is η_b.

There are several states with this system: all populations go extinct [0, 0, 0], only the prey survives [K_b, 0, 0], only the mesopredator survives [0, S/η_s, 0], only the superpredator disappears [B^*, $S/\eta_s + B^*/\eta_b$, 0] (B^* has the same value than in system (1–2)), only the prey disappears [0, $S/\eta_s(1 - 1/r_r)$, $S/\mu_r\eta_s(1 - 1/r_r)$], only the mesopredator disappears [K_b $(1 - 1/r_b)$, 0, $K_b(1 - 1r_b)/\mu_b$], and, finally, no species disappears [B_6^*, R_6^*, C_6^*]. There can be between 0 and 5 stationary states with the equilibrium value of B between 0 and K_b, as solutions of an equation of the fifth degree. As its expression is very long and complex for the last point, it will not be presented here, but the authors will provide the Maple file upon request. For the same reason, the comparison between different points is too complex to be presented here analytically. The deterministic nature of the model allows, however, a numerical study.

It can be noted that the fourth, fifth and sixth equilibrium points are equivalent to some from the models 1–2 and 3–4. The conditions of existence of these points are described in the Appendix.

SUPERPREDATOR PRESENCE AND MESOPREDATOR RELEASE

The behaviour of the model is studied analytically (see Appendix), but simulations are presented for heuristic purposes. It can be seen from Fig. 2 that, under some conditions, while the rat alone would extirpate the bird (a) and the cat alone would not (b), the cat prevents extinction of the bird by the rat when both predators are present by controlling rat (c), or even by extirpating the rat (d).

One can see that, in some cases, the presence of the superpredator can indirectly protect a shared prey from a mesopredator. Even in circumstances where this is not the case, the elimination of the superpredator might be more harmful to the prey, through the 'mesopredator release', which arises when the pressure on mesopredators by superpredators is suppressed. To mimic this process, the effect of the suppression of the superpredator when the three species are present in equilibrium is studied. First one has to find values for which the bird population does not go extinct when the two other species are introduced. A range of parameters must be defined at which all three populations persist and reach an equilibrium state. This range of parameters implies high values of intrinsic growth rate of the prey ($>1{\cdot}3$) if it is to survive the presence of the two predators. From this equilibrium state ([B_6^*, R_6^*, C_6^*]), the extinction of the superpredator population can be simulated and the outcome of the two remaining populations monitored: new simulations are run with the following initial conditions: [B_6^*, R_6^*, 0]. This is repeated for different values of sensible parameters, to obtain a pattern displayed Fig. 3. This shows that prey extinction through mesopredator release does occur in this system. Moreover, it is avoided only for higher values of prey intrinsic growth rate ($>1{\cdot}6$). These correspond to values too high to be biologically realistic, and will not often be reached *in natura* by insular bird species. Indeed, in the absence of similar predation pressure,

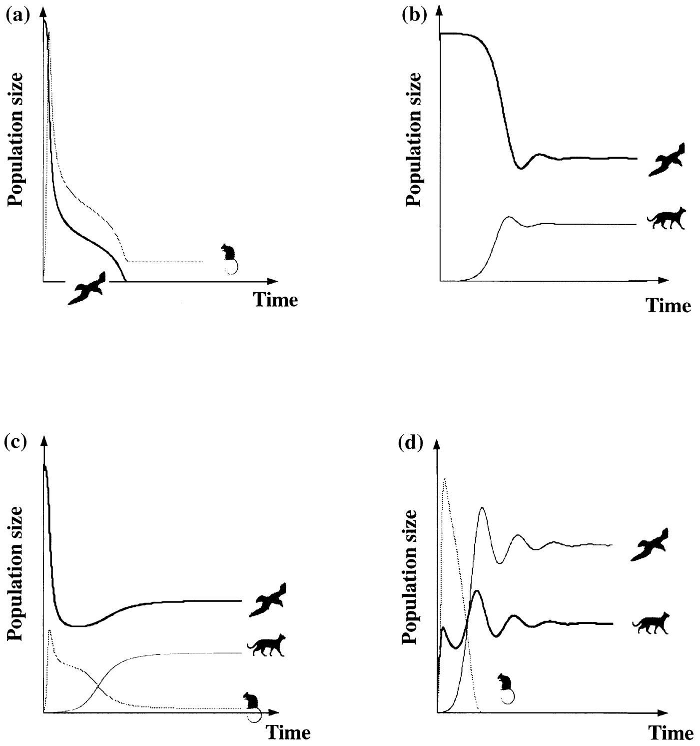

Fig. 2. Simulations showing the dynamics of the three population sizes plotted against time: (a) the model with only prey and mesopredator (system 1–2); (b) the model with only prey and superpredator (system 3–4); (c) and (d) the model with prey and both mesopredator and superpredator (system 5–7). The values used for the simulations show that the superpredator can lower the mesopredator population, to such a point that it prevents the prey elimination [simple mesopredator control in (c), total mesopredator eradication in (d)]. Values used are 1·5, 4·0 and 0·75 for r_b, r_r and r_c, respectively, 100 000 for K_b and 10000 for S, 54 for μ_b and 200 for μ_r, 6 for η_b and 365 for η_s. Initial conditions are in all cases 100 000 birds, 100 rats and 1 cat (which corresponds to the introduction of 100 rats and/or 1 cat into a healthy population of 100 000 birds). The scale is different for the three species.

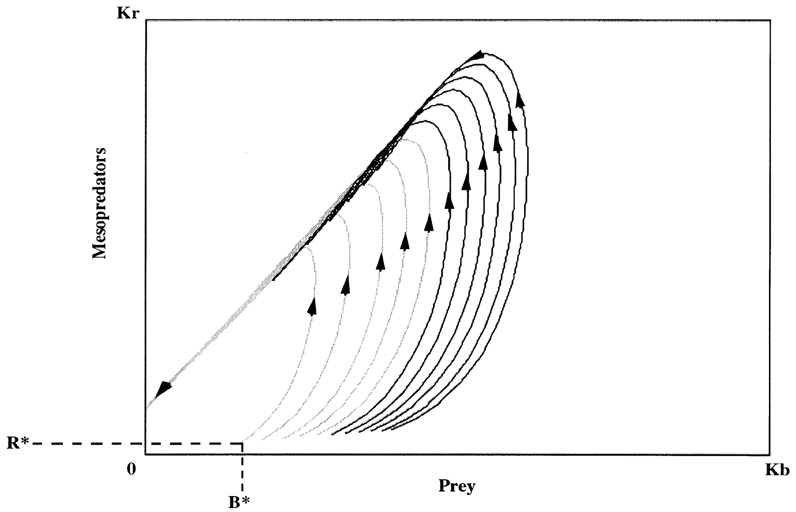

Fig. 3. Phase portrait of the bird vs. the rat populations, displaying the effect of the eradication of the superpredator on the prey, for different values of the prey intrinsic growth rate. Initial conditions are here the equilibrium point of the model where all three species are present (cat population is set to zero to simulate its eradication). This point changes because different values are used for the prey intrinsic growth rate leading to different equilibrium values. Elimination of the superpredator without elimination of the mesopredator results in elimination of the prey population through 'mesopredator release', when the prey intrinsic growth rate is lower than 1·6 (curves in light grey).

these endemic species seldom have developed anti-predator life history traits, such as a high intrinsic growth rate. These results show that the only endemic species with intrinsic growth rates high enough to survive the introduction of both a superpredator and a mesopredator will normally be extirpated through mesopredator release if the control strategy implies only the superpredator eradication. The strategy of control therefore appears essential in these particular ecosystems.

CONTROL STRATEGY

Mesopredator release can occur following eradication of the superpredator and the presence of the superpredator also has negative effects on the prey population, therefore a study of control strategies is necessary to determine an optimal strategy. If one applies a control effort of λ_r on the rat population and of λ_c on the cat population, the model (5–7) becomes:

$$\begin{cases} \dfrac{dB}{dt} = \mathrm{r_b}B\left(1 - \dfrac{B}{\mathrm{K_b}}\right) - \dfrac{B}{\mathrm{S} + B}\eta_b R - \dfrac{B}{B + R}\mu_b C & \text{eqn 8} \\[2ex] \dfrac{dR}{dt} = \mathrm{r_r}R\left(1 - \dfrac{\eta_b \eta_s R}{\eta_b \mathrm{S} + \eta_s B}\right) - \dfrac{R}{B + R}\mu_r C - \lambda_r R & \text{eqn 9} \\[2ex] \dfrac{dC}{dt} = \mathrm{r_c}C\left(1 - \dfrac{\mu_b \mu_r C}{\mu_r B + \mu_b R}\right) - \lambda_c C & \text{eqn 10} \end{cases}$$

This provides the same number of equibrium points as model (5–7), although with different values. Values of these points are provided in the Appendix, together with their conditions of existence and stability.

Analysis of this model shows that when superpredator control is high enough ($\lambda_c > r_c$), the superpredator disappears. As a result, the prey also disappears when the mesopredator control is not high enough [$\lambda_r < r_r(1 - r_b\eta_s/\eta_b) < r_r$), because of mesopredator release. In contrast, and surprisingly, the prey does not disappear when the superpredator control is below a certain threshold [i.e. $r_c(1 - r_b) < \lambda_c < r_c$], provided the mesopredator control is high enough [$\lambda_r > r_r - \mu_r(1 - \lambda_c/r_c)/\mu_b$]. This illustrates the importance of the presence of the superpredator in the system, and the need to take it into account in control programmes.

Discussion

This study examined, through a mathematical model, the fate of a prey species in an insular ecosystem into which both a mesopredator and a superpredator have been introduced. Although other species could have been considered, such as mongooses and reptiles (Case *et al.* 1992), the rat, feral cat and endemic bird species were taken as examples. Indeed, as Diamond (1989) stated, 'rats and cats are the most notorious killers and island birds the most notorious victims, in this regard [extinctions due to introduced predators].' This work shows several interesting features of direct concern to conservation biology. First, the result of this theoretical work shows that the presence of one predator only is sufficient to induce the extinction of the endemic prey. This is not new, as indicated by too many examples *in natura*. Second, when both the mesopredator and the superpredator are present, seven different situations may arise, among which is the case where the three species are present with stable dynamics. Interestingly, there is another case where both predator species can coexist indefinitely, even after the eradication of the prey species. Finally, and most interestingly, is the case where the superpredator causes the extinction of the mesopredator, but not of the prey.

It has been shown here that presence of a superpredator may have a global positive effect in insular ecosystems in which an introduced mesopredator threatens an endemic prey. Indeed, in the model presented here the presence of the superpredator may preclude the elimination of the prey by the mesopredator (or allow a larger prey population size). In addition, it has been demonstrated that superpredator eradication should be avoided, as a means to prevent what has been termed 'mesopredator release' (Soulé *et al.* 1988): a sudden burst of mesopredators, once the superpredator pressure is suppressed. Rats have a lower predation rate on birds than cats, but they are much more numerous and can have a higher impact on the prey (Newman & McFadden 1990). Moreover, as they are omnivores, they can maintain a high population and a high predation pressure, even when the prey population size is low, which the cat cannot. This explains why rats alone eliminate the prey more easily than cats alone in the model (Fig. 2), and why the cat presence is sometimes beneficial to shared prey. In fact, over the last 400 years, rats and cats are said to be responsible for 54% and 26% of island extinctions caused by predators, respectively (King 1985). The study of the control strategies clearly shows that the fate of the prey will depend on the superpredator control level. Although counterintuitive, if the superpredator control is too high, the prey will disappear. This may be a further argument in favour of the use of biological control, especially with pathogens with a steady long-term impact (see Courchamp & Sugihara 1999), which are unlikely to be too brutal.

Despite its mathematical complexity, this model remains very simple in its representation of the biological reality. In particular, spatial and temporal population heterogeneities, which are important components of insular ecosystems, were not taken into account. Similarly, the fact that different prey species are present in these ecosystems has not been taken into account. Instead, only one species, which is supposed to represent the 'average' of all prey species, was considered. As the rats and the cats are opportunistic predators, which switch prey species according to their relative availability (Clark 1980; Fitzgerald 1988), it would be interesting to study the effect of the presence of several prey species. This model is robust enough to be extended to other ecosystems that can be well described by the prey–mesopredator–superpredator trophic web. It therefore holds for systems where several prey species are present (e.g. landbirds, seabirds and lizards) provided that they are prey of both the mesopredator and the superpredator. Some changes may occur in the solutions of the model according to the characterics of the species (e.g. if they have different antipredation response), but the general conclusions should remain the same. Similarly, the results will be the same if another superpredator, say a bird of prey, is present. Different efficiencies in hunting different preys would here again add more complexity. In contrast, the model results will undoubtedly be different if another species is present which does not fully fit into one of these three trophic levels, because it would describe a totally different system. It is the case, for example, if a prey species (e.g. the rabbit) is present which is not preyed upon by both the superpredator and the mesopredator: islands where cats, rats and rabbits have been introduced should therefore be described by a different model. Despite these possible improvements, this theoretical work shows that it is crucial to take into account the presence of other alien species when designing control programmes for one introduced species (see also Courchamp *et al.*, in press for another example). Emphasis is placed on the following important distinction that should be understood from this work: in some ecosystems where rats are present, introduced cats might play a positive role (implying that their removal could have negative aspects on local fauna); however, their introduction cannot be recommended, whatever the circumstances.

Several points allow optimism about this particular area of conservation biology. First, the recovery and/or preservation of the ecosystems involved is not in conflict with local economic or politic interests, even if the governments of many concerned islands can hardly afford costly programmes such as mammal eradications. Second, eradication of introduced mammals such as domestic cats (Bloomer & Bester 1992), rabbits (Flux 1993), rats (Taylor & Thomas 1993), possums (Cowan 1992), foxes (Bailey 1992), goats (Parkes 1990) or others, once thought impossible, is now known to be feasible; for example, 120 successful 'pest' eradications have already been conducted on New Zealand islands (Veitch *et al.* 1992). Third, many studies show that, when the introduced species has been successfully removed from the whole ecosystem, the threatened species (plant or animal) generally recovers, sometimes rapidly, from the effects of these alien species (e.g. Cruz & Cruz 1987; Brothers & Copson 1988; Towns 1991, 1994; Newman 1994; Cooper *et al.* 1995). Fourth, in the cases where alien species induced the complete extinction of the population, local populations were often concerned; species or subspecies extinctions are less frequent (Moors & Atkinson 1984). Moreover, seabird populations are not dependent on the land for food, and breeding can continue on isolated islets and stacks free from predators (Atkinson 1985). In most cases of colony or population extinctions as a result of alien predators, there are, in nearby islets, populations able to recolonize the ecosystem once the predator eradication is achieved (Moors & Atkinson 1984; Case *et al.* 1992; Jouventin & Micol 1995). Last, in some cases (as in the well known case of the kakapo, Clout & Craig 1995; Powlesland *et al.* 1995) it is suspected that only a small number of individuals (cats as well as rats) have learned to kill the prey or eat the eggs (Grant, Pettit & Whittow 1981; Moors & Atkinson 1984). In these cases, when heavy programmes, such as complete eradication or long-term control, are not possible, selective control to eliminate these particular individuals may be sufficient in the short term, and should thus be implemented.

However, the situation is critical in many cases, and the media and scientific coverage of the situation on most islands does not seem to be proportionate to the problems faced by these often unique ecosystems (Crystal 1989). Despite numerous indications of catastrophic effects of introduced mammals on most oceanic islands, politically organized policies to resolve, or even prevent these effects remain comparatively few. Recent examples, and other older ones, show that solutions do exist. It is often the high financial constraints on eradication programmes that preclude them (Powlesland *et al.* 1995), or that impose undesired priorities in the order of their attainment (Brothers & Copson 1988). In these cases, a predictive study on the feasibility of the eradication and its potential effects on the ecosystem is needed, especially when there is more than one introduced species, in order to maximize the efficiency of eradication programmes. Theoretical studies, such as mathematical modelling could fulfil this task. This study shows that the intuitively evident need for feral cat eradication may not be the best solution in some specific cases, such as when introduced rodents are present. This is well illustrated by the case of Raoul Island, where it has been said that eradication of feral cats might bring little benefit to bird populations, because Norway rats are present on this island and constitute a major part of the diet of the cats (Fitzgerald *et al.* 1991). Empirical examples remain, however, scarce regarding the effects of eradication of predators (top predators or mesopredators) on population dynamics of coexisting species.

The idea that top predators may be important species for conservation biology is not new. It has been suggested that they have a disproportionate importance in food webs because their extinction can generate a cascade of unexpected secondary extinctions (Paine 1966; Pimm 1980). For example, the extinction of several prey species has been attributed to the increase of generalist and/or medium-sized predatory mammals because of the lack of top predators in different ecosystems (Terborgh & Winter 1980; Diamond & Case 1986; Wilcove, McLellan & Dobson 1986; Diamond 1989; Böhning-Gaese, Taper & Brown 1993; Goodrich & Buskirk 1995). With the example of lynx, mongooses and rabbits, it has been shown, both theoretically and empirically, that top predators actually benefit their prey through intraguild predation on other smaller predators which share the prey (Palomares *et al.* 1995). What is new here is rather the application of this idea to an already perturbed ecosystem, a rather counter-intuitive idea: in some cases the removal of one of the causes of perturbation may lead to increased damage. This is the case with the mesopredator release (Soulé *et al.* 1988). In some systems, only the direct negative effects of the top predator on endemic threatened prey have been examined, while in some cases greater positive effects may be present on the same species. Obviously, outcomes of changes of these already perturbed trophic webs are not intuitive, and intervention as dramatic as species eradication should always be preceded by careful empirical and theoretical studies of the whole ecosystem. Indeed, in the present case, eradicating the rats before the cats (at first a seemingly sound strategy) might in fact lead to another case of mesopredator release, as shown by the recent example of Bird Island in the Seychelles. Here, a recent eradication of the introduced black rat population led to an explosion of the exotic crazy ant *Anoplolepis longipes*, Jerdon, which has been shown to be threatening the bird colonies which rat eradication was intended to protect (Feare 1998). As complete removal of those alien predators is most of the time (and often rightly) the only envisaged solution (Veitch 1985; Ashmole, Ashmole & Simmons 1994; Rainbolt & Coblentz 1997), this idea of possible positive effects of top predators should be kept in mind in conservation biology.

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References

van Aarde, R.J. (1978) Reproduction and population ecology in the feral house cat, *Felis catus* on Marion Island. *Carnivore Genetics Newsletter*, **3**, 288–316.

van Aarde, R.J. (1983) Demographic parameters of the feral cat *Felis catus* population at Marion Island. *South African Journal of Wildlife Research*, **13**, 12–16.

Amarasekare, P. (1993) Potential impact of mammalian nest predators on endemic forest birds of Western Mauna Kea Hawaii. *Conservation Biology*, **7**, 316–324.

Arnaud, G., Rodriguez, A., Ortega-Rubio, A. & Alvarez-Cardenas, S. (1993) Predation by cats on the unique endemic lizard of Socorro Island *Urosaurus auriculatus* Revillagigedo Mexico. *Ohio Journal of Science*, **93**, 101–104.

Ashmole, N.P., Ashmole, M.J. & Simmons, K.E.L. (1994) Seabird conservation and feral cats on Ascension Island, South Atlantic. *Seabirds on Islands, Threats, Case Studies and Action Plans* (eds D. N. Nettleship, J. Burger & M. Gochfeld), pp. 39–67. Birdlife Conservation Series no. 1, Hamilton.

Atkinson, I.A.E. (1985) The spread of commensal species of *Rattus* to oceanic islands and their effect on island avifaunas. *Conservation of Island Birds* (ed. P. J. Moors), pp. 35–81. ICBP Technical Publication no. 3. Cambridge.

Atkinson, I.A.E. (1989) Introduced animals and extinctions. *Conservation for the Twenty-First Century* (eds D. Western & M. C. Pearl), pp. 54–75. Oxford University Press, Oxford.

Bailey, E.P. (1992) Red foxes, *Vulpes vulpes*, as biological control agents for introduced arctic foxes, *Alopex lagopus*, on Alaskan Islands. *Canadian Field Naturalist*, **106**, 200–205.

Bell, B.D. (1978) The Big South Cape Island rat irruption. *The Ecology and Control of Rodents in New Zealand Nature Reserves* (eds P. R. Dingwall, I. A. E. Atkinson & C. Hay), pp. 33–46. Dept. Land and Surveys, Private Bag, Wellington. Inf. Ser. 4.

Bertram, D.F. (1995) The roles of introduced rats and commercial fishing in the decline of ancient murrelets on Langara Island, British Columbia. *Conservation Biology*, **9**, 865–872.

Bertram, D.F. & Nagorsen, D.W. (1995) Introduced rats, *Rattus* spp., on the Queen Charlotte Islands: Implications for seabird conservation. *Canadian Field Naturalist*, **109**, 6–10.

Bloomer, J.P. & Bester, M.N. (1992) Control of feral cats on sub-Antarctic Marion Island, Indian Ocean. *Biological Conservation*, **60**, 211–219.

Böhning-Gaese, K., Taper, M.L. & Brown, J.H. (1993) Are declines in North-American insectivorous songbirds due to causes on the breeding range? *Conservation Biology*, **7**, 76–85.

Brooke, M. de L. (1995) The breeding biology of the gadfly petrels *Pterodroma spp.* of the Pitcairn Islands: Characteristics, population sizes and controls. *Biological Journal of the Linnean Society*, **56**, 213–231.

Brosset, A. (1963) Statut actuel des mammifères des îles Galapagos. *Mammalia*, **27**, 323–338.

Brothers, N.P. & Copson, G.R. (1988) Macquarie Island flora and fauna management – interpreting progress and predictions for the future. *Papers and Proceedings of the Royal Society of Tasmania*, **122**, 129–135.

Campbell, E.W. (1991) The effect of introduced roof rats on bird diversity of Antillean cays. *Journal of Field Ornithology*, **62**, 343–348.

Case, T.J. & Bolger, D.T. (1991) The role of introduced species in shaping the distribution and abundance of island reptiles. *Evolutionary Ecology*, **5**, 272–290.

Case, T.J., Bolger, D.T. & Richman, A.D. (1992) Reptilian extinctions: the last ten thousand years. *Conservation Biology, the Theory and Practice of Nature Conservation Preservation and Management* (eds P. L. Fielder & K. J. Subodh), pp. 91–125. Chapman & Hall, London.

Ceballos, G. & Brown, J.H. (1995) Global patterns of mammalian diversity, endemism and endangerment. *Conservation Biology*, **9**, 559–568.

Chapuis, J.L. (1995) Alien mammals in the French Subantarctic Islands. *Progress in Conservation of the Subantarctic Islands* (ed. P. R. Dingwall), pp. 127–132. IUCN–The World Conservation Union. Conservation of the Southern Polar Region No 2. Paimpont.

Clark, D.A. (1980) Age- and sex-dependant foraging strategies of a small mammalian omnivore. *Journal of Animal Ecology*, **49**, 549–564.

Clark, D.A. (1981) Foraging patterns of black rats across a desert-montagne forest gradient in the Gualapagos Islands. *Biotropica*, **13**, 182–194.

Clout, M.N. & Craig, J.L. (1995) The conservation of critically endangered flightless birds in New Zealand. *Ibis*, **137**, S181–S190.

Cooper, J. (1995) Conservation status of the Prince Edward Islands. *Progress in Conservation of the Subantarctic Islands* (ed. P. R. Dingwall), pp. 21–30. IUCN–The World Conservation Union. Conservation of the Southern Polar Region No, 2. Paimpont.

Cooper, J., Marais, A.V.N., Bloomer, J.P. & Bester, M.N. (1995) A success story: breeding of burrowing petrels (Procellariidae) before and after the eradication of feral cat *Felis catus* at subantartic Marion Island. *Marine Ornithology*, **23**, 33–37.

Courchamp, F. & Sugihara, G. (1999) Biological control of introduced predator populations to protect native island species from extinction. *Ecological Applications*, in press.

Courchamp, F., Langlais, M. & Sugihara, G. (in press) Rabbits killing birds: modelling the hyperpredation process. *Journal of Animal Ecology* (in press).

Cowan, P.E. (1992) the eradication of introduced Australian brushtail possums, *Trichosurus vulpecula*, from Kapiti Island, a New Zealand nature reserve. *Biological Conservation*, **61**, 217–226.

Cree, A., Daugherty, C.H. & Hay, J.M. (1995) Reproduction of a rare New Zealand reptile, the Tuatara *Sphenodon punctatus*, on rat-free and rat-inhabited islands. *Conservation Biology*, **9**, 373–383.

Cruz, J.B. & Cruz, F. (1987) Conservation of the dark-rumped petrel *Pterodroma Phaeopygia* in the Galapagos Islands, Ecuador. *Biological Conservation*, **42**, 303–312.

Crystal, L. (1989) American Broadcast journalism: its coverage of conservation crises. *Conservation for the Twenty-First Century* (eds D. Western & M. C. Pearl), pp. 289–293. Oxford University Press, Oxford.

Derenne, P. (1976) Notes sur la biologie du chat haret de Kerguelen. *Mammalia*, **40**, 531–595.

Diamond, J. (1989) Overview of recent extinctions. *Conservation for the Twenty-First Century* (eds D. Western & M. C. Pearl), pp. 37–41. Oxford University Press, Oxford.

Diamond, J. & Case, T. (eds) (1986) Overview: introductions, extinctions, exterminations and invasions. *Community Ecology*, pp. 65–79. Harper & Row Publishers, New York.

Domm, S. & Messersmith, J. (1990) Feral cat eradication on a barrier reef island, Australia. *Atoll Research Bulletin*, **338**, 1–4.

Feare, C. (1998) *The sustainable exploitation of sooty tern eggs in the Seychelles*. 6th annual unpublished report to the Division of Environment, Government of the Republic of Seychelles.

Fitzgerald, B.M. (1988) Diet of domestic cats and their impact on prey populations. *The Domestic Cat, the Biology of its Behaviour* (eds D. C. Turner & P. Bateson), pp. 123–147. Cambridge Academic Press, Cambridge.

Fitzgerald, B.M., Karl, B.J. & Veitch, C.R. (1991) The diet of feral cats (*Felis catus*) on Raoul Island, Kermadec group. *New Zealand Journal of Ecology*, **15**, 123–129.

Flux, J.E.C. (1993) Relative effect of cats, myxomatosis, traditional control or competitors in removing rabbits from islands. *New Zealand Journal of Zoology*, **20**, 13–18.

Goodrich, J.M. & Buskirk, S.W. (1995) Control of abundant native vertebrates for conservation of endangered species. *Conservation Biology*, **9**, 1357–1364.

Grant, G.S., Pettit, T.N. & Whittow, G.C. (1981) Rat predation on Bonin petrel eggs on Midway atoll. *Journal of Field Ornithology*, **52**, 336–338.

Holdgate, M.W. & Wace, N.M. (1961) The influence of man on the floras and faunas of Southern Islands. *Polar Record*, **10**, 475–493.

Honnegger, R.E. (1981) List of amphibians and reptiles either known or thought to have become extinct since 1600. *Biological Conservation*, **19**, 141–158.

Iverson, J.B. (1978) The impact of feral cats and dogs on populations of the west Indian rock iguana, *Cyclura carinata*. *Biological Conservation*, **14**, 63–73.

Johnstone, G.W. (1985) Threats to birds on subantarctic islands. *Conservation of Island Birds* (ed. P. J. Moors), pp. 101–121. ICBP Technical Publication no. 3. Cambridge.

Jouventin, P. & Micol, T. (1995) Conservation status of the French Subantarctic Islands. *Progress in Conservation of the Subantarctic Islands* (ed. P. R. Dingwall), pp. 31–52. IUCN—The World Conservation Union. Conservation of the Southern Polar Region No 2. Paimpont.

Jouventin, P., Stahl, J.C., Weimerskirch, H. & Mougin, J.L. (1984) The seabirds of the French Subantarctic Islands & Adelie Land, their status and conservation. *Status and Conservation of the World's Seabirds* (eds J. P. Croxall, P. G. H. Evans & R. W. Schreiber), pp. 609–625. ICBP Technical Publication no. 2. Cambridge.

Karl, B.J. & Best, H.A. (1982) Feral cats on Stewart Island: their foods and their effects on kakapo. *New Zealand Journal of Zoology*, **9**, 287–294.

Kepler, C.B. (1967) Polynesian rat predation on nesting Laysan Albatrosses and other Pacific seabirds. *Auk*, **84**, 426–430.

King, W.B. (1985) Island birds: will the future repeat the past? *Conservation of Island Birds*. ICBP Technical Publication no. 3 (ed. P. J. Moors), pp. 3–15. Cambridge.

Konecny, M.J. (1987) Food habits and energetics of feral house cats in the Galàpagos Islands. *Oikos*, **50**, 24–32.

Lovegrove, T.G. (1996) A comparison of the effects of predation by Norway (*Rattus norvegicus*) and Polynesian rats (*R. exulans*) on the saddleback (*Philesturnus carunculatus*). *Notornis*, **43**, 91–112.

MacCallum, J. (1986) Evidence of predation by kiore upon lizards from the Mokohinau islands. *New Zealand Journal of Ecology*, **9**, 83–87.

Mellink, E. (1992) The Status of Neotoma anthonyi Rodentia Muridae Cricetinae of Todos Santos Islands Baja California Mexico. *Bulletin Southern California Academy of Sciences*, **91**, 137–140.

Monteiro, L.R., Ramos, J.A. & Furness, R.W. (1996) Past and present status and conservation of the seabirds breeding in the Azores Archipelago. *Biological Conservation*, **78**, 319–328.

Moors, P.J. & Atkinson, I.A.E. (1984) Predation on seabirds by introduced animals, and factors affecting its severity. *Status and Conservation of the World's Seabirds*. (eds J. P. Croxall, P. G. H. Evans & R. W. Schreiber), pp. 667–690. ICBP Technical Publication no. 2. Cambridge.

Murphy, E. & Bradfield, P. (1992) Change in diet of stoats following poisoning of rats in a New-Zealand forest. *New Zealand Journal of Ecology*, **16**, 137–140.

Newman, D.G. (1994) Effects of a mouse, *Mus musculus*, eradication programme and habitat change on lizard populations of Mana Island, New Zealand, with special reference to McGregor's skink, *Cyclodina macgregori*. *New Zealand Journal of Zoology*, **21**, 443–456.

Newman, D.G. & McFadden, I. (1990) Seasonal fluctuations of numbers, breeding, and food of kiore (*Rattus exulans*) on Lady Alice Island (Hen and Chickens group), with a consideration of kiore: Tuatara (*Sphenodon punctatus*) relationships in New Zealand. *New Zealand Journal of Zoology*, **17**, 55–64.

Nogales, M. & Medina, F.M. (1996) A review of the diet of feral domestic cats (*Felis silvestris* L. *catus*) on the Canary Islands, with new data from the laurel forest of La Gomera. *Zeitschrift für Säugetierkunde*, **61**, 1–6.

Nogales, M., Rodriguez, J.L., Delgado, G., Quilis, V. & Trujillo, O. (1992) The diet of feral cats (*Felis catus*) on Alegranza island (north of Lanzarote, Canary islands). *Folia Zoologica*, **41**, 209–212.

Paine, R.T. (1966) Food web complexity and species diversity. *American Naturalist*, **100**, 65–75.

Palomares, F., Gaona, P., Ferreras, P. & Delibes, M. (1995) Positive effects on game species of top predators by controlling smaller predator populations: an example with lynx, mongooses and rabbits. *Conservation Biology*, **9**, 295–305.

Parkes, J.P. (1990) Feral goat control in New Zealand. *Biological Conservation*, **54**, 335–348.

Pimm, S.L. (1980) Food web design and the effect of species deletion. *Oikos*, **35**, 139–149.

Powlesland, R.G., Roberts, A., Lloyd, B.D. & Merton, D.V. (1995) Number, fate, and distribution of kakapo (*Strigops habroptilus*) found on Stewart Island, New Zealand, 1979–92. *New Zealand Journal of Zoology*, **22**, 239–248.

Rainbolt, R.E. & Coblentz, B.E. (1997) A different perspective on eradication of vertebrate pests. *Wildlife Society Bulletin*, **25**, 189–191.

Rodriguez-Estrella, R., Arnaud, G., Cardenas, S.A. & Rodriguez, A. (1991) Predation by feral cats on birds at Isla Socorro Mexico. *Western Birds*, **22**, 141–143.

Schoener, T.W. & Spiller, D.A. (1987) Effect of lizards on spider populations: manipulative reconstruction of a natural experiment. *Science*, **236**, 131–134.

Seitre, R. & Seitre, J. (1992) Causes of land-bird extinction in French Polynesia. *Oryx*, **26**, 215–222.

Seto, N.W.H. & Conant, S. (1996) The effects of rat (*Rattus rattus*) predation on the reproductive success of the Bonin Petrel (*Pterodroma hypoleuca*) on Midway Atoll. *Colonial Waterbirds*, **19**, 171–185.

Soulé, M.E., Bolger, D.T., Alberts, A.C., Wright, J., Sorice, M. & Hill, S. (1988) Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology*, **2**, 75–92.

Spencer, P.B.S. (1991) Evidence of predation by a feral cat, *Felis catus* (Carnivora: Felidae) on an isolated rock-wallaby colony in tropical Queensland. *Australian Mammalogy*, **14**, 143–144.

Taylor, R.H. & Thomas, B.W. (1989) Eradication of Norway rats (*Rattus norvegicus*) from Hawea island, Fiordland, using Brodifacoum. *New Zealand Journal of Ecology*, **12**, 23–32.

Taylor, R.H. & Thomas, B.W. (1993) Rats eradicated from rugged Breaksea Island 170 ha Fiordland New Zealand. *Biological Conservation*, **65**, 191–198.

Terborgh, J. & Winter, B. (1980) Some causes of extinction. *Conservation Biology: an Evolutionary–Ecological Perspective* (eds M. E. Soulé & B. A. Wilcox), pp. 119–133. Sinauer Assoc. Inc., Sunderland, Massachusetts.

Thurley, T. & Ben, B.D. (1994) Habitat distribution and predation on a western population of terrestrial Leiopelma (Anura: Leiopelmatidae) in the northern King Country, New Zealand. *New Zealand Journal of Zoology*, **21**, 431–436.

Tidemann, C.R., Yorkston, H.D. & Russack, A.J. (1994) The diet of cats, *Felis catus*, on Christmas Island, Indian Ocean. *Wildlife Research*, **21**, 279–286.

Towns, D.R. (1991) Response of lizard assemblages in the Mercury Islands, New Zealand, to removal of an introduced rodent: The kiore (*Rattus exulans*). *Journal of the Royal Society of New Zealand*, **21**, 119–136.

Towns, D.R. (1994) The role of ecological restoration in the conservation of Whitaker's skink (*Cyclodina whitakeri*), a rare New Zealand lizard (Lacertilia: Scincidae). *New Zealand Journal of Zoology*, **21**, 457–471.

Towns, D.R. (1996) Changes in habitat use by lizards on a New Zealand island following removal of the introduced Pacific Rat *Rattus exulans*. *Pacific Conservation Biology*, **2**, 286–292.

Towns, D.R. & Daugherty, C.H. (1994) Patterns of range contractions and extinctions in the New Zealand herpetofauna following human colonisation. *New Zealand Journal of Zoology*, **21**, 325–339.

Veitch, C.R. (1985) Methods of eradicating feral cats from offshore islands in New-Zealand. *Conservation of Island Birds* (ed. P. J. Moors), pp. 35–81. ICBP Technical Publication no. 3. Cambridge.

Veitch, C.R., Fitzgerald, B.M., Innes, J. & Murphy, E. (1992) Proceedings of the National Predator Management Workshop, Threatened Species Occasional Publication. No 3.

Wilcove, D.S., McLellan, C.H. & Dobson, A.P. (1986) Habitat fragmentation in the temperate zone. *Conservation Biology, the Science of Scarcity and Diversity*. (ed. M. E. Soulé), pp. 237–256. Sinauer Assoc. Inc., Sunderland, Massachusetts.

Williamson, M. (1996) *Biological Invasion*. Chapman and Hall, London.

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Appendix

SYSTEM (1–2)

There are several stationary states for the first system (eqns 1,2). The first two equilibrium states [0, 0] and [K_b, 0] are always unstable. The third state [0, S/η_s] is globally asymptotically stable if and only if $r_b \leqslant \eta_b/\eta_s$. These three points always exist. When no populations go extinct, the system reaches [B^*, $S/\eta_s + B^*/\eta_b$], where B^*, the bird population size at equilibrium, is the solution of a quadratic equation and therefore one can have 0, one or two equilibria with both populations present between 0 and K_b: $B^* = [-t + \sqrt{(t^2 - 4\eta_s r_b u)}]/2\eta_s r_b$, with $t = \eta_s K_b - \eta_s r_b\ (K_b - S)$, and $u = (\eta_b - \eta_s r_b)(SK_b)$. Numerically, when there are two points with admissible coexistence, one only, at most, is stable. If $0 < \eta_b \leqslant \eta_s$, then there are two cases: if $\eta_b/\eta_s \leqslant r_b$, the point is stable, otherwise it does not exist. If $0 < \eta_s \leqslant \eta_b$, then there are two cases: if $\eta_b/\eta_s < r_b$, it is stable, if $r_b \leqslant 1 < \eta_b/\eta_s$ it does not exist. If $1 < r_b < \eta_b/\eta_s$, then if $\eta_b > \eta_b{}^*$, it does not exist, if $\eta_b = \eta_b{}^*$, it is stable, if $\eta_b < \eta_b{}^*$ there are two values for this point. $\eta_b{}^* = (\eta_s B_{max}{}^2 + r_b \eta_b SK_b)/K_b S$, with $B_{max} = [(r_b - 1)K_b - r_b S]/2r_b > 0$.

SYSTEM (3–4)

The second system (eqns 3, 4) has 3 stationary states. $P1_{34}$: [0, 0], $P2_{34}$: [K_p, 0], and $P3_{34}$: [$K_p(1 - 1/r_p)$, $(1/\mu_p)K_p(1 - 1/r_p)$]. The dynamic behaviour of this system is given by four cases.

1 Case 1: $r_c > 1$: if $r_p \leqslant 1$ the system reaches $P1_{34}$, otherwise it reaches $P3_{34}$.

2 Case 2: $0 < r_p \leqslant r_c < 1$: the system reaches $P1_{34}$.

3 Case 3: $0 < r_c < 1$, $r_c \leqslant r_p$: in this case, the dynamics depend on the initial proportion of prey and predator. If $C(0)/P(0) > \mu_p(r_p - r_c)/(1 - r_c)$, then the system reaches $P1_{34}$. If $0 < r_c \leqslant r_p < 1$, then the system reaches $P1_{34}$. If $1 < r_p$, then: (i) if $r_c + r_p > 2$, then the system reaches $P3_{34}$; (ii) if $r_c + r_p = 2$, then this stationary state becomes a centre, all nearby trajectory being periodical; (iii) if $r_c + r_p < 2$, then this point is unstable.

4 Case 4: $r_c = 1$: if $0 < r_p \leqslant 1$, the system reaches $P1_{34}$, otherwise it reaches $P3_{34}$.

SYSTEM (5–7)

There are several equilibrium points for this system. The two equilibrium points $[K_b, 0, 0]$ and $[0, S/\eta_s, 0]$ always exist but are never stable. There are 0, one or two equilibrium points where only the cat population disappears, since it is the solution of an equation of the second degree $[B^*, S/\eta_s + B^*/\eta_b, 0]$. These points are never stable when they exist. The point where only the prey disappears $[0, S(1 - 1/r_r)/\eta_s, (1/\mu_r)\ (S/\eta_s)\ (1 - 1/r_r)]$ is admissible if $r_r > 1$ and is stable if $r_b < [\mu_b/\mu_r + \eta_b(1 - 1/r_r)/\eta_s]$ and $r_c + r_r > 2$. The point where only the mesopredator disappears $[K_b(1 - 1/r_b), 0, (1/\mu_b)K_b(1 - 1/r_b)]$ is admissible if $r_b > 1$ and is stable if $r_r < \mu_r/\mu_b$ and $r_c + r_b > 2$. In numerical simulations, at least one equilibrium point with persistence of the three species $[B_6^*, R_6^*, C_6^*]$ is found if the above conditions are not fulfilled.

SYSTEM (8–10)

Several equilibirum points arise. Only the prey survive: $[K_b, 0, 0]$. This point is stable if $\lambda_r > r_r$ and $\lambda_c > r_c$. Only the mesopredator survives: $[0, (1 - \lambda_r/r_r)S/\eta_s, 0]$. This point is stable if $\lambda_r < r_r$, $\lambda_c > r_c$ and $\lambda_r < r_r(1 - r_b\eta_s/\eta_b)$. Only the mesopredator disappears: $[K_b(1 - 1/r_b + \lambda_c/r_b r_c), 0, K_b(1 - 1/r_b + \lambda_c/r_b r_c)(1 - \lambda_c/r_c)/\mu_b]$. This point is admissible if: $r_c > \lambda_c > r_c(1 - r_b)$. It is stable if $r_c > \lambda_c > r_c(1 - r_b)$, $\lambda_r > r_r - \mu_r/\mu_b(1 - \lambda_c/r_c)$ and $\lambda_c > (2 - r_c - r_b)/(2 - r_c)$. The last condition implies $r_c < 2$, which is fulfilled by studied cat populations *in natura* (e.g. $r_c = 0{\cdot}43$–$0{\cdot}55$: Derenne 1976; or 0·233–1·171: van Aarde 1978, 1983). If not, one would have to replace it by: $(2 - r_c)\lambda_c > (2 - r_c - r_b)$. Only the prey disappears: $[0, (1 - 1/r_r + \lambda_c/r_r r_c - \lambda_r/r_c)S/\eta_s, (1 - 1/r_r + \lambda_c/r_r r_c - \lambda_r/r_c)(1 - \lambda_c/r_c)S/\mu_r\eta_s]$. This point is admissible if: $r_c > \lambda_c > r_c(1 - \lambda_r r_r/r_c - r_r)$. It is stable if $r_c > \lambda_c > r_c(1 - \lambda_r r_r/r_c - r_r)$, $r_b < \mu_b(1 - \lambda_c/r_c)/\mu_c + \eta_b(1 - 1/r_r + \lambda_c/r_r r_c - \lambda_r/r_c)/\eta_s$ and $\lambda_c > r_c(\lambda_r + 2 - r_c - r_r)/(2 - r_c)$. The same comment holds for the last condition ($r_c > 2$). Only the superpredator disappears: as in the case without control, there are 0, 1 or 2 points, given by the solutions of an equation of the second degree. $[-t \pm \sqrt{(t^2 - 4r_r\eta_s\eta_b u)}/2r_r\eta_s\eta_b, S/\eta_s + B^*/\eta_b, 0]$, with here $t = \lambda_r\eta_s K_b + r_r\ [\eta_s K_b - \eta_s r_b\ (K_b - S)]$, and $u = \lambda_r\eta_b SK_b + r_r\ (\eta_b - \eta_s r_b)(SK_b)$. The point where the superpredator disappears is unstable if $\lambda_c < r_c$ (new introductions lead to other states). Numerically, this point can be stabilized by increasing the value of λ_c (increasing the control of the superpredator). In numerical simulations, at least one equilibrium point with persistence of the three species $[B_6^*, R_6^*, C_6^*]$ is found if the above conditions are not fulfilled.