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Control of rabbits to protect island birds from cat predation

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Abstract

Both introduced predators (e.g. domestic cats) and introduced small grazers (e.g. rabbits) are harmful to many island vertebrate species. The effects of cats on indigenous species are direct (predation), whereas the most obvious effects of rabbits are often indirect and in the longer term. Thus, in situations where both cats and rabbits are present, priority is frequently given to control of cats. However, the presence of rabbits can allow an increased predator population which can lead to extinction of the indigenous and less well adapted prey species, and increase the difficulty of predator control. Through a mathematical model, we show that control of introduced prey facilitates the control of the introduced predator population. Moreover, predator control may fail to protect the indigenous prey if control of the introduced prey is not undertaken simultaneously. Therefore, control of both introduced species is the best strategy.

Keywords: Bird conservation; Control strategies; Feral cats; Hyperpredation process; Introduced mammals; Mathematical model; Rabbits

1. Introduction

Two major problems in alien species introduction on oceanic islands are predation and overgrazing (e.g. Diamond, 1989). Predators frequently have a dramatic effect on local prey, often inducing a decrease in their populations, and sometimes even driving them to extinction (e.g. Moors and Atkinson, 1984). Among the most notorious and harmful introduced predators are domestic cats *Felis catus*, rats *Rattus* spp. and mongooses *Hagolestes auropunctatus*, *H. edwardsii*. Cats and mongoose have often been introduced deliberately, in a vain attempt to control rats, which generally get ashore from infested ships (Moors and Atkinson, 1984). However, these introduced predators have often attacked native prey (Moors and Atkinson, 1984; Case et al., 1992), which have no antipredation behaviour (Moors and Atkinson, 1984) having not evolved in the presence of such mammal predators (Diamond, 1989).

Similarly, successful grazers, such as goats *Capra hircus* or rabbits *Oryctolagus cuniculus* are generally able to eat a very large variety of native plants, and the result is frequently a dramatic impoverishment of the quantity and quality of indigenous flora. On Laysan Island in the Hawaiian chain, rabbits alone were responsible for eliminating 26 species of plants between 1903 and 1923, a rate of loss exceeding one species per year (Christophersen and Caum, 1931, cited in Atkinson, 1989). They are also believed to have been responsible for the decline or extinction of several reptile and bird species (King, 1985; North et al., 1994; Smith and Quin, 1996), including the loss of at least three species of land birds from Laysan Island (Warner, 1963, cited in Atkinson, 1989). Direct effects include: competition for existing burrows (or places to dig them) with many burrowing seabird species (e.g. Young, 1981); prevention of large-scale regeneration following fires (Norman, 1967) or cyclones (Kirk and Racey, 1992); colony desertion by seabirds due to interference (Gillham, 1963), or even sometimes egg destruction (Brown, 1974); death of as much as 10% of Hooker's sea lion pups being trapped and suffocated in burrows each year on Enderby and Rose Islands (Sanson and Dingwall, 1995). Indirect effects of rabbits overgrazing include: reduction of the plant cover for terrestrial nesting birds, affecting their reproductive success (Gillham, 1963); direct competition for food among birds depending directly (e.g. granivorous) or indirectly (e.g. insectivorous) on the terrestrial

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vegetation (Gillham, 1963); denudation of the soil from the exposure to frost-heaving, rain and wind erosion (Watt, 1981; Scott, 1988; Wallage-Drees and Croin Michielsen, 1989); and acceleration of soil erosion due to burrowing (Norman, 1967; Chapuis, 1995a).

Control of alien species has been recommended by both theoretical and field conservationists (e.g. Wilson et al., 1998). Rabbit control methods are becoming increasingly efficient, and rabbits have been eradicated, by one method or another, from at least 87 islands (Flux, 1993). Successful cat eradication has been reported for several islands (Rauzon, 1985; Veitch, 1985; Domm and Messersmith, 1990), including large ones, such as the 29 000 ha Marion Island (Cooper, 1995). Even rat eradication, historically thought to be impossible, is now being achieved regularly (Taylor and Thomas, 1989, 1993; Towns, 1996). In many cases, introduced predators and prey both occur together; for example at least 80 islands have both alien cats and rabbits (Flux, 1993). Priority is then generally given to the control of the predators, since they have the most direct and obvious short term effects. Often, only direct effects of grazers are taken into account for control program decisions, and when there are no important direct effects, control may not be considered at all.

Effects of rabbits on indigenous vertebrate species can, however, be very complex, especially when introduced cats are also present. Cats are opportunistic predators, which switch prey according to their availability (Fitzgerald, 1988). When rabbits are more abundant than birds, reptiles or other mammals, they constitute a larger part of the cats' diet than when they are less abundant (e.g. Nogales et al., 1992; Nogales and Medina, 1996). On Cochon island, rabbits are only a secondary prey item in months when seabirds are present, but appear to enable cats to subsist over winter, when seabirds are absent (Derenne and Mougin, 1976). Spatial fluctuations of prey abundance can be as important as temporal ones. Rabbits may sustain cats in areas where indigenous prey are not present, thereby enabling them to reach remote colonies or populations of indigenous prey (Brothers and Copson, 1988). It is also known that in Raoul, Dassen, Deserta Grande, Marion and Kerguelen Islands, introduced mammals such as rabbits, rats and mice, *Mus musculus* are the main prey of cats in winter, allowing them to maintain high density during the absence of migrating birds (e.g. Derenne and Mougin, 1976; Taylor, 1979a; Cook and Yalden, 1980; van Aarde, 1980; Brothers and Copson, 1988; Chapuis, 1995a,b).

Another effect rabbits may have on indigenous prey is through a process that has been called hyperpredation (Smith and Quin, 1996), which is close to "apparent competition" as described by Holt (1977). This process predicts that an introduced prey species, well adapted to high predation pressure, could induce the extinction of an indigenous prey, by increasing population size of a shared predator. This is the mechanism suspected to have caused the extinction of the Macquarie parakeet *Cyanoramphus novaezelandiae erythrotis* (Taylor, 1979b).

We have previously demonstrated in theory the existence of this process (Courchamp et al., unpublished). We argue here that introduced prey should be controlled when a predator has been introduced, in order to prevent such a predator population increase, even when no direct effect is visible. In addition, removing an introduced predator population without controlling the introduced prey may be difficult to achieve, since they constitute a constant source of food to the predator. Even if it is was not difficult, it would not be a good solution, because removing the predation pressure would increase the difficulties of later coping with introduced prey, which are often characterised by high reproductive rates. On the other hand, controlling the introduced prey only is not satisfactory in the long term, because predators have a strong direct negative effect on the indigenous prey and should eventually be removed. In this work, we focus on the control strategies in islands where both a predator and its prey grazer have been introduced. Although many field conservationists are now aware of the existence of such complex relationships, theoretical demonstration and characterisation is still lacking. We believe that not only could the cost of eradication programs be substantially decreased by conducting control of both introduced species simultaneously, but also that it would be a more efficient method.

2. Methods

We constructed a mathematical model that features the interactions of three populations: indigenous prey, introduced prey and introduced predator (Fig. 1), which, for the sake of simplicity, we call bird, rabbit and cat, respectively. The dynamic of each population is modelled by a logistic equation linked to the others by simple parameters. We did not take potential population cycles into account, since this is not observed in all islands, would make the model analysis too complex, and would not change its main conclusions. The number of individuals at time t in the bird, rabbit and cat populations are B, R and C, respectively, and the intrinsic growth rates are r_b, r_r and r_c, respectively. The predation rate is μ_b on the bird population and μ_r on the rabbit population. The carrying capacity of the environment for the bird population is K_b and the carrying capacity of the environment for the rabbit is K_r. We chose to give the carrying capacity of the habitat for the predator the value of the maximum number of predators that can be fed by the ecosystem. This corresponds

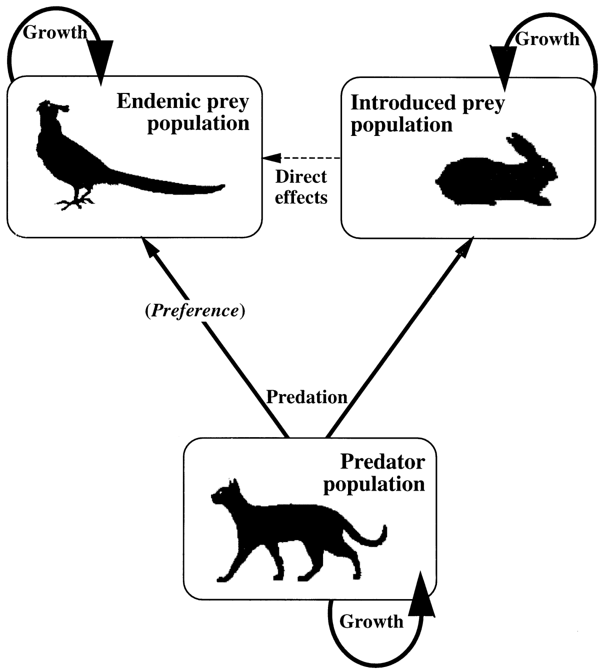

Fig. 1. Compartmental representation of the mathematical model. Each box represents a species population: the endemic prey (bird), the introduced prey (rabbit) and the introduced predator (cat). The arrows represent the flux within or between populations: the curved arrows represent the growth of each population and the straight arrows represent the predation on a population. The dashed arrow represents the direct effects of rabbits on birds, and is set to zero in this work.

to the number of prey at time t, divided by the predation rate. The carrying capacity of the cat is thus

$$\frac{B}{\mu_b}+\frac{R}{\mu_r},\ \text{i.e.}\ \frac{(\mu_r B+\mu_b R)}{\mu_b\mu_r}.$$

Domestic cats are known to prey on different species accordingly to their availability (Fitzgerald, 1988). We therefore take into account the proportion of each prey species, $\frac{B}{B+R}$ and $\frac{R}{B+R}$, in the predation term. Finally, given equal availability, the cat will select the indigenous prey (bird) over the introduced prey (rabbit), because the native species are not adapted to this predation (e.g. lack of dissimulation and escape). This preference is given by α, the bird/rabbit ratio in the diet of cats (the predator will prey upon the bird α times more often than on the rabbit). The predation terms are thus given by $\frac{\alpha B}{\alpha B+R}\mu_b C$ and $\frac{R}{\alpha B+R}\mu_r C$ on the bird and rabbit, respectively. We assume that the rabbit induces a decrease of the bird population at a rate η (for all the causes cited in introduction), without suffering a reciprocal effect. In this paper, this parameter η will be set to 0 to account for cases where introduced prey have no direct effect on indigenous prey. This allows the study of only indirect effect (hyperpredation) of introduced prey on indigenous prey. We chose to keep the parameter in the model so that direct effects of rabbits can easily be deduced from this study. We model the control effort by introducing in the model separates terms for controlling rabbits, λ_r, and cats, λ_c. Setting one of these to 0, allows for the strategy where there is control of the other species only.

So, we have the following system:

$$\begin{cases}\text{Rate of change of birds} = \text{natural growth of birds}\\ \qquad - \text{direct effect of rabbit}\\ \qquad - \text{predation of cats}\\ \text{Rate of change of rabbits} = \text{natural growth of rabbits}\\ \qquad - \text{predation of cats}\\ \qquad - \text{control of rabbits}\\ \text{Rate of change of cats} = \text{natural growth of cats}\\ \qquad \text{(which depends on prey populations)}\\ \qquad - \text{control of cats}\end{cases}$$

which mathematically may translate to:

$$\begin{cases}\frac{dB}{dt}=r_bB\left(1-\frac{B}{K_b}\right)-\eta_bBR-\frac{\alpha B}{\alpha B+R}\mu_bC & (1)\\ \frac{dR}{dt}=r_rR\left(1-\frac{R}{K_r}\right)-\frac{R}{\alpha B+R}\mu_rC-\lambda_rR & (2)\\ \frac{dC}{dt}=r_cC\left(1-\frac{\mu_b\mu_rC}{\mu_rB+\mu_bR}\right)-\lambda_cC & (3)\end{cases}$$

3. Results

Seven different equilibrium points are possible, all of which are found by the mathematical model. (1) First, all populations become extinct. This may be the case when insufficiently controlled cats eliminate both prey populations, and then naturally die out. (2) Both the introduced prey and predator populations may be destroyed by the combined effects of cat predation on rabbits, and human control. The bird population will then completely recover, reaching the carrying capacity of its habitat. This equilibrium will arise if controls on cats and on rabbits are sufficient (for each point, conditions are given according to the level of cat control and of rabbit control, in the Appendix). (3) Only the rabbit population survives if the control of cats is too low to prevent eradication of the bird, but is high enough subsequently to eradicate the cat population. The equilibrium point where only the cat population survives does not exist since cats need prey to subsist. (4) Only the predator population may be destroyed by the combined effects of reduction of the introduced prey numbers and human control. In this case, both the bird and the rabbit populations survive. It is noteworthy that the conditions for cat eradication imply a control of the rabbit as well (see Appendix). Indeed, this point is reached if control of cats, but also of rabbits, is sufficiently high. (5) The rabbit population only may be destroyed by the combined effects of cat predation and human control if control of rabbits is sufficiently high but control of cats is not. (6) Only the bird population disappears, destroyed by both an increased number of rabbits and an increased predation pressure of cats. This happens if the control of neither cats nor rabbits is sufficiently high and is the worst situation: the full failure of the eradication programme, with extinction of the indigenous prey. (7) Finally, all three populations survive and reach a stable equilibrium

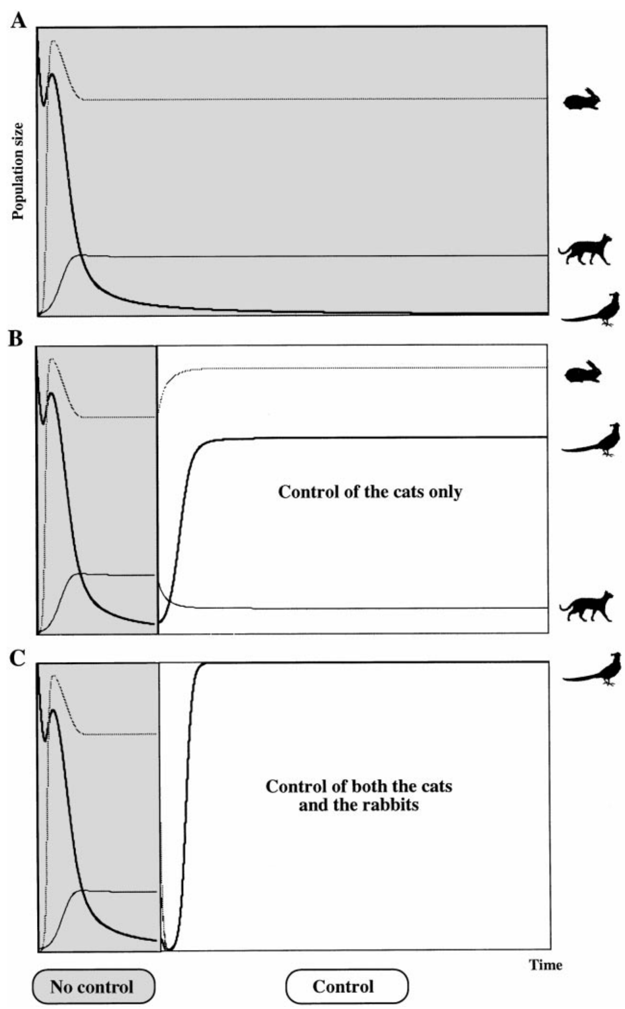

Fig. 2. Model simulations given different control strategies. Population numbers vs time, (A) when there is no control, (B) control of cats only or (C) simultaneous control of both rabbits and cats. When there is no control (shaded area), the bird population goes extinct. If control of cat (B, white area) is started 20 years after introduction of cats and rabbits, both prey (birds and rabbits) partially recover. When rabbits are also controlled (C, white area) and cat control is the same as in B, then the extinction of the rabbit leads the cat population to extinction, allowing the total recovery of the bird population. For the sake of clarity, the scale is different for all three populations: the maximum population size is set to 1000 for birds, 100 for cats and 10 000 for rabbits; initial conditions are 1000 birds, introduction of 1 cat and 10 rabbits. The intrinsic growth rate of the cats and rabbits are $r_c = 0.75$ and $r_r = 4$, the control efforts are $\lambda_c = 0.56$ and $\lambda_r = 3$; the predation rate of the cat is $\mu_r = \mu_b = 365$ (one prey per day); the cat selection of birds over rabbits, $\alpha = 1.5$ (given equal availability, the cat will kill birds 1.5 times more often than rabbits).

point, if controls are insufficient, and the bird population parameters are high enough to cope with cat predation exacerbated by rabbit presence. An analysis of this bird–rabbit–cat system with control is detailed in the Appendix, and the analysis of a similar system without control is described elsewhere (Courchamp et al., unpublished).

Fig. 2 shows the effect of the control of the introduced predator only (2B) and of both introduced species (2C), by comparison with the case when there is no control at all (cats are at their maximum, 2A). This figure illustrates how control of rabbit can facilitate the eradication of cats. When no control is undertaken (shaded areas in A, B and C), the cat population, mainly because of rabbit presence, stays large and can eliminate the birds in the long term (2A). Parts B and C of Fig. 2 illustrate the start of control programs after 20 years of uncontrolled presence of cats and rabbits. Parameters are tuned for a high growth rate for both introduced populations, high predation rate, and high preference for birds over rabbits. Provided the effort is sufficient, control programs (white areas in B and C) can save the bird population, even when the situation has become critical and parameters are largely unfavourable to birds, as simulated here. When cats only are controlled, the presence of rabbits precludes cat eradication (2B), and the bird population recovery is only partial. In contrast, for the same cat control effort, eradication of rabbits allows eradication of cats, and total recovery of birds (2C), after a slight decrease (see Discussion).

The importance of taking into account the introduced prey is further shown by the fact that the extinction of the indigenous species (bird) occurs if the control efforts are below a value linked with the intrinsic growth rates of both introduced species (see Appendix). Actually, if the control of introduced prey is not sufficient, the indigenous prey will be destroyed, even if the predator population is being controlled. This is illustrated in Fig. 3, where different efforts of cat control cannot prevent bird extinction in the absence of rabbit control (3A), whereas the same cat control efforts can save the bird population if rabbits are also controlled (3B). In these simulations, the level of cat control was lower than the simulation in Fig. 2. This reflects the case when the island situation prevents a high predator control effort (e.g. accessibility or financial problems). Under these conditions, even a relatively low cat control effort may be sufficient to save the bird population if rabbits are also controlled. We emphasise the fact that, in the model, the rabbit has no direct effect on the bird. It only allows an increase of their mutual predator, which is deleterious for the bird.

4. Discussion

The aim of this three-species model was to assess the impact of the introduction of both a prey and a predator in an insular ecosystem (Courchamp et al., unpublished), together with the implications of control strategies on the population of an indigenous prey species. We used domestic cats and rabbits as examples of the introduced predator and prey, and birds as an example of an indigenous prey, since these species account for most real cases. Most conclusions of this work are also valid for rodents as introduced prey, since they can induce hyperpredation. However, since they are also important predators, control strategies must also take mesopredator release into account in the case of simultaneous presence of cats and rodents (Courchamp et al., 1999). Whenever cats, rabbits and rats have all been introduced (which we did not try to model here), all three species should be removed concurrently, but control of rats should be high enough to prevent their increase following control of cats. In the present case, the presence of the introduced predator is directly deleterious to the indigenous prey, and the presence of the introduced prey induces an increase of the predator population, thus exacerbating the predation pressure on the indigenous prey. We took into account the control effort of both introduced species.

Although biologically simple, the model shows a relatively high mathematical complexity. Therefore, the aim of this model was not to provide precise values of control measures in the field. This would not be possible accurately, since the values for the parameters used in the model (which are basic ecological parameters) are often unknown or only roughly estimated from the field. Neither the nature of the model, nor the state of current knowledge in the field would allow such value with precision. The aim of this exercise was rather to emphasise the link between control effort and the life-history parameters of both introduced species. We aimed to demonstrate unambiguously that, even if it is difficult to achieve in the field, the concurrent control of both introduced species is clearly the best strategy for maximum recovery of indigenous species. Increasingly, such theoretical demonstrations may be required by management agencies before control programs will be launched.

The higher efficiency of dual control is not due to direct effects of rabbits on birds (habitat destruction and competition for food and shelter), since they are not taken into account here. Nor is the predicted success of dual control due to the preference of the predator since this preference is set in favour of the indigenous prey in the model. This success is due to the hyperpredation process, where introduction of a prey induces an increase of the introduced predator beyond a level that can be sustained by an ill-adapted indigenous prey. Because the birds can only sustain a low predation pressure, controlling rabbits causes the cat population to drop to lower levels than when rabbits are uncontrolled.

Concurrent control would, of course, also have the major advantage of greatly reducing rabbit numbers, thereby lowering their impact on vegetation and associated animal species, as well as decreasing their direct impact on birds. We have not simulated the direct impact of rabbits on birds, although we have incorporated this possibility in the model (direct impacts of rabbits can be studied from the results of this study by giving a positive value to this parameter; e.g. the presence of ten rabbits induce the direct death of two birds each year, $\eta = 0.2$). In addition to being more efficient for cat control, starting both control programs together would also result in advantages due to synergetic effects: costs may be reduced (if costs related to transportation, or hunting and trapping can be shared by the two programs) and efficiency might be increased (e.g. through the additive effects of primary and secondary poisoning of predators, Rammel et al., 1984; Flux, 1993; Robertson et al., 1994).

The simulations in Fig. 2 have been tuned to illustrate an extreme situation: cat and rabbit population parameters extremely unfavourable for the bird, and start of control programs when the bird population is dangerously low. Under these conditions, it is noteworthy that the bird population could undergo a period of time dangerously close to extinction after control of both cats and rabbits is started. This is due to the fact that when the rabbit population decreases suddenly, cats may prey more heavily on the birds (prey-switching by hungry cats). This demonstrates, first, that the control programs should not be delayed until the bird population is critically endangered (< 40 individuals in the simulation). Secondly, the control of rabbits may have to be staggered with that of cats to allow birds to recover after release from predation pressure (as shown Fig. 3B). It should, however, not be delayed too much because an increase of the rabbit population, due to the release from cat predation, is likely to follow rapidly. Unfortunately, the model cannot in its present state provide values of timing for control measures; these should be estimated by field workers from the empirical knowledge they have of the island(s) where they work. The timing of such measures will probably be among most difficult factors for concurrent control, but the last decade has been characterised by major progress in control methods for alien species, which is encouraging for the future.

Despite the generalised concurrent presence of both introduced predators and prey, hyperpredation and similar processes have still rarely been studied. In addition to the extinction of the Macquarie parakeet, this process seems to be responsible for increased predation, for example, of cats on banded rails *Rallus philippensis*, (Taylor, 1979b), of skuas *Stercorarius skua* on petrels (Jones and Skira, 1979), and of kiore *Rattus exulans* on endemic lizards (MacCallum, 1986). The harm caused by introduced species on oceanic islands is widely known, and control programs are largely recognised as the best way to restore ecosystems (Atkinson, 1988). Eradication of rabbits has already been achieved in several islands

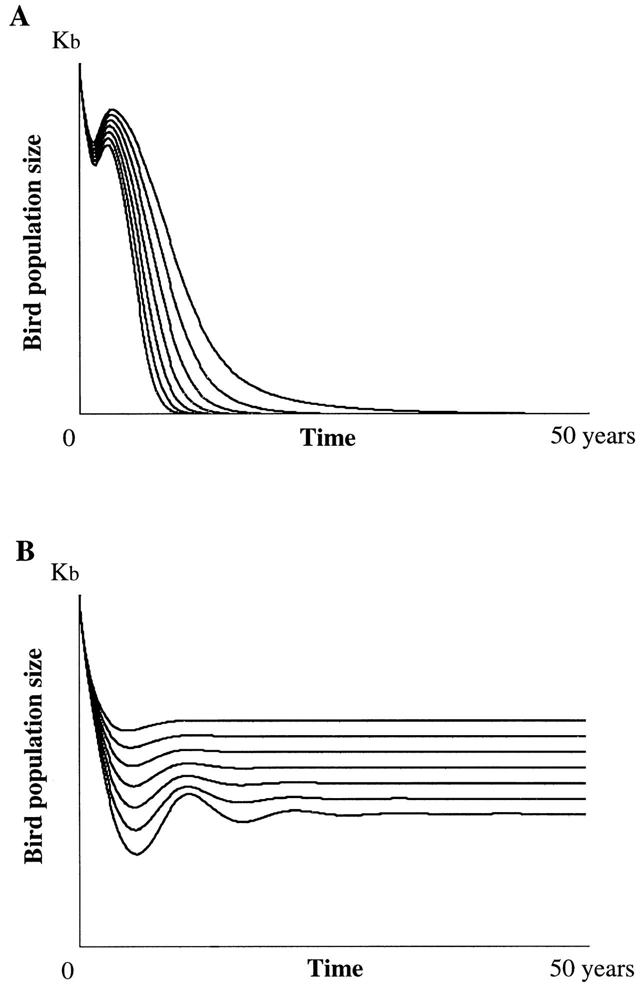

Fig. 3. Bird population dynamics for different values of the cat population control effort, λ_c from 0.05 to 0.35, (A) in absence of rabbit control and (B) in presence of rabbit control, $\lambda_r = 4$. The control of rabbits, although they have no direct effect on the bird population, allows the recovery of the bird population, when cat control alone is insufficient.

(Young, 1981; Merton, 1987; Flux, 1993; North et al., 1994; Chapuis, 1995b). Introduced domestic cats have also been the subject of many control attempts, and have been effectively removed from several islands (e.g. Rauzon, 1985; Veitch, 1985; Domm and Messersmith, 1990). However, despite its major importance, the concurrent control of both species is not always undertaken. We show here that species interactions should be taken into account in control program designs, since concurrent control of both these introduced species will often be the most efficient solution, and because control of the predator alone, which is less efficient, may fail to prevent extinction of endemic prey species.

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Appendix A.

All points represent the population sizes of the Bird, the Rabbit and the Cat, respectively.

1. $P0 = [0, 0, 0]$. Although ecologically correct, this point is not mathematically admissible, because setting both R and B to zero yields a null denominator.
2. $P1 = [K_b, 0, 0]$. This point exists if and only if: $\lambda_r > r_r$ and $\lambda_c > r_c$. This stationary point is not stable if the control efforts are null: if $\lambda_r = \lambda_c = 0$, which means that any change in the population numbers will lead to another stationary point.
3. $P2 = [0, K_r(1 - \frac{\lambda_r}{r_r}), 0]$. This point is admissible if and only if $\lambda_r < r_r$ and is stable if and only if $\lambda_c > r_c$ and $\lambda_r < r_r(\frac{r_b}{\eta_b K_r} - 1)$. Here again, this point is not stable if the control efforts are null.
4. $P3 = [K_b(1 - \frac{\eta \boldsymbol{b}}{r_b})K_r(1 - \frac{\lambda_r}{r_r}), K_r(1 - \frac{\lambda_r}{r_r}), 0]$. It is admissible if and only if $r_r > \lambda_r > r_r(1 - \frac{r_b}{\eta_b K_r})$. It is stable if $\lambda_c > r_c$. Again, this point is not stable if the control efforts are null. The above conditions show that these three points $P1$, $P2$ and $P3$ are mutually incompatible.
5. $P4 = [K_b(1 - \frac{r_c - \lambda_c}{r_c r_b}), 0, \frac{r_c - \lambda_c}{r_c \mu_b} B^*]$. This point exists if and only if $r_c > \lambda_c > r_c(1 - r_b)$, and is stable if and only if $\lambda_r > r_r - \frac{1}{\alpha}\frac{\mu_r}{\mu_b}\frac{r_c - \lambda_c}{r_c}$ and $\lambda_c > \frac{r_c(r_b + r_c - 2)}{r_c + 2}$.
6. $P5 = [0, K_r(1 - \frac{r_c - \lambda_c + r_c\lambda_r}{r_r r_c}), \frac{r_c - \lambda_c}{r_c \mu_r} R^*]$ is reached if: $\lambda_c < r_c$ and $\lambda_r < r_r - 1 + \frac{\lambda_c}{r_c}$. This point is stable if the two following conditions are true: $\lambda_r < \frac{(r_c - \lambda_c)(r_c - 2)}{r_c)}$ and $\lambda_r < r_r + \frac{\lambda_c}{r_c} - 1 - \frac{r_r}{\eta_b K_r}(r_b - \alpha\mu_b \frac{r_c - \lambda_c}{r_c \mu_r})$.
7. $P6 = [B6^*, R6^*, C6^*]$ is reached if none of the above conditions is fulfilled. The value of these equilibrium point is too complex to be given here, but the Mapple file is available upon request to the authors.

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