

Rabbits killing birds: modelling the hyperpredation process

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Summary

1. Introduced rabbits are known to have catastrophic effects on oceanic islands, either by direct destruction of the vegetative cover, or by the resulting disturbance of indigenous vertebrates.

2. Another dramatic effect, less well known, but potentially of major importance, is the hyperpredation process. This process, related to apparent competition, predicts that an introduced prey species, well adapted to high predation pressure, could induce the extinction of an indigenous prey, through the sudden increased population size of an introduced predator. In many island ecosystems, the simultaneous presence of introduced feral cats and rabbits is thus potentially a further threat for small vertebrates endemic of these islands.

3. Through a mathematical model, we tested this hypothesis, using a tri-trophic system comprising an indigenous prey (birds), an introduced prey (rabbits) and an introduced predator (cats), and we demonstrated the theoretical existence of the hyperpredation process.

4. In addition, the numerical analysis of the model allowed a quantification of this process. It shows that the conditions required for an indigenous species to cope with the hyperpredation process imply very high intrinsic growth rates and/or carrying capacity, as well as behavioural anti-predator response to the introduced predator. Since these conditions are unlikely to be met, this process is a further potential threat to most indigenous vertebrate prey.

5. Finally, our model shows that, although it can be induced by both types of adaptation together or alone, behavioural adaptations alone are more powerful in generating the hyperpredation process, than are life history traits adaptations.

Key-words: apparent competition, bird extinction, feral cats, introduced mammals, mathematical model.

Journal of Animal Ecology (2000) **69**, 154–164

Introduction

Recent history has shown that oceanic insular ecosystems are particularly sensitive to human induced disturbances. Among these, successful introduction of alien species is a major cause of ecosystem perturbation (Lever 1994; Williamson 1996). Successful introductions often involve highly adaptable species (e.g. Lésel 1968; Apps 1986; van Aarde 1986; Flux

1993). In addition, these species often find exceptionally good conditions in these islands. Having not co-evolved with the introduced species, indigenous species constitute inefficient competitors or predators (Holdgate & Wace 1961; van Aarde & Skinner 1981). In addition, introduced species generally encounter only a small subset of pathogens or parasites (which species are, in general, less virulent than on the mainland; Dobson 1988), but plenty of non-adapted food for grazers and predators (Moors & Atkinson 1984; Atkinson 1985; Burger & Gochfeld 1994). In many cases, the outcome of these successful introductions is the dramatic

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decline, sometimes to complete extinction, of indigenous prey or competitors.

Extinction of many plant and animal species provides direct examples of the detrimental effect of species introductions. The most obvious examples are provided by predators, among which carnivores have played a major role (Boitani 1999). For example, domestic cats, *Felis catus*, L., have been, accidentally or on purpose, introduced to many oceanic islands, and are the direct cause of decline of numerous land and seabird species (Atkinson 1989; Lever 1994; Dickman 1996). Similarly, of Guam's 11 native forest birds extant at the time of introduction of the brown tree snake (*Boiga irregularis*, Fitzinger), seven are now extinct and four critically endangered (Haig, Ballou & Derrickson 1990; Savidge 1987). This snake is also suspected to be a major factor in the possible extirpation of at least three species of skinks and two geckos (Case, Bolger & Richman 1992). In fact, this snake may now have been introduced to several nearby islands and represents the most serious threat to all species of birds, lizards and small mammals of Micronesia (Reichel 1991). Introduced predatory snails, together with introduced rats (*Rattus* sp., F.), are believed to be responsible for the decimation of at least 20 species of Hawaiian tree snails (Hadfield, Miller & Carwile 1993). Examples for extinction through competition by introduced alien species, be it invertebrates, reptiles, birds or small mammals are also numerous (Brosset 1963; Atkinson 1985; Moulton & Pimm 1986; Bolger 1991).

One of the most documented introduced mammal species, often referred to for its dramatic impact on endemic plant species, is the rabbit (*Oryctolagus cuniculus*, Lilljeborg). Rabbits have been introduced (most of the time voluntarily) to more than 800 oceanic islands so far (Flux & Fullagar 1992). Rabbits have a high ecological adaptability and introductions easily succeed (Flux 1993). They can adapt to harsh conditions, eat a wide range of plant species and have an exceptional growth rate for their body weight (Smith & Quin 1996). The very rapid increase of their populations in ecosystems where indigenous grazer are, in general, much less numerous and competitive, leads to a dramatic impoverishment of the vegetation, both quantitatively and qualitatively (Costin & Moore 1960; Holdgate & Wace 1961; Norman 1967; Lésel 1968), and resulting severe impact on associated indigenous fauna. Because of this, rabbits are believed to have been directly responsible for the decline or extinction of several reptile and bird species (e.g. King 1985; North, Bullock & Dulloo 1994; Smith & Quin 1996).

Effects of rabbits on indigenous vertebrate species can be more complex. These mammals are indeed preyed upon by other introduced vertebrates, in par-

ticular by feral domestic cats. Cats are opportunistic predators, which switch prey according to their relative spatial and/or temporal availability (Fitzgerald 1988). When rabbits are abundant, domestic cats are known to prey largely upon them, whereas rabbits can constitute a smaller part of the cat diet when birds, reptiles or other mammals are relatively more abundant (e.g. Nogales *et al.* 1992; Dickman 1996; Nogales & Medina 1996). In several sub-Antarctic islands, 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 & Mougin 1976; Chapuis 1995a,b). A similar effect is documented on the spatial dimension: rabbits often enable cats to reach remote colonies or populations of indigenous prey in islands with heterogeneous indigenous prey distribution (Brothers & Copson 1988). In these cases, the presence of rabbits has an indirect effect on other prey species used by introduced cats.

A comparable process has occurred on Macquarie Island. On this island, predation by introduced cats caused the decline of burrow-nesting petrels (Brothers 1984), and the extinction of an endemic parakeet and a banded rail (Taylor 1979a). Cats were introduced to this island 60 years before the introduction of rabbits. However, the dramatic impact of cat predation on bird populations dates back to just 10 years following the introduction of rabbits (Taylor 1979a). The variation in numbers of these species is reproduced Fig. 1. There, rabbits are the main prey during winter months, when seabirds are absent from the island (Jones 1977; Brothers,

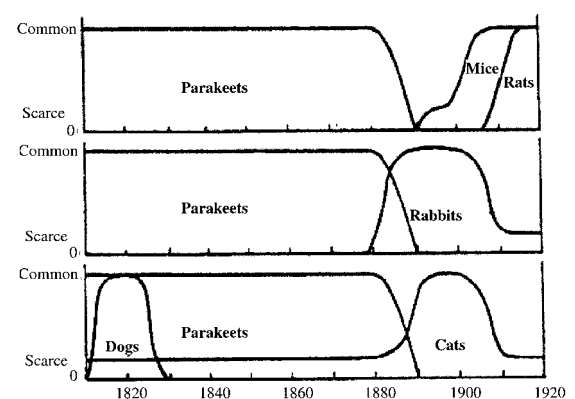


Fig. 1. Diagrammatic reconstruction of changes in numbers of parakeets, rats, mice, feral rabbits, feral dogs and feral cats on Macquarie Island 1810–1920. Modified from Taylor 1979a. Decrease in parakeet numbers coincides with increase of cat and rabbit numbers. It is likely that the increase of rabbit numbers induced the increase in the cat numbers, which in turn induced the decrease in parakeet numbers. No direct effect of rabbit on parakeet has been observed. Dogs and rodents do not seem to be involved in parakeet extinction.

Skira & Copson 1985). It is believed that the rabbit population allowed not only the maintenance of the cat population in winter, but also a significant increase, therefore resulting in increased predation pressure on the land bird species. No direct effect of the rabbit on the birds was observed and no correlated change seemed to be involved. Although it does not necessarily involve very high levels of predation (but rather 'higher than normal'), this process has been termed hyperpredation (Smith & Quin 1996), a term we will use throughout this work. This process is related to the more general 'apparent competition', already largely studied theoretically (e.g. Holt 1977; Abrams 1987; Abrams, Holt & Roth 1998), but which has received relatively little attention in conservation biology programmes. However, hyperpredation would be a rather restrictive case of apparent competition: it is a process occurring in specific conditions, when apparent competition is unlikely to occur, because two of the three species are not naturally in contact with the third. Two species (a prey and the predator) have to be introduced in a new ecosystem (e.g. an island) in order to encounter the indigenous prey, for this process to occur. It describes 'a sudden increase in the ratio of predators to indigenous prey [which] is not brought about by natural climatic phenomena, but by the introduction of an exotic prey with a greatly elevated reproductive rate [and with] ... no opportunity for populations to escape ...' (Smith & Quin 1996). Moreover, unlike pure apparent competition, as defined by Holt (1977, 1984), hyperpredation is unilateral (or amensal, Bonsall & Hassell 1998): even if the introduced prey population might be slightly reduced by the presence of the indigenous prey, the process can be regarded as one-sided, in favour of the indigenous prey. For all these reasons, hyperpredation is more specific to closed ecosystems, such as oceanic islands. In an eloquent discussion of the causes of Australian rodent extinction, Smith & Quin (1996) discussed the characteristics of a prey species, such as the rabbit, which can induce the 'hyperpredatory extinction' of an indigenous prey. It is assumed that life history traits and behaviour of this introduced prey make it resistant to high levels of predation. A highly superior reproductive rate, high density and efficient anti-predator responses (which are often lacking in the indigenous species) could confer on the introduced prey a possibility to induce an increase of the predator without suffering too much from it. The lack of serious competitors and often few parasites in these introduced prey, can also increase their potential for dramatic increase. These features imply a possibility to sustain high predation pressure, as cats are supposed to remove only the reproductive surplus (dispersing young, sick and dead, Smith & Quin 1996). The resulting increased population of predators cannot,

however, be sustained by the indigenous prey species, which has inferior (less well adapted) reproductive and anti-predator characteristics compared with the introduced prey species. The conjunction of a low adaptation to predation and an artificially high predation pressure can lead to dramatic indigenous prey population decrease, up to total extirpation.

This particular hypothetical process has been described on several insular ecosystems subject to introductions, but has neither been the object of documented field studies nor of theoretical investigation. Furthermore, there is so far no indication of which, if any, of the two kinds of anti-predation adaptation, life-history traits vs. behaviour, would be predominantly responsible for this process. As recently concluded by Caughley & Gunn (1996): 'The trajectory of a declining population and its demographic components are rarely described, and, as well as data, we lack theories with which to predict and test ideas about how species decline'. In this work, we test, qualify and quantify the hyperpredation process, through a mathematical model coupling the population dynamics of an indigenous prey, an introduced prey and a predator, in the context of island ecosystem conservation biology.

The model

TWO-SPECIES MODEL

In order to present heuristically the hyperpredation model, we first present a two-species model. In a further step, the three species are considered together by modifying this two-species model. This also allows comparisons of the effects of one or both introduced species, and will be used to quantify the hyperpredation process (see below).

The models are deterministic coupled differential equations based on the classical Lotka–Volterra predation model. Each prey population is described by a simple logistic equation, modified to take into account its relationship with the other species. For heuristic purposes, we will often refer to the indigenous prey population as the bird population (although it can also be a reptile species for example), to the introduced prey population as the rabbit population (although rodents can play a similar role) and to the predator population as the cat population (mongooses *Herpestes* sp., Illiger or wekas *Gallirallus australis* Grey, for example, could be used instead). When the term 'prey' only is used, it refers indiscriminately to either the bird or to the rabbit.

The number of individuals at time t in the bird, rabbit and cat populations are B , R and C , respectively. The intrinsic growth rates of the bird and the rabbit populations are r_b and r_r , respectively. In order to study hyperpredation only, we do not consider potential direct effects of the rabbit on the

birds. 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 . The rate at which eaten prey are turned into new predators is λ_b for birds and λ_r for rabbits, and v is the predator mortality rate. The model bird–cat and rabbit–cat are the same, so that we will treat only the bird–cat model.

$$\begin{cases} \frac{dB}{dt} = r_b B \left(1 - \frac{B}{K_b}\right) - \mu_b CB \\ \frac{dC}{dt} = \lambda_b \mu_b BC - vC \end{cases} \quad \text{eqn 1}$$

This prey–predator model leads to three equilibrium points: extinction of both populations $[0, 0]$, of the predator only $[K_b, 0]$ or stable coexistence of both populations

$$\left[\frac{v}{\lambda_b \mu_b}, \frac{r_b (K_b \lambda_b \mu_b - v)}{K_b \lambda_b \mu_b^2} \right]$$

This last point is admissible and stable if $K_b \lambda_b \mu_b > v$.

THREE-SPECIES MODEL

The complete hyperpredation model easily arises from this system. The main change is in the formulation of the predation rates and of the growth rate of the predator, which now take into account the presence of both prey simultaneously. Since we have two species of prey, with different predation rates, and since the cat adjusts its predation pressure accordingly to the relative numbers of birds and rabbits, instead of $\mu_b C$ and $\mu_r C$, we chose the form $[B/(B + R)]\mu_b C$ and $[R/(B + R)]\mu_r C$ for the bird and the rabbit predation rates, respectively, so that the predation rate is still function of the availability of the prey but now varies with prey relative proportions. The adaptation of the introduced prey in terms of an anti-predator behavioural response is given by a preference of the predator for the indigenous prey (which is more easily detected and/or caught) over the introduced prey. This preference is a ratio, α , with a simple biological meaning: given equal availability, the predator will prey upon the indigenous prey α times more often than on the introduced prey. We assume that $\alpha \geq 1$, and that one rabbit and one bird prey items are energetically equally valuable to the cat. The predation terms are now given by $[\alpha B/(\alpha B + R)]\mu_b C$ and $[R/(\alpha B + R)]\mu_r C$ on the indigenous and introduced prey, respectively. This change is reflected in a similar way in the predator growth rate: $\lambda_b B[\alpha B/(\alpha B + R)]\mu_b C + \lambda_r R[R/(\alpha B + R)]\mu_r C$: it depends on both the numbers and

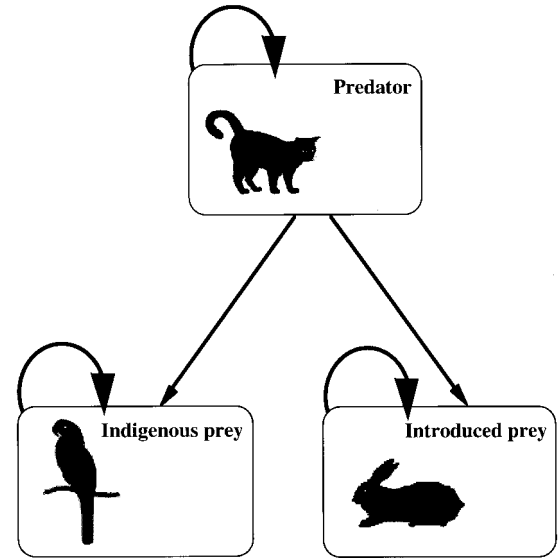


Fig. 2. Compartmental representation of the mathematical model. Each box represents a species population: the predator (cat), indigenous prey (bird) and the introduced prey (rabbit). The arrows represent the flux within or between populations. The curved arrows represent the intrinsic increase of each population (r_b , r_r). The straight black arrows represent the predation suffered by a population (μ_b , μ_r).

the proportion of prey. Figure 2 gives the compartmental representation of the three-species system described by the model.

We have now the following system:

$$\begin{cases} \frac{dB}{dt} = r_b B \left(1 - \frac{B}{K_b}\right) - \frac{\alpha B}{\alpha B + R} \mu_b CB \\ \frac{dR}{dt} = r_r R \left(1 - \frac{R}{K_r}\right) - \frac{R}{\alpha B + R} \mu_r CR \\ \frac{dC}{dt} = \frac{\lambda_b \mu_b \alpha B^2 + \lambda_r \mu_r R^2}{\alpha B + R} C - vC \end{cases} \quad \text{eqn 2}$$

Biologically, several different outcomes may arise from this system. The first of them is the extinction of the three populations (P0). Two others are the extinction of both the rabbit and the cat populations, the bird population reaching its carrying capacity in the absence of alien populations (P1), or the extinction of both the bird and the cat populations, the rabbit reaching its carrying capacity (P2). Three other possibilities involve the disappearance of the cat only (P3), of the bird only (P4) or of the rabbit only (P5). The last one is the presence of all three species together (this can give 1 or 2 points, labelled P6 and P7 in the sequel).

The analysis of this system indicates that all these outcomes are found by the model (except P0, see below). The equilibrium value of the remaining populations are given below for the six different cases with at least one population going extinct:

$$P0 : \begin{cases} B_0^* = 0 \\ R_0^* = 0 \\ C_0^* = 0 \end{cases} \quad P1 : \begin{cases} B_1^* = K_b \\ R_1^* = 0 \\ C_1^* = 0 \end{cases}$$

$$P2 : \begin{cases} B_2^* = 0 \\ R_2^* = K_r \\ C_2^* = 0 \end{cases} \quad P3 : \begin{cases} B_3^* = K_b \\ R_3^* = K_r \\ C_3^* = 0 \end{cases}$$

$$P4 : \begin{cases} B_4^* = 0 \\ R_4^* = \frac{v}{\lambda_r \mu_r} \\ C_4^* = \frac{v r_r (K_r \lambda_r \mu_r - v)}{K_r \lambda_r^2 \mu_r^3} \end{cases}$$

$$P5 : \begin{cases} B_5^* = \frac{v}{\lambda_b \mu_b} \\ R_5^* = 0 \\ C_5^* = \frac{v r_r (K_b \lambda_b \mu_b - v)}{K_b \lambda_b^2 \mu_b^3} \end{cases}$$

The expression for P6 and P7, which represents the points where all three populations are in equilibrium, depends on a complex fashion on the solutions of a quadratic equation whose coefficients are functions of the population dynamics parameters. Their explicit expression is too involved to be presented here, but a Maple file is available upon request. Since the deterministic nature of this model allows a numerical analysis, it will be substituted for the analytical study of this point. In addition to being heuristically clearer, this will allow us a quantification of the hyperpredation process (see below). Although it is ecologically correct, the point P0 is not mathematically admissible, because of a null divider (the case is, however, encountered in the simulations). The points P0, P1 and P2 are not stable (which means that new introductions will lead to other equilibrium points). The point P3 is always admissible; it is stable when

$$v > \frac{\lambda_b \mu_b \alpha K_b^2 + \lambda_r \mu_r K_b^2}{\alpha K_b + K_r},$$

that is when cat mortality rate is not compensated by the predation on the two prey population at their maximum size. P4 exists and is stable if

$$r_b < \frac{\alpha \mu_b r_r (K_r \lambda_r \mu_r - v)}{\mu_r^2 K_r \lambda_r}$$

and

$$v < K_r \lambda_r \mu_r < 2v.$$

P5 exists and is stable iff

$$r_r < \frac{\mu_r r_b (K_b \lambda_b \mu_b - v)}{\mu_b^2 K_b \lambda_b \alpha}$$

and

$$v < K_b \lambda_b \mu_b < 2v.$$

Numerically, at most, one stable equilibrium point with persistence of the three populations was found, so that whenever two exist simultaneously one of them is unstable; we shall denote this stable point P6 in the sequel.

Figure 3 shows some typical results of simulations of the two- and three-species models. The passage from the two- to the three-species model illustrates the effect of prey introduction on the prey-predator system: the predator population increases, and as a result, the indigenous prey disappears.

Results

EVIDENCE FOR THE HYPERPREDATION PROCESS

The main aim of this work is to assess the effect of the introduced prey on the indigenous prey. The simplest way to study the hyperpredation process quantitatively is to compare the value of the indigenous prey population at equilibrium (B^*) under different ecological conditions: when the predator alone is present and when the introduced prey is also present. Point B_5^* of the full model gives the value of the bird population size at equilibrium in absence of rabbit and presence of cats. The point B_6^* represents the equilibrium value of the bird population when both rabbits and cats are present, corresponding to a stable equilibrium point P6. The value of the ratio B_6^*/B_5^* thus illustrates the decrease induced on the indigenous prey (bird), by the presence of the introduced prey (rabbit) when a generalist predator (cat) is introduced. If this value is lower than one, then the hyperpredation process exists. We present this ratio Fig. 4, as a function of the bird life history traits (r_b and K_b), to allow a comparison between bird species types. This shows that, according to the values of the parameters, the indirect effect of the introduced prey may be very important, since through hyperpredation it can induce its complete extinction. The effect of hyperpredation is the strongest for species with low intrinsic growth rate and with low environmental carrying capacity. It can also be seen from Fig. 4 that in presence of a two-fold preference of the cat for the bird over the rabbit, this ratio does not exist (i.e. the bird goes extinct) for species with an intrinsic growth rate of less than $\approx 400\%$. If α is set to as low as 1, then the bird extinction occurs if its intrinsic growth rate is lower than that of the rabbit (see also Fig. 5A). Since such high intrinsic growth rates cannot realistically be attributed to island endemic birds, the hyperpredation process is likely to have a major influence in islands where both predators and their prey have been introduced.

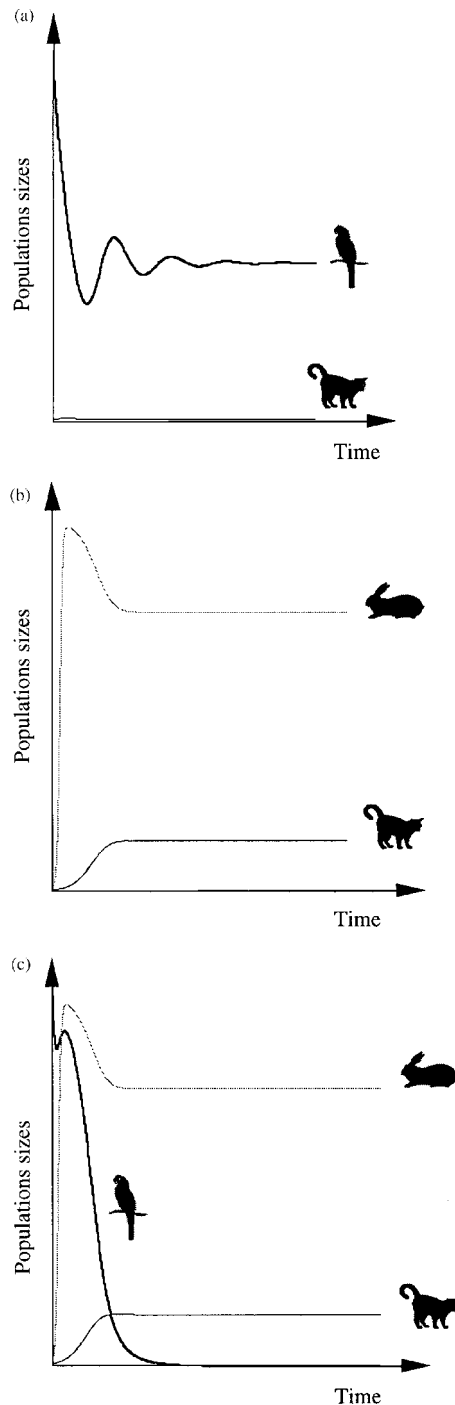


Fig. 3. Simulations of two of the two-species models (a) bird–cat, and (b) rabbit–cat, and of the three species model (c) bird–rabbit–cat: evolution of the size of the populations with time. The simulations show that, taken two by two, the rabbit population allows a much higher cat population than does the bird population. The presence of an introduced prey in a system with indigenous prey and introduced predator induces an important increase of the predator population, and the extinction of the indigenous prey population. The scale is different for predator and prey populations.

CHARACTERIZATION OF THE HYPERPREDATION PROCESS

The assumptions found in the literature (Smith & Quin 1996) are that the predator increase is due to a better resistance of the introduced prey to high predation pressure based on two mechanisms: life-history traits (e.g. high reproductive potential) and behaviour (low detectability, high escape efficiency). Our model allows us to test the role of each of these two kinds of anti-predator adaptation. Life history traits are given by the intrinsic growth rate of the indigenous prey r_b , and its carrying capacity K_b , whereas behavioural response is reflected by the ratio of anti-predator response efficiency α (which depends on prey dissimulation and escape response). By varying these two sets of parameters, one can determine the effect of each on the outcome of the system. This can be visualized as the fraction of the indigenous prey population that would be removed as a result of hyperpredation (the ratio B^*_6/B^*_5), as a function of these parameters. Figure 5A shows this ratio as a function of α and r_b , which allows a comparison of the relative influence of these two parameters on the strength of the hyperpredation process (in percentage). This figure shows that high values of r_b lessen this process, but only for low values of α . Higher values of the preference of the cat for the bird over the rabbit imply increasingly unrealistically high values of the bird intrinsic growth rate for it to avoid extinction. Similarly, Fig. 5B shows that high values of K_b decrease the amplitude of the hyperpredation process, but only for low values of α . All other things being equal, if the preference of the cat for the bird over the rabbit is more than 1.5, then the bird becomes extinct whatever its carrying capacity. We conclude that the hyperpredation process is due to a combination of well adapted life history traits and efficient behavioural response of prey, but that the ‘better-adapted’ behavioural response may have more importance than ‘better-adapted’ life history traits.

Discussion

In this paper, we have studied the indirect effect of an introduced prey species on an indigenous prey species, through a population of introduced predators, a mechanism which has been termed hyperpredation (Smith & Quin 1996). We used the rabbit, feral cat and indigenous bird species as examples. We have shown with a mathematical model, that the introduction of a more adapted prey species could lead to the decline, up to extinction, of an ill-adapted indigenous prey species, through an introduced generalist predator. The model confirms the detrimental effect of the rabbit presence, even in absence of direct effects (taking into account direct effects would worsen the fate of the indigenous

Ratio of bird population size in absence of rabbit over its size in presence of rabbits

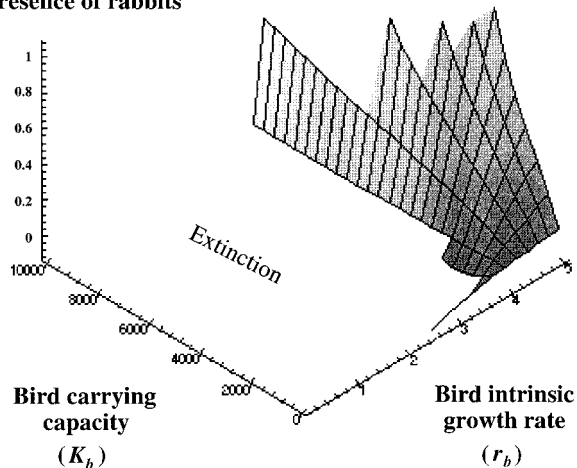


Fig. 4. Quantitative representation of the hyperpredation process: value of the ratio of the bird population size when only the cats are present vs. when both rabbits and cats are present (vertical axis, in percentage), for different values of the indigenous species life history traits: K_b (carrying capacity of the habitat) and r_b (intrinsic growth rate). Values used for these graphs are: $\lambda_b = \lambda_r = 0.01$; $\mu_b = \mu_r = 0.1$; $K_r = 10000$; $r_r = 2$; $\nu = 0.5$; $\alpha = 2$.

prey). With this model, we were also able to quantify this process and to predict that it can cause a very important decrease of the indigenous prey population. Most indigenous species able to cope with introduced predators will not be able to withstand this predation if a prey species is also introduced, because of the hyperpredation process. The condition for them to resist this process implies very high intrinsic growth rates, a high carrying capacity (with density dependence, typical of colonial birds) and low preference of the predator over the introduced prey. This may not be realistic for endemic birds.

Moreover, this indirect effect depends more on the ratio of anti-predator response efficiency, than on the indigenous prey life history traits we studied, that is intrinsic growth rate and carrying capacity. However, this model remains biologically simple and effects of more pertinent life-history traits would be interesting to study. This means that if predators show a preference for the indigenous prey, for example, because it is easier to detect and/or capture, then the increase of the predator population induced by the introduced prey will lead to decline or even extinction of the indigenous prey. As indigenous prey have not co-evolved with mammalian predators, they often lack adequate anti-predator defences (e.g. Kepler 1967; Brooke 1995; Powlesland *et al.* 1995; Seto & Conant 1996), and the predator preference for naive indigenous vs. introduced prey species might be very high *in natura*. The model shows that very low values for this parameter (typically less than two-fold) are, however,

sufficient to induce the extinction. Anti-predator response might be the key factor for most endangered endemic small vertebrates (Bunin & Jamieson 1995). Since indigenous bird species generally show both moderate intrinsic growth rates and poor anti-predation responses, the hyperpredation process is likely to have a major impact in ecosystems where both predator and prey have been introduced. This process remains, however, to be tested experimentally.

Despite its ecological importance as an interesting concept, as well as a potentially threat for endemic species, the hyperpredation process has still received relatively little attention in conservation biology. For example, it has not been studied *per se* in these ecosystems and is not always taken into account in control programmes. Still, this is not due to an absence of awareness of its existence. A more general process, called 'apparent competition' has been largely studied theoretically (e.g. Holt 1977; Abrams 1987; review in Holt & Lawton 1994) or through laboratory experiments (e.g. Bonsall & Hassell 1998; see also Hudson & Greenman 1998). The hyperpredation process and similar ones has also received some attention in the field. On continental undisturbed ecosystems, Davis (1957) explored the role of a buffer (cat food) in the problem of predation, with the example of farm cats and rats infesting farms. The buffer has been shown to maintain the cat population during a period of scarcity (low population) of the rat. The conclusion of his work was that a buffer should be readily available at a time of scarcity of the main prey, so that the predator popula-

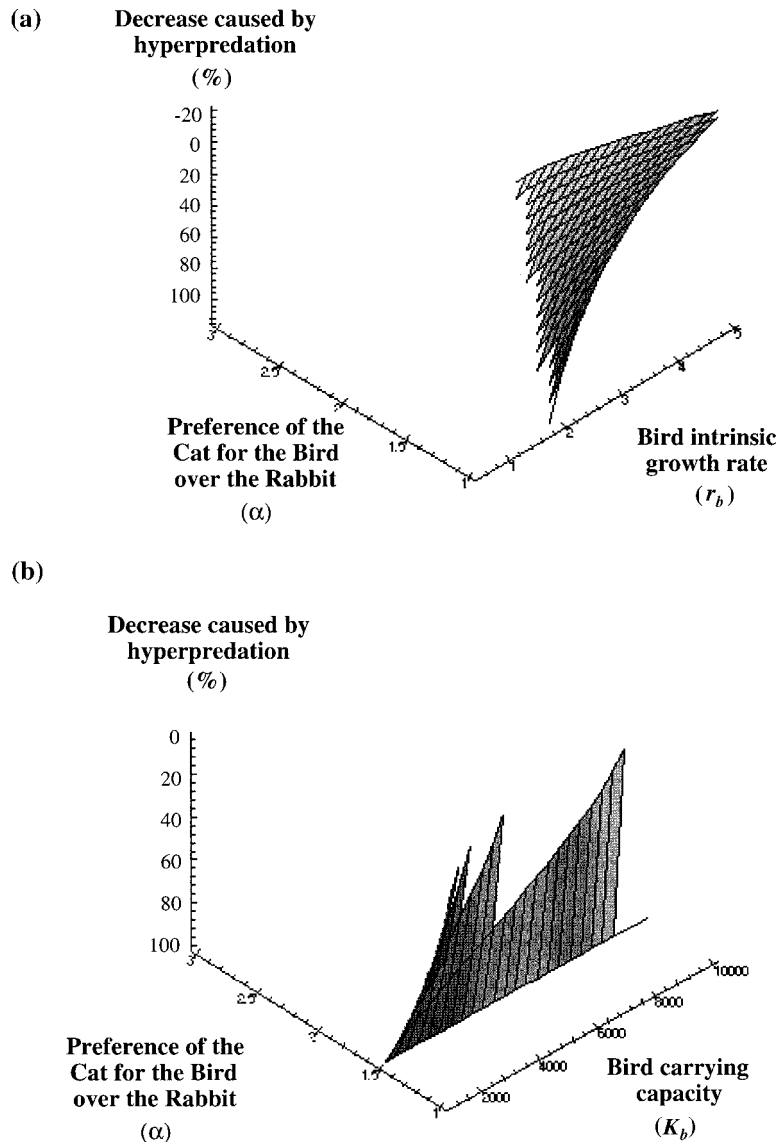


Fig. 5. Relative effects of the bird anti-predator behavioural response (preference of the cat for the bird over the rabbit: α) and the bird life history traits [(a) r_b , intrinsic growth rate; (b) K_b , carrying capacity] on the strength of the hyperpredation process. Missing values are due to complete extinction of the bird owing to hyperpredation. Values used for these graphs are the same than in Fig. 4. These graphs show that a better behavioural adaptation to predation (lower values of α) has a more dramatic effect on the strength of the hyperpredation process than does a better life history traits adaptation (higher values of K_b and r_b). For example, even in absence of preference from the cat, the bird population gets extinct if its intrinsic growth rate is not at least that of the rabbit ($\alpha = 1$, $r_b = 2$).

tion can be kept high. We can translate this to the present topic: in the islands under study here, a buffer (rabbit) should not be available so that the predator population has difficulty to maintain a high level. Pearson (1966) also found that the impact of feral cats on a vulnerable species was exaggerated if they had an alternative food when numbers of the preferred prey were low. Moreover, the hyperpredation process has been described in a few independent studies in different insular ecosystems. As in the cases of Macquarie, it is known that in Kerguelen, Raoul, Dassen, Marion, Deserta Grande and

Cochon islands among others, introduced mammals, such as rabbits, rats and mice (*Mus musculus*, L.), occupy a key position in food-webs as the main prey of cats in winter, allowing them to maintain high density during the absence of migrating birds (Derenne & Mouglin 1976; Taylor 1979b; Cook & Yalden 1980; van Aarde 1980; Brothers & Copson 1988; Chapuis 1995a). There are many cases where introduced prey constitute the main component of introduced cats' diet, threatened indigenous vertebrates being preyed upon to lesser extent (e.g. Dilks 1979; Karl & Best 1982; Konecny 1987; Nogales

et al. 1992). These relationships have been mostly observed in cat populations (Moors & Atkinson 1984), but also for other introduced predators, such as rats, mongooses or mustelids (Atkinson 1985). In the Mokohinau islands, it is seabirds, present for just a few months, which enable an increase of the kiore (*Rattus exulans*) population, but not rapidly enough to inflict massive predation when young seabirds are available. By the end of the nesting season, however, the kiore become sufficiently numerous to inflict increased predation on endemic lizards once the birds have fledged (MacCallum 1986). In this regard, rats can thus act as introduced predator, as well as introduced prey and, therefore, their effects on indigenous fauna can take several forms (see Courchamp, Langlais & Sugihara 1999a).

The countless direct and indirect ecological effects of introduced rabbits can be partly assessed by studying the changes occurring to ecosystems, following their decline or complete removal, by eradication programmes on small islands (Brothers & Copson 1988; Norman 1988; North *et al.* 1994), as well as biological control by myxomatosis in Europe and Australia (reviewed in Sumption & Flowerdew 1985). Most of the time, these effects are of primary importance, and eradication of introduced rabbits has been advocated for a long time (Norman 1967; Bullock 1977; North & Bullock 1986; Sanson & Dingwall 1995). Eradication has already been achieved in several islands (Young 1981; Merton 1987; Flux 1993; North *et al.* 1994; Chapuis 1995b). Current control or eradication programmes are currently being carried out on several islands of high conservation value. These programmes are unfortunately often very expensive and studies often must be conducted to prove that control of rabbits is warranted (Brothers & Copson 1988). Among the many reasons for the need for rabbit eradication, one should take into account the risk of maintaining or increasing the population size of alien predators, as one of the most devastating deleterious consequences of the presence of the introduced prey. A study of the efficiency of different control strategies (predator alone, introduced prey alone or both alien species simultaneously, with different degrees) is of importance in this context and is presented elsewhere (Courchamp, Langlais & Sugihara 1999b).

Insular ecosystems have a major importance in conservation biology, not only because they represent an important part of biodiversity (Olson 1989; Stone, Snell & Snell 1994), but also because they present many advantages for research. Among these advantages, their trophic webs are simpler when compared to most continental ecosystems (Holdgate & Wace 1961; Terborgh & Winter 1980; Bousset, Arthur & Chapuis 1988). This allows a better understanding of the ecological processes taking place in these systems. This also enables the testing of

hypotheses through mathematical modelling. Indeed, to be useful to the conservation biologist, models must remain mathematically simple, but also relatively realistic biologically, which is still possible in insular ecosystems. Here, we show that the hyperpredation process should be accounted for in conservation biology programmes, emphasizing that it is important to be aware of the possible indirect effect that may occur when manipulating predator-prey systems (Abrams 1987).

Acknowledgements

This work was supported by a Lavoisier fellowship from the French Foreign Office, by Biological Oceanography Grant ONR: N00014-95-1-0034, and endowment funds from the John Dove Isaacs Chair in Natural Philosophy, and was part of the IFRTP Program No. 279. We thank Susan Lingle, Bryan Grenfell, Tim Clutton-Brock, M. de L. Brooke, Bob Holt and an anonymous referee for their helpful comments on the manuscript. We are especially grateful to Bob Holt for several important suggestions leading to the current version of the mathematical model.

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Received 3 June 1998; revision received 27 April 1999