

Intraguild predation and mesopredator release effect on long-lived prey

James C. Russell^{a,*}, Vincent Lecomte^a, Yves Dumont^b, Matthieu Le Corre^a

^a ECOMAR, Université de la Réunion, 15 avenue René Cassin, Saint Denis, 97715, France

^b IREMA, Université de la Réunion, 15 avenue René Cassin, Saint Denis, 97715, France

ARTICLE INFO

Article history:

Received 28 October 2008

Received in revised form 15 January 2009

Accepted 25 January 2009

Available online 27 February 2009

Keywords:

Cats
Eradication
Island
Rats
Seabird

ABSTRACT

Complete extirpation of a species can generate cascading effects throughout an ecosystem, yet are precisely the goal of island eradications of pest species. “Mesopredator release effect”, an asymmetrical special case of intraguild predation, has been hypothesised as a possible indirect effect from eradications, where superpredator removal can generate a mesopredator increase which may increase the impact on their shared prey. Theoretically this suggests that for intraguild predators, the superpredator may protect the shared prey from mesopredation, and removal of superpredators alone is not recommended. We create a model of long-lived age-structured shared prey and explore the non-equilibrium dynamics of this system. The superpredator can impact all prey life-stages (adult survival and reproductive success) whereas the smaller mesopredator can only impact early life-stages (reproductive success). This model is independently tested with data from a closed oceanic island system where eradication of introduced intraguild predators is possible for conservation of threatened birds. Mesopredator release only occurs in strongly top-down moderated (resource-abundant) systems. Even when mesopredator release can occur, the negative impact of more mesopredators is outweighed by the benefit of superpredator removal, allowing recovery of the prey population. Results are robust to 10% variation in model parameters. The consideration of age-structured prey contradicts previous theoretical results for mesopredator release effect and intraguild predation. Superpredator eradication is vital for population recovery of long-lived insular species. Nonetheless island conservation must retain a whole-ecosystem perspective given the complex trophic relationships among multiple species on islands.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

Communities represent complex assemblages of interacting species, where population fluctuations in one species can have cascading effects on other species and trophic levels (Shurin et al., 2002). Severe alteration of community dynamics, such as removing top predators (Bergstrom et al., 2009) or herbivores (Palmer et al., 2008), can have unexpected effects throughout an ecosystem. Such removals are becoming increasingly common as a result of human alteration of natural environments (Novacek and Cleland, 2001). One such dynamical change can occur in an intraguild predation system (Polis and Holt, 1992; Arim and Marquet, 2004), where two predators compete for a shared prey, but predation can also occur between the predators. For asymmetrical intraguild predation (Polis et al., 1989), where a superpredator preys upon a mesopredator, if the superpredators are removed, the mesopredators are released from predation; a ‘mesopredator release effect’ (Soulé et al., 1988; Litvaitis and Villafuerte, 1996). Any subsequent

increase in mesopredator density may increase the impact on the shared prey species (e.g. Rogers and Caro, 1998). In the extreme case, this new dynamic may even drive the shared prey to extinction (Crooks and Soulé, 1999).

One of the greatest threats to biodiversity is the introduction of non-native species, which embed themselves within, and alter, ecosystem functioning (Ebenhard, 1988; Courchamp et al., 2003). The direct impacts of some invasive species have been so severe so as to drive entire species to extinction (Townsend et al., 2006). These impacts have been particularly pronounced on oceanic islands, where evolutionarily isolated species have been poorly adapted to predation by introduced species, especially introduced mammals (Courchamp et al., 2003; Clout and Russell, 2008). Eradication of introduced pest species is the most powerful conservation tool currently available to restore these island communities (Donlan et al., 2003); however, experience has shown that if these manipulations are not viewed within a whole-ecosystem context, then unexpected outcomes can occur (Zavaleta et al., 2001; Tompkins and Veltman, 2006).

Mesopredator release has been theoretically demonstrated as one such unexpected outcome from island eradications where intraguild predation occurs (Courchamp et al., 1999). Invasive

* Corresponding author. Tel.: +262 262 938145; fax: +262 262 938686.
E-mail address: james.russell@univ-reunion.fr (J.C. Russell).

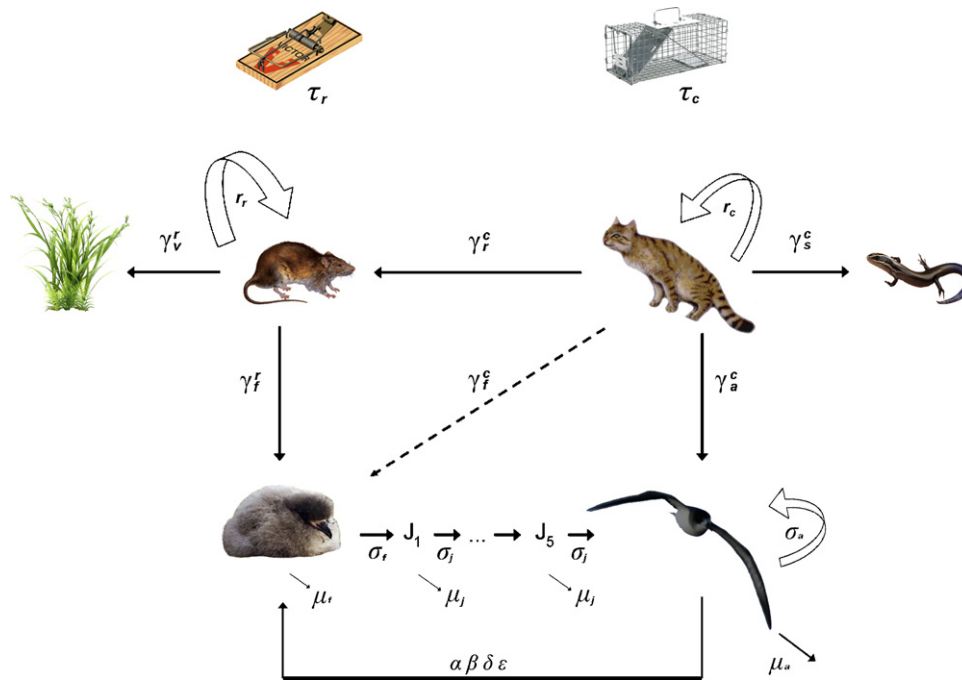


Fig. 1. Conceptual representation of the age-structured differential predation model. γ_j^i is the predation rate of population i on population j where $c = \text{cats}$, $r = \text{rats}$, $f = \text{fledglings}$, $a = \text{adult bird}$, $v = \text{vegetation}$ and $s = \text{skinks}$. r_i is the annual intrinsic growth rate of population i . For birds, α is the adult sex-ratio, β the proportion of breeding adults, δ the adult pair fecundity, ε the number of clutches, σ_j the fledgling survival, σ_j the juvenile survival and σ_a the adult survival. μ is the corresponding mortality where $\sigma + \mu = 1$.

cats (*Felis catus*) and rats (*Rattus* spp.) are common asymmetrical intraguild predator introductions on islands around the world, both impacting bird populations (Nogales et al., 2004; Howald et al., 2007; Jones et al., 2008). Cats are widely perceived to have the greatest impact on seabird populations on islands, and so their removal is often considered a priority (e.g. Rodríguez et al., 2006). However, if cats are regulating rat numbers in a top-down manner, the removal of cats would cause an explosion in rat numbers. The decrease in cat predation on birds may be offset by the increase in rat predation, counter-intuitively accelerating the decline of the bird population. This led Courchamp et al. (1999) to argue that cats may theoretically be protecting birds through their regulation of rats. Such a claim would have major implications in the planning of island conservation projects, in the extreme case suggesting that eradication of intraguild superpredators should not be undertaken at all, unless intraguild mesopredators can simultaneously be eradicated.

Empirical evidence has been lacking for the mesopredator release effect on oceanic islands, but recently Rayner et al. (2007) provided evidence from a 25-year study that the endemic seabird Cook's petrel (*Pterodroma cookii*) was the victim of an unanticipated mesopredator release effect on reproductive success following superpredator (cat) eradication. However, whereas cats can prey on every life-stage of seabirds, rat predation is limited by factors such as body-size and life-stage, with the greatest impact on reproductive success (Jones et al., 2008). For long-lived species with low reproductive rates such as seabirds, it is already well established that population growth rates are much more sensitive to changes in adult survival, relative to reproductive success (Doherty et al., 2004; Peck et al., 2008). Therefore any decrease in reproductive success following mesopredator irruption may be offset by a corresponding increase in adult survival (Le Corre, 2008). Previous work has only investigated asymmetrical intraguild predators which prey identically upon their shared prey. We test the hypothesis that when the shared prey are age-structured, much longer-lived than either predator, and undergoing differential predation by the super and mesopredator, they will not be subject to a mesopredator release effect.

2. Methods

Courchamp et al. (1999) theoretically demonstrated a mesopredator release effect at equilibrium dynamics using a series of three coupled logistic differential equations. This model has a number of stable states, notably including coexistence of all three species, complete extirpation of the bird species, and coexistence with cats only but not rats only. Fan et al. (2005) mathematically developed the equilibrium model of Courchamp et al. (1999), incorporating more realistic time budgeting into predation rates. This solves a number of model anomalies from Courchamp et al. (1999). Fan et al. (2005) still found that mesopredator release can occur, resulting in both a mild (coexistence) and severe (extinction) state for the bird species.

We model an intraguild predator age-structured prey system (Fig. 1). We conceptually develop previous ordinary logistic differential equations by incorporating biologically plausible age-structured populations. This allows us to define more realistic differential predation mechanisms by the super and mesopredators, mediated by the body-size relationship between predator and prey (Emmerson and Raffaelli, 2004; Bonnaud et al., 2008), and in concurrence with observation of cat and rat predation on island bird populations. The prey is a long-lived seabird species with a 5-year at-sea juvenile phase, typical of medium-sized (>300 g) gadfly petrels (*Pterodroma* spp.). We chose gadfly petrels because they are an average-sized seabird, found throughout the world, are usually endangered, and are amongst the most heavily impacted upon seabirds by introduced predators (Le Corre, 2008). Hence introduced mammal eradication is regularly proposed for their conservation (Jones et al., 2008). Cats are large enough to prey upon both breeding adults and chicks while rats can generally only prey upon chicks. This is generally the case for most other seabird species except those which are very large and hence immune to any predation (e.g. albatross), or very small and hence vulnerable to predation at all life-stages (e.g. storm petrels).

We consider this system of coupled non-linear differential equations using independent data from the dark-rumped petrel, *P.*

sandwichensis (Simons, 1984) and Barau's petrel, *P. barau* (Faulquier et al., in press), investigating whether a mesopredator release effect is possible which impacts medium-sized long-lived seabird species subjected to differential predation mechanisms by introduced cats and rats. Introduced mammal invasions on islands have occurred recently in ecological time (Blackburn et al., 2004) and on many island systems new stable states (e.g. species extinction or coexistence) are yet to be reached. Previous mesopredator release effect studies, however, have assumed such equilibrium dynamics, which may not be appropriate. We consider the non-equilibrium dynamics of such a model for the first time, i.e. during invasion by predators. We then investigate whether the obvious mitigation measure of superpredator control or eradication would benefit the prey population, or generate a mesopredator release effect exacerbating the decline.

Time is measured annually, corresponding to the seasonal breeding of bird species. No senescence is assumed, although some can occur very late in life for seabirds (Nisbet, 2001), and juvenile birds remain at-sea and hence are immune to any predation. We independently parameterise the age-structured model using previously published parameter estimates (Table 1).

Hence for the entire bird population:

$$\begin{aligned}\frac{dF}{dt} &= \alpha\beta\delta\varepsilon A \left(1 - \frac{A}{K_a}\right) - \sigma_f F - \mu_f F - \frac{F}{F+A+R+S} \gamma_f^c R - \frac{F}{F+A+R+S} \gamma_f^c C \\ \frac{dJ_k}{dt} &= \sigma_j J_{k-1} - \mu_j J_{k-1} - \sigma_j J_k \quad \text{for } k = 1, \dots, 5 \quad \text{and } J_0 = F \\ \frac{dA}{dt} &= \sigma_j J_5 - \mu_a A - \frac{A}{F+A+R+S} \gamma_a^c C\end{aligned}$$

where F , J_k , A , R , C , V and S are the population size of fledglings, juvenile age-class k ($k = 1, \dots, 5$), adult birds, rats, cats, vegetation (rat alternative food) and skinks (cat alternative food), respectively. α , β , δ and ε are the sex-ratio, adult breeding proportion, adult pair fecundity and number of clutches for birds, respectively. σ_i and μ_i are survival and mortality of age-class i (F, J, A), respectively (note that $\sigma_i + \mu_i = 1$ but we explicitly distinguish between mortality and survival in each age-class). γ_j^i is the annual predation rate (number of prey per predator) of i (cats and rats) on j (rats, adults, fledglings, vegetation and skinks).

For the predators we use typical logistic population growth models, following Courchamp et al. (1999). Both species can breed in their first year and so there is no need to distinguish age-classes. Following previous work the presence of alternative prey (V and S) is set at an arbitrarily large fixed abundance. This allows biologically realistic population persistence despite seabird extinction, addressing the concerns of Fan et al. (2005). This also allows us to manipulate the mode of system regulation. We define simple predator functional responses where predation is relative to prey availability, and all prey items have equal value. Although Fan et al. (2005) introduce more mathematically complex behavioural time-budgeting arguments for the functional response of predation, their conclusions were qualitatively the same as those of Courchamp et al. (1999) and in the interest of parsimony we do not incorporate these. We independently parameterise predation rates using estimates from previously published diet analysis of cats and rats on seabird islands (Table 1).

Hence for the predators:

$$\begin{aligned}\frac{dR}{dt} &= r_r R \left(1 - \frac{R}{K_r}\right) - \tau_r R - \frac{R}{F+A+R+S} \gamma_r^c C \\ \frac{dC}{dt} &= r_c C \left(1 - \frac{C}{K_c}\right) - \tau_c\end{aligned}$$

where r_i and K_i = the annual intrinsic growth rate and carrying capacity of species i , τ_i is the removal rate (simulated control) of species i and γ_j^i is as stated earlier.

Carrying capacities are given by

$$K_a = \text{fixed}$$

$$K_r = \frac{F}{\gamma_f^r} + \frac{V}{\gamma_f^v}$$

$$K_c = \frac{F}{\gamma_f^c} + \frac{A}{\gamma_a^c} + \frac{R}{\gamma_r^c} + \frac{S}{\gamma_s^c}$$

giving realistic carrying capacities for predators determined by the consumption of available food resources. We do not model any irruptive population dynamics of rats, where alternative food sources can increase by orders of magnitude and hence alter the carrying capacity of rats. Such irruptions are common in continental systems but much rarer on islands (Adler and Levins, 1994).

The right-hand side of the whole system is Lipschitz continuous. Thus, from classical analysis, we deduce that there exists a unique maximal (positive) solution. In particular, depending on the parameters, various equilibria may exist that are locally (globally) stable/unstable. The models are analysed using numerical simulation of the prey population at demographic equilibrium prior to the (non-equilibrium) invasion by either one or both species of intraguild predators. We use a non-standard finite difference scheme obtained following Mickens' rules (1994, 2000) for this reasonably complex model:

$$\begin{aligned}F_{n+1} &= \frac{F_n + (\alpha\beta\delta\varepsilon A_n(1 - (A_n/K_a)))\Delta t}{1 + (\sigma_f + \mu_f - (R_n/(F_n + V)))\gamma_f^r + (C_n/(F_n + A_n + R_n + S))\gamma_f^c}\Delta t \\ J_{k,n+1} &= \frac{J_{k,n} + \sigma_j J_{k-1,n}\Delta t}{1 + (\mu_j + \sigma_j)\Delta t} \quad \text{for } k = 1, \dots, 5 \quad \text{and } J_0 = F \\ A_{n+1} &= \frac{A_n + \sigma_j J_{5,n}\Delta t}{1 + (\mu_a + (C_n/(F_n + A_n + R_n + S))\gamma_a^c)\Delta t} \\ R_{n+1} &= R_n \frac{1 + r_r \Delta t}{1 + ((r_r/((F_n/\gamma_f^r) + (V/\gamma_f^v)))R_n + \gamma_r^c(C_n/(F_n + A_n + R_n + S)) + \tau_r)\Delta t} \\ C_{n+1} &= C_n \frac{1 + r_c \Delta t}{1 + ((r_c/((F_n/\gamma_f^c) + (A_n/\gamma_a^c) + (R_n/\gamma_r^c) + (S/\gamma_s^c)))C_n + \tau_c)\Delta t}\end{aligned}$$

After long but straightforward computations, it is possible to show that the non-standard scheme has the same equilibria as the continuous system. Moreover, since the right-hand side of the scheme is positive, it is clear that, for any positive initial data, we will obtain positive approximations in the feasible region.

We first model non-equilibrium system dynamics over time with initial predator introduction (invasion). Seabird (prey) populations start at equilibrium prior to the introduction of a single pregnant female rat and/or cat. We then model non-equilibrium system dynamics over time with predator control for conservation. Seabird (prey) and rat (mesopredator) populations start at equilibrium prior to the introduction of a single pregnant female cat. Cat control then occurs at time $t = 40$ years following cat arrival. We investigate differences between bottom-up systems where food is a limiting resource to the mesopredator, and top-down systems where the mesopredator is not limited by food (10 times alternative food availability). We also investigate the conservation impact of annual 20% ($\tau_c = 0.2$; ongoing) versus 80% ($\tau_c = 0.8$; effectively a 5-year eradication program) cat control. All results are tested for robustness to $\pm 10\%$ sensitivity in demographic and predation rate parameters, given these parameters will have had associated statistical variation from the studies in which they were estimated.

3. Results

Seabirds are K -selected species, with high adult survival and low reproductive output, as reflected in the low growth rate of our populations ($\lambda_b = 1.04$). Seabirds and mesopredators could coexist but at a lower seabird population size due to predation on chicks (Fig. 2a).

Table 1
Biological parameters for model.

Parameter	Symbol	Value	Source
Annual demographic parameters			
Adult sex-ratio	α	0.5	Simons (1984)
Proportion of adults breeding	β	0.9	Simons (1984)
Adult pair fecundity	δ	1	Simons (1984)
Number of clutches	ε	1	Simons (1984), Brooke (1995)
Sub-adult classes	n	5	Simons (1984), Brooke (1995)
Fledgling mortality	μ_f	0.34	Simons (1984), Brooke (1995)
Sub-adult mortality	μ_j	0.2	Simons (1984), Brooke (1995)
Adult mortality	μ_a	0.07	Simons (1984), Brooke (1995)
Expected adult lifetime (years)	$E(\omega)$	18	Derived ^a
Maximum adult lifetime (years)	$\max(\omega)$	48	Derived ^{a,b}
Bird growth rate	r_b	0.03	Derived ^a
Bird annual reproduction	$\lambda_b (e^{r_b})$	1.04	Derived ^a
Adult bird carrying capacity	K_a	100,000	Fixed
Cat growth rate	r_r	0.25	Bester et al. (2002)
Rat growth rate	r_c	4.00	Russell et al. (2008)
Annual per capita predation rates			
Cats on rats	γ_r^c	244	Bonnaud et al. (2007)
Cats on adult birds	γ_a^c	70	Faulquier et al. (in press)
Cats on fledglings	γ_f^c	22	Faulquier et al. (in press)
Cats on alternative (skinks)	γ_s^c	150	Fixed
Rats on fledglings	γ_f^r	8	Faulquier et al. (in press)
Rats on alternative (vegetation)	γ_v^r	300	Fixed
Alternative food sources			
Skinks (cat alternative food)	S	100,000	Fixed
Vegetation (rat alternative food)	V	100,000	Fixed (bottom-up system)
		1,000,000	Fixed (top-down system)

^a Estimates are derived from the life table given the above parameters.

^b Maximum lifetime is calculated as the age at which cumulative lifetime survival falls below 1%.

Seabirds and superpredators could not coexist, with rapid extinction within 50 years following superpredator introduction (Fig. 2b). In the presence of both predators, the superpredator exerted some control on the mesopredator, but the prey still rapidly went extinct (Fig. 2c).

Superpredator control must occur rapidly following introduction ($t=40$ years) given their severe impact. Only superpredator eradication rescued the seabird population (Fig. 3a–d). As expected, a strong mesopredator release only occurred in the top-down system following superpredator control or eradication (Fig. 3c and d), but the increase in mesopredators following superpredator eradication did not significantly alter the recovery rate of the seabird population, given the abundance of alternative food for mesopredators in the top-down system (Fig. 3b vs. d). The seabird population

recovered to a stable population size (in the presence of mesopredators) after 500 years (results not shown). Subsequent mesopredator eradication would further benefit the recovery of the seabird population. All results were robust to $\pm 10\%$ variation in demographic and predation parameter estimates.

4. Discussion

The relationships among species, particularly vertebrates, in asymmetrical intraguild predator systems are complex, and generalisms remain elusive (Litvaitis and Villafuerte, 1996), but have important implications for conservation biology (Polis and Holt, 1992). The equilibrium coexistence of all three species has been theoretically demonstrated in both intraguild predation and

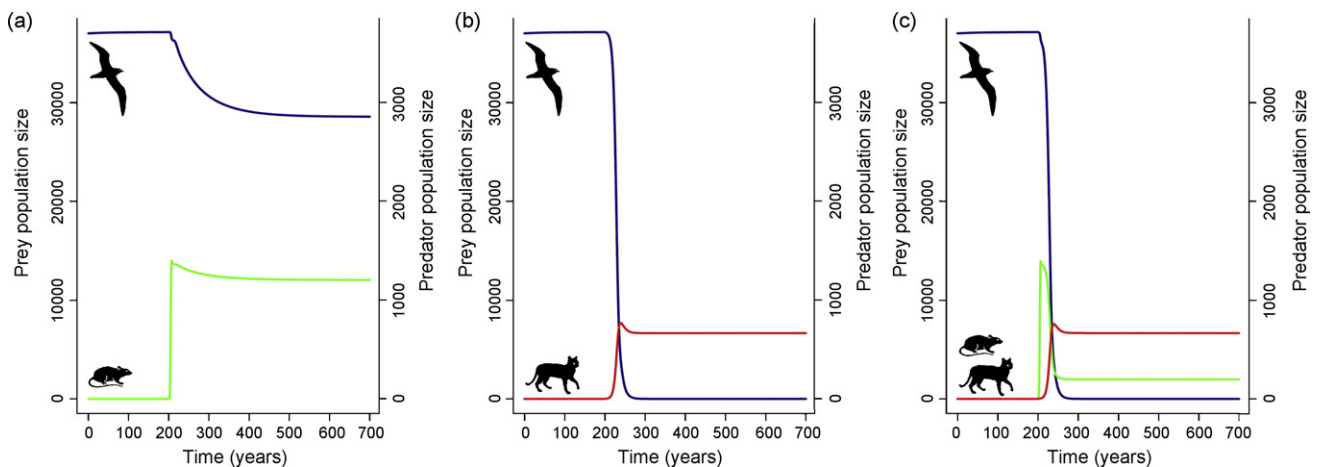


Fig. 2. Simulations of non-equilibrium system dynamics over time with predator introduction. Seabird (prey) populations start at equilibrium prior to the introduction of a single pregnant female rat or cat. (a) With rat (mesopredator) introduction seabird population size is reduced over 50 years but stabilises at a new equilibrium; (b) with cat (superpredator) introduction seabirds rapidly go extinct in 50 years; (c) with rat and cat (mesopredator + superpredator) introduction seabirds rapidly go extinct in 50 years and the rat population is limited by both cat predation and a lack of seabird prey. Results are robust to $\pm 10\%$ variation in demographic and predation parameter estimates.

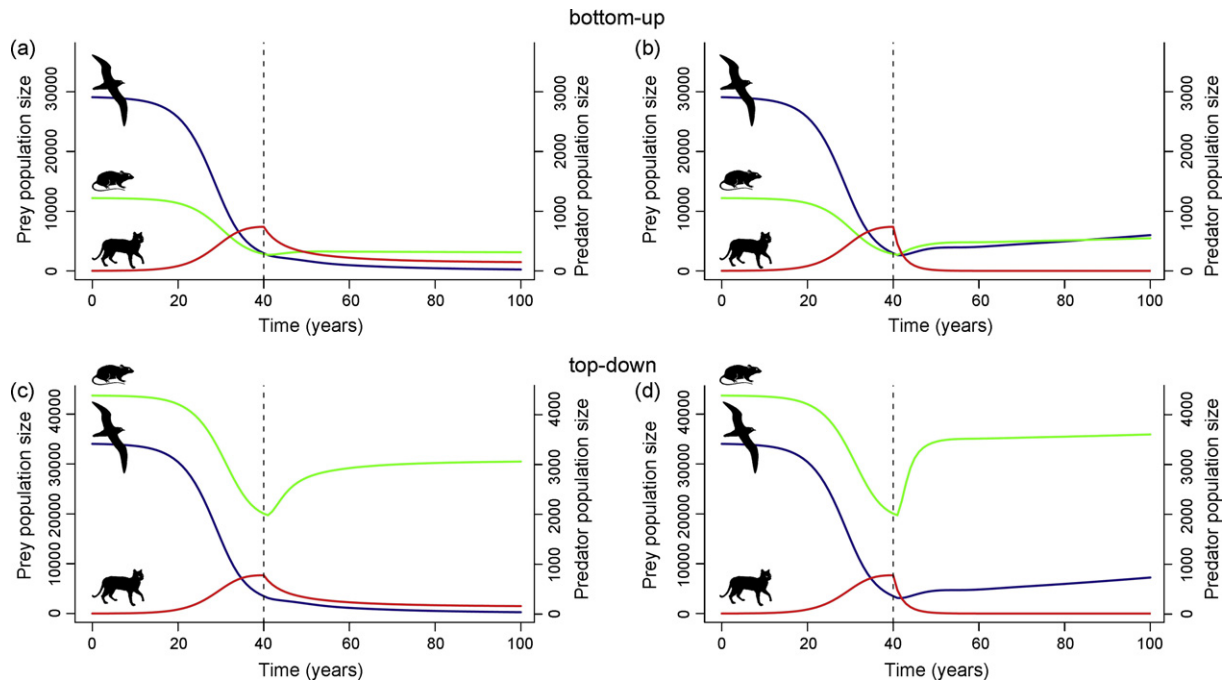


Fig. 3. Simulations of non-equilibrium system dynamics over time with predator control. Seabird (prey) and rat (mesopredator) populations start at equilibrium prior to the introduction of a single pregnant female cat. Cat control then occurs at time $t=40$ years. (a) Bottom-up (food limited) system, with 20% annual cat control; (b) bottom-up (food limited) system, with 80% annual cat control (effectively a 5-year eradication program); (c) top-down (predator mediated) system, with 20% annual cat control; (d) top-down (predator mediated) system, with 80% annual cat control (effectively a 5-year eradication program). Dotted line indicates cat control initiated. Seabird and rat populations start at equilibrium prior to the introduction of a single pregnant female cat. Results are robust to $\pm 10\%$ variation in demographic and predation parameter estimates.

mesopredator release models (Holt and Polis, 1997; Courchamp et al., 1999), but empirical evidence has been restricted to microcosms and invertebrate systems (Arim and Marquet, 2004). Species coexistence is predicted when the mesopredator is the more efficient predator (Polis and Holt, 1992; Holt and Polis, 1997; Arim and Marquet, 2004), but when we accounted for the differential predation of super and mesopredators, the superpredator being able to exploit all life stages, coexistence was not possible. Important effects of age-structure between intraguild predators have previously been demonstrated (Polis et al., 1989), and here age-structure in the shared prey also played a major role in determining equilibrium states. Strong intraguild predation also prevents species coexistence (Holt and Polis, 1997), and can prevent trophic cascades, such as mesopredator release, from occurring when superpredator abundance changes (Polis and Holt, 1992).

For a mesopredator release effect to occur, as defined by Courchamp et al. (1999), two conditions must be met. Firstly, a mesopredator release following superpredator eradication must occur, i.e. there must be a demographic explosion of the mesopredator, as measured by an increased density. Such a release is only expected in a strongly top-down moderated system (Litvaitis and Villafuerte, 1996). Bottom-up driven changes in resource availability can also increase mesopredator abundance and impact prey, e.g. mast-seeding seasons (Tompkins and Veltman, 2006), but are initially independent of superpredator density. Secondly, the impact of the released mesopredator must outweigh the previous combined impact of both intraguild predators on the shared prey, i.e. the prey species growth rate is reduced following mesopredator release.

Our results differ markedly from those of other models (Courchamp et al., 1999; Fan et al., 2005), who investigated 'average' bird species at equilibrium (i.e. assuming species coexistence), with traits typical of small r -selected species, such as forest passerines. Whereas they found mesopredators had the greatest impact on birds, we found that superpredators did, and that species coexistence (e.g. Fig. 1 in Courchamp et al., 1999) could not occur when

the superpredator was the most efficient. Invasion and extinction times were rapid in our models, as is observed during island invasion and extinction events (e.g. five species extinct within 5 years of rat invasion on Big South Cape Island, New Zealand; Towns, in press). Rayner et al. (2007) empirically demonstrated a reduced reproductive success of seabirds in the presence of mesopredators only, as would be expected from our model, but without data on adult survival the overall impact on population growth rate cannot be known. Conversely, Rodríguez et al. (2006) found increased adult seabird survival in the presence of mesopredators (rats) following superpredator (cat) eradication. Other studies of rat populations following cat eradication have found changes in rat behaviour and trapping indices, but are confounded by simultaneous rat control during cat eradication and by only indexing rat abundance (Hughes et al., 2008; Rauzon et al., 2008). In both cases seabirds nonetheless benefited overall from cat eradication, despite rat persistence. Avian coexistence with both cats and rats is only possible if some alternative mechanism such as anti-predator response is invoked, which insular avifauna often lack (Moors and Atkinson, 1984). Such behaviour may alter the functional form of predation and cause the predators to focus on alternate types of prey which are easier to capture. Given certain initial conditions of alternative food (i.e. top-down or bottom-up control) and differential predation rates on fledglings and adults (i.e. impact on reproductive success or adult survival), the empirical observations of previous studies (Rodríguez et al., 2006; Rayner et al., 2007; Hughes et al., 2008; Rauzon et al., 2008) are supported by our age-structured asymmetrical intraguild predation model. Nonetheless a truly experimental evaluation of mesopredator release effect; eradicating cats and monitoring rat density before and after, as well as associated changes in seabird demographic parameters, is still required.

In demonstrating the first condition of the mesopredator release effect (i.e. release) a tangible increase in mesopredator population density must be found. The strength of such a release will depend on the level of top-down control in the system (Sinclair et al., 2003;

Elmhagen and Rushton, 2007). In a diverse system with abundant alternative food for rats, rat density may be controlled by cat predation (top-down). This is usually not the case for rats however, which have a large intrinsic growth rate which can sustain high levels of predation (Krebs, 1999). In contrast if rats are limited by food, then even following cat eradication, they will be unable to substantially increase their density, especially if their prey population has been greatly reduced by shared cat predation (bottom-up). In such a food-limited system however, the impact of rats on birds may be much more severe given the scarcity of alternative food, regardless of superpredator presence. This was postulated by Rayner et al. (2007) as a reason Polynesian rat (*R. exulans*) impact on Cook's petrels was greater at high-altitude sites. In demonstrating the second condition of the mesopredator release effect (i.e. effect), the entire suite of prey population biology parameters must be considered, and not adult survival or reproductive success in isolation. Ultimately these factors combine to determine whether the overall population growth rate is positive or negative. Alternative forms of mesopredator release, such as a behavioural mesopredator release where predation rates change relative to super and mesopredator densities, may be possible, but we do not consider these, and expect them to be small in magnitude relative to numerical responses.

Seasonality plays an important role in bird breeding and is a logical extension to our model. On islands, the breeding season coincides with a massive influx of seabirds, changing the food availability for introduced mammals. Such predator 'swamping' has been hypothesised to facilitate seabird persistence, due to a presumed lag in the predator growth rate following off-season population collapse (e.g. Taylor, 1979; Catry et al., 2007). Preliminary modelling of seasonality suggests the same model outcomes, although time to extinction is longer for the seabird prey. Such an off-season collapse in cats could be compensated by the presence of rats as an alternative food-supply. If this were the case, the system dynamics would better characterise hyperpredation (Courchamp et al., 2000) rather than mesopredation, where the presence of an alternative food supply can maintain the key superpredator at an elevated density (e.g. Bonnaud et al., 2007; Peck et al., 2008). The dynamics of such single predator models have been explored elsewhere, and also lead to prey extinction attributable to the super-predator (Gaucel and Pontier, 2005).

We used a simple predator functional response for our model, assuming no prey preference beyond numerical availability. Observations of introduced cats on islands have shown that seabirds appear to be preferentially preyed, followed by introduced mammals such as rats, mice and rabbits, and only then do land birds form a small part of cat diet (e.g. Harper, 2005; Bonnaud et al., 2007; Peck et al., 2008). In addition introduced rats will often prefer birds to vegetation (e.g. Brooke, 1995). Such preferences could be readily incorporated in our model by weighting the functional response towards specific food groups (e.g. α parameter in Courchamp et al., 2000), although more complex functional responses used by Fan et al. (2005) had little effect on the model outcome, and we expect the same here.

Conservation is often a crisis activity (Soulé, 1991), and any reactive actions must be rapid, and not dictated to by the requirement for thorough baseline data (Simberloff, 2003). We recommend cat eradication on islands as an immediate mitigation measure to reverse the decline of vulnerable long-lived seabird populations. That is not to say that rat eradication is not also important, as rats can suppress small seabirds and many other insular species (Townes et al., 2006; Jones et al., 2008), but concerns of mesopredator release should not unnecessarily delay cat eradication. This mirrors other work showing that the direct impacts of introduced predators are much greater in strength and regularity than indirect effects (Schoener and Spiller, 1999). Furthermore, mesopredator release is unlikely due to frequent bottom-up regulation of islands

(Polis et al., 1997; Sanchez-Piñero and Polis, 2000). We also expect these results to hold for long-lived terrestrial bird species, such as the kakapo (*Strigops habroptilus*), which can coexist with rats but not cats (Powlesland et al., 1995).

Ultimately island conservation must take a holistic and adaptive approach, viewing the island as the unit of conservation, and not its constituent species (either invasive or threatened) in isolation (Zavaleta et al., 2001). Managers must be prepared to react appropriately to cascading unexpected outcomes of ecosystem manipulations (Ebenhard, 1988), but also recognise that these are not the primary concern of control operations, where the direct impact of predators on prey is usually greater and more immediate. Conservation efforts on islands, particularly for seabirds, should focus on reducing mortality in the relatively valuable adult age class, through targeting terrestrial predation on adults (e.g. cat eradication) or marine mortality of adults (e.g. reducing fisheries by-catch). Only when breeding recruitment is drastically reduced will conservation measures be urgently necessary, and such measures (e.g. rat eradication) should not be at the cost of reducing adult mortality, as others have argued (Wilcox and Donlan, 2007). Although we have demonstrated that a mesopredator release effect does not threaten *K*-selected seabird populations, the bird community most commonly found on oceanic islands, further theoretical and empirical work is required investigating mesopredator release effect on *r*-selected species.

Acknowledgments

We wish to thank Laurence Humeau, Patrick Pinet and David Towns for comments on the manuscript. This work was supported by the French National Research Agency (ANR-05-BDIV-003-03) and the French Ministry of Ecology and the Environment.

References

- Adler, G.H., Levins, D., 1994. The island syndrome in rodent populations. *Q. Rev. Biol.* 69, 473–489.
- Arim, M., Marquet, P.A., 2004. Intraguild predation: a widespread interaction related to species biology. *Ecol. Lett.* 7, 557–564.
- Bergstrom, D.M., Lucieer, A., Kiefer, K., Wasley, J., Belbin, L., Pedersen, T.K., Chown, S.L., 2009. Indirect effects of invasive species removal devastate World Heritage Island. *J. Appl. Ecol.* 46, 73–81.
- Bester, M.N., Bloomer, J.P., van Aarde, R.J., Erasmus, B.H., van Rensburg, P.J.J., Skinner, J.D., Howell, P.G., Naude, T.W., 2002. A review of the successful eradication of feral cats from sub-Antarctic Marion Island, Southern Indian Ocean. *S. Afr. J. Wildl. Manage.* 32, 65–73.
- Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L., Gaston, K.J., 2004. Avian extinction and mammalian introductions on oceanic islands. *Science* 305, 1955–1958.
- Bonnaud, E., Bourgeois, K., Vidal, E., Kayser, Y., Tranchant, Y., LeGrand, Y., 2007. Feeding ecology of a feral cat population on a small Mediterranean island. *J. Mammal.* 88, 1074–1081.
- Bonnaud, E., Vidal, E., Zarzoso-Lacoste, D., Torre, F., 2008. Measuring rodent incisors from scats can increase accuracy of predator diet studies. An illustration based on island cats and rats. *C. R. Biol.* 331, 686–691.
- Brooke, M., 1995. The breeding biology of the gadfly petrels *Pterodroma* spp. of the Pitcairn Islands: characteristics, population sizes and controls. *Biol. J. Linn. Soc.* 56, 213–231.
- Catry, P.M., Silva, M.C., MacKay, S., Campos, A., Masello, J., Quillfeldt, P., Strange, I.J., 2007. Can thin-billed prions *Pachyptila belcheri* breed successfully on an island with introduced rats, mice and cats? The case of New Island, Falkland Islands. *Pol. Biol.* 30, 391–394.
- Clout, M.N., Russell, J.C., 2008. The invasion ecology of mammals: a global perspective. *Wildl. Res.* 35, 180–184.
- Courchamp, F., Langlais, M., Sugihara, G., 1999. Cats protecting birds: modelling the mesopredator release effect. *J. Anim. Ecol.* 68, 282–292.
- Courchamp, F., Langlais, M., Sugihara, G., 2000. Rabbits killing birds: modelling the hyperpredation process. *J. Anim. Ecol.* 69, 154–164.
- Courchamp, F., Chapuis, J.-L., Pascal, M., 2003. Mammal invaders on islands: impact, control and control impact. *Biol. Rev.* 78, 347–383.
- Crooks, K.R., Soulé, M.E., 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400, 563–566.
- Doherty, P.F., Schreiber, E.A., Nichols, J.D., Hines, J.E., Link, W.A., Schenk, G.A., Schreiber, R.W., 2004. Testing life history predictions in a long-lived seabird: a population matrix approach with improved parameter estimation. *Oikos* 105, 606–618.

- Donlan, C.J., Tershy, B.R., Campbell, K., Cruz, F., 2003. Research for requiems: the need for more collaborative action in eradication of invasive species. *Conserv. Biol.* 17, 1850–1851.
- Eberhard, T., 1988. Introduced Birds and Mammals and Their Ecological Effects. Svenska Jaegarefoerbundet, Stockholm.
- Elmhagen, B., Rushton, S.P., 2007. Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? *Ecol. Lett.* 10, 197–206.
- Emmerson, M.C., Raffaelli, D., 2004. Predator-prey body size, interaction strength and the stability of a real food web. *J. Anim. Ecol.* 73, 399–409.
- Fan, M., Kuang, Y., Feng, Z., 2005. Cats protecting birds revisited. *Bull. Math. Biol.* 67, 1081–1106.
- Faulquier, L., Fontaine, R., Vidal, E., Salamolard, M., Le Corre, M., in press. Feral cats *Felis catus* threaten the endangered endemic Barau's petrel *Pterodroma baraui* at Reunion Island (Western Indian Ocean). *Waterbirds*.
- Gaucel, S., Pontier, D., 2005. How predator food preference can change the destiny of native prey in predator-prey systems. *Biol. Inv.* 7, 795–806.
- Harper, G.A., 2005. Numerical and functional response of feral cats (*Felis catus*) to variations in abundance of primary prey on Stewart Island (Rakiura), New Zealand. *Wildl. Res.* 32, 597–604.
- Holt, R.D., Polis, G.A., 1997. A theoretical framework for intraguild predation. *Am. Nat.* 149, 745–764.
- Howald, G.R., Donlan, C.J., Galván, J.P., Russell, J.C., Parkes, J., Samaniego, A., Wang, Y., Veitch, C.R., Genovesi, P., Pascal, M., Saunders, A., Tershy, B.R., 2007. Invasive rodent eradication on islands. *Conserv. Biol.* 21, 1258–1268.
- Hughes, B.J., Martin, G.R., Reynolds, S.J., 2008. Cats and seabirds: effects of feral domestic cat *Felis silvestris catus* eradication on the population of sooty terns *Onychoprion fuscatus* on Ascension Island, South Atlantic. *Ibis* 150, 122–131.
- Jones, H.J., Tershy, B.R., Zavaleta, E.S., Croll, D.A., Keitt, B.S., Finkelstein, M.E., Howald, G.R., 2008. Severity of the effects of invasive rats on seabirds: a global review. *Conserv. Biol.* 22, 16–26.
- Krebs, C.J., 1999. Current paradigms of rodent population dynamics—what are we missing? In: Singleton, G.R., Hinds, L.A., Leirs, H., Zhang, Z. (Eds.), *Ecologically Based Rodent Management*. ACIAR, Canberra, pp. 33–48.
- Le Corre, M., 2008. Cats, rats and seabirds. *Nature* 451, 134–135.
- Litvaitis, J.A., Villafuerte, R., 1996. Intraguild predation, mesopredator release, and prey stability. *Conserv. Biol.* 10, 676–677.
- Mickens, R.E., 1994. *Nonstandard Finite Difference Models of Differential Equations*. World Scientific, Singapore.
- Mickens, R.E., 2000. *Applications of Nonstandard Finite Difference Schemes*. World Scientific, Singapore.
- Moors, P.J., Atkinson, I.A.E., 1984. Predation on seabirds by introduced animals, and factors affecting its severity. In: Croxall, J.P., Evans, P.G.H., Schreiber, R.W. (Eds.), *Status and Conservation of the World's Seabirds*. International Council for Bird Preservation, Cambridge, pp. 667–690.
- Nisbet, I.C.T., 2001. Detecting and measuring senescence in wild birds: experience with long-lived seabirds. *Exp. Gerontol.* 36, 833–843.
- Nogales, M., Martín, A., Tershy, B.R., Donlan, C.J., Veitch, C.R., Puerta, N., Wood, B., Alonso, J., 2004. A review of feral cat eradication on islands. *Conserv. Biol.* 18, 310–319.
- Novacek, M.J., Cleland, E.E., 2001. The current biodiversity extinction event: scenarios for mitigation and recovery. *Proc. Natl. Acad. Sci. U.S.A.* 98, 5466–5470.
- Palmer, T.M., Stanton, M.L., Young, T.P., Goheen, J.R., Pringle, R.M., Karban, R., 2008. Breakdown of an ant-plant mutualism follows the loss of large herbivores from an African savanna. *Science* 319, 192–195.
- Peck, D.R., Faulquier, L., Pinet, P., Jaquemet, S., Le Corre, M., 2008. Feral cat diet and impact on sooty terns at Juan de Nova Island, Mozambique Channel. *Anim. Conserv.* 11, 66–74.
- Polis, G.A., Holt, R.D., 1992. Intraguild predation: the dynamics of complex trophic interactions. *Trends Ecol. Evol.* 7, 151–154.
- Polis, G.A., Myers, C.A., Holt, R.D., 1989. The ecology and evolution of intraguild predation: potential competitors that each other. *Ann. Rev. Ecol. Syst.* 20, 292–330.
- Polis, G.A., Hurd, S.D., Jackson, C.T., Sanchez-Piñero, F., 1997. El Niño effects on the dynamics and control of an island ecosystem in the Gulf of California. *Ecology* 78, 1884–1897.
- Powlesland, R., Roberts, G.A., Lloyd, B.D., Merton, D.V., 1995. Number, fate and distribution of kakapo (*Strigops habroptilus*) found on Stewart Island, New Zealand, 1979–1992. *N. Z. J. Zool.* 22, 239–248.
- Rauzon, M.J., Everett, W.T., Boyle, D., Bell, L., Gilardi, J., 2008. Eradication of feral cats at Wake Atoll. *Atoll Res. Bull.* 560, 1–21.
- Rayner, M.J., Hauber, M.E., Imber, M.J., Stamp, R.K., Clout, M.N., 2007. Spatial heterogeneity of mesopredator release within an oceanic island system. *Proc. Natl. Acad. Sci. U.S.A.* 104, 20862–20865.
- Rodríguez, C., Torres, R., Drummond, H., 2006. Eradicating introduced mammals from a forested tropical island. *Biol. Conserv.* 130, 98–105.
- Rogers, C.M., Caro, M.J., 1998. Song sparrows, top carnivores and nest predation: a test of the mesopredator release hypothesis. *Oecologia* 116, 227–233.
- Russell, J.C., Towns, D.R., Clout, M.N., 2008. Review of Rat Invasion Biology: Implications for Biosecurity. Science for Conservation 286, Department of Conservation, Wellington.
- Sanchez-Piñero, F., Polis, G.A., 2000. Bottom-up dynamics of allochthonous input: direct and indirect effects of seabirds on islands. *Ecology* 81, 3117–3132.
- Schoener, T.W., Spiller, D.A., 1999. Indirect effects in an experimentally staged invasion by a major predator. *Am. Nat.* 153, 347–358.
- Shurin, J., Borer, E., Seabloom, E., Anderson, K., Blanchette, C., Broitman, B., Cooper, S., Halpern, B., 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecol. Lett.* 5, 785–791.
- Simberloff, D., 2003. How much information on population biology is needed to manage introduced species? *Conserv. Biol.* 17, 83–92.
- Simons, T.R., 1984. A population model of the endangered Hawaiian dark-rumped petrel. *J. Wildl. Manage.* 48, 1065–1076.
- Sinclair, A.R.E., Mduma, S., Brashares, J.S., 2003. Patterns of predation in a diverse predator-prey system. *Nature* 425, 288–290.
- Soulé, M.E., 1991. Conservation: tactics for a constant crisis. *Science* 253, 744–750.
- Soulé, M.E., Bolger, D.T., Alberts, A.C., Wright, J., Sorice, M., Hill, S., 1988. Reconstructed dynamics of rapid extinctions of chapparral-requiring birds in urban habitat islands. *Conserv. Biol.* 2, 75–92.
- Taylor, R.H., 1979. Predation of sooty terns at Raoul Island by rats and cats. *Notornis* 26, 199–202.
- Tompkins, D.M., Veltman, C.J., 2006. Unexpected consequences of a vertebrate pest control: predictions from a four species community model. *Ecol. Appl.* 16, 1050–1061.
- Towns, D.R., Atkinson, I.A.E., Daugherty, C.H., 2006. Have the harmful effects of introduced rats on islands been exaggerated? *Biol. Inv.* 8, 863–891.
- Towns, D.R., in press. Eradications as reverse invasions: lessons from Pacific rat (*Rattus exulans*) removals on New Zealand islands. *Biol. Inv.*
- Wilcox, C., Donlan, C.J., 2007. Resolving economic inefficiencies: compensatory mitigation as a solution to fisheries bycatch-biodiversity conservation conflicts. *Front. Ecol. Environ.* 5, 325–331.
- Zavaleta, E.S., Hobbs, R.J., Mooney, H.A., 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends Ecol. Evol.* 16, 454–459.