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Rabbits protecting birds: Hypopredation and limitations of hyperpredation

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ABSTRACT

Biological invasions often damage island ecosystems. One such damaging consequence of biological invasions is *hyperpredation*. Hyperpredation is the increase in predation pressure from a generalist predator following the introduction of an alternative prey, typically a consequence of *apparent competition* between the two prey. Models for this have been devised that demonstrate this effect. However, hyperpredation may not always occur or may not always occur at the same strength. Here, we investigate how different mechanisms affect the magnitude of hyperpredation: (i) saturation of the predator's functional response, (ii) predator interference and (iii) non-predatory competition among predators. We find that all three mechanisms generally reduce hyperpredation. Predator saturation can actually overturn hyperpredation into *hypopredation*, an increase in native prey, as a result of *apparent predation* between the two prey. This occurs when the alternative prey is '*poisoned prey*', i.e. prey that have a handling time cost greater than the nutritional benefit for the predator. Consuming 'poisoned prey' can result in an increase or decrease in predator density. Conversely, we also identify scenarios in which interference and competition may increase hyperpredation. Based on these insights, we conclude that the invasion of established ecosystems by non-native prey can lead to more diverse consequences than previously thought. Potential control measures should take these effects into account.

1. Introduction

Hyperpredation is the increase in predation pressure upon a native prey following the introduction of an alien prey under a common predator. The term hyperpredation is relatively recent as it was first used in Smith and Quin (1996). It has since been found to be a common phenomenon. A classical example of hyperpredation is the Cat–Rabbit–Bird problem on subantarctic Macquarie Island (Taylor, 1979; Courchamp et al., 1999, 2000). Originally, cats (*Felis catus*) were introduced onto the island which caused many problems for several native bird species, but eventually the ecosystem stabilised with an endemic cat population. Following this, rabbits (*Oryctolagus cuniculus*) invaded. The now naturalised cats switched prey to this new prey source. This new food supply allowed for greater cat numbers, which in turn increased predation pressure on many native birds. This increase in predation pressure has been linked with the extinction of two species of native flightless birds (a parakeet and a banded rail) (Taylor, 1979).

There are other systems where hyperpredation has been demonstrated. For example, in laboratory conditions with a parasitoid wasp and two moth hosts (Bonsall and Hassell, 1997), and in the wild with an Eagle–Pig–Fox system on the Californian Channel Islands (Roemer et al., 2001, 2002; Courchamp et al., 2003). However, in the latter, some have suggested that Allee effects are also involved (Angulo et al., 2007).

Since the term hyperpredation was coined, studies have either developed models that demonstrate hyperpredation (Courchamp et al., 2000; Roemer et al., 2001, 2002) or have used such models for understanding the consequences of possible control strategies (Courchamp et al., 1999; Zhang et al., 2006). However, as far as the authors are aware, there has not been either a measure of the strength of hyperpredation or a study on the limitations of hyperpredation. On the other hand, there are such studies in the related topic of *apparent competition*.

Apparent competition is the negative indirect effect that two prey have on each other when they share a common predator (Holt, 1977). Although the first theoretical work suggesting that prey can compete via a 'controlling factor' like a common predator was Williamson (1957), it was Holt (1977) that triggered research into apparent competition. Apparent competition is the typical mechanism that leads to hyperpredation, although it is not necessarily the only mechanism. *Apparent predation* where the native prey is the *apparent prey* will also lead to hyperpredation (Fig. 1). In fact, Fig. 1 also demonstrates that negative hyperpredation, or *hypopredation* exists, when there is *apparent mutualism* or the native prey is the *apparent predator*. Given the possible existence of apparent mutualism and apparent predation in Fig. 1,

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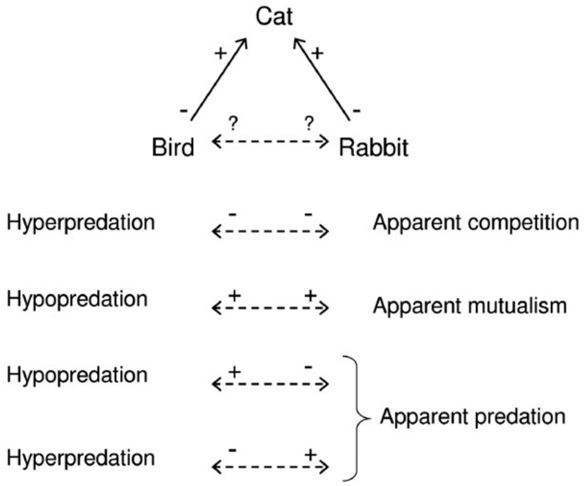


Fig. 1. The many guises of shared predation: the links between hyper-/hypopredation of the bird (native prey) and the signs of the indirect interactions between the bird and rabbit (introduced prey). Hyper-/hypopredation is determined by the sign of the indirect effect on the bird whereas both signs are used to determine the nature of the indirect interaction.

apparent competition is not necessarily equivalent to shared predation. The latter is therefore a more appropriate name for this food web module.

Of these different indirect effects, only apparent competition caught the imagination of others. However, Holt (1977) also mentioned apparent mutualism and apparent predation as indirect links, although he did not demonstrate such links in a one predator–two prey system. Apparent mutualism was discovered in a one predator–two prey system by Abrams and Matsuda (1996). Their model considered both a saturating functional response and density dependence in the predator. Likewise, Abrams et al. (1998) suggested that apparent predation may exist under oscillating dynamics when considering the time average of populations. Our main result is that apparent predation can exist even in the absence of population cycles—and lead to hypopredation in considerably more circumstances than previously thought.

In this paper, we develop some simple measures of the strength of hyperpredation and then compare several models to establish which assumptions limit, eliminate or even overturn hyperpredation. This is done by using the one predator–two prey model in Holt (1977) (and before that in MacArthur, 1970) as a basic model, i.e. the classic apparent competition model. We construct three other models by adding (i) a Holling type II functional response, (ii) predator interference and (iii) non-predatory competition to the basic model. These are chosen as possible limiting factors as they should restrict either the functional response or the growth of predator numbers. By doing so we find that all such factors reduce hyperpredation for most parameter ranges, especially when the introduced prey is the stronger *apparent competitor*. In particular, a reduction in predation pressure, i.e. negative hyperpredation or hypopredation, is found in the Holling type II model. This contrasts with Abrams and Matsuda (1996), where they combine a Holling type II functional response with non-predatory competition.

The hypopredation is the result of '*poisoned prey*', prey that takes more time being handled than they are worth in nutritional benefit. In extreme (and hypothetical) cases, predators become extinct from preying on poisoned prey. In mild cases, preying on poisoned prey can increase predator density. This supports a hypothesis from Whelan et al. (2003, p. 339) (and implicit in Holt, 1977) about apparent predation occurring in a two-prey Holling type II functional response where prey have a low energy to handling time ratio. Our example of hypopredation is distinct from that in Abrams and Matsuda (1996) as here we have apparent predation (Holt, 1977) between the native and invading poisoned prey and not apparent mutualism. In fact, the native prey is the apparent predator whereas the invading poisoned prey is the apparent prey. Although no specific examples of poisoned prey have come to the authors' attention, introduced prey that are difficult for a predator to handle or catch, or have low nutritional benefit for the predator are prime candidates.

Throughout this paper for ease of language and to conform with previous models (Courchamp et al., 1999, 2000; Zhang et al., 2006), the predator, native prey and introduced/alternative prey are interchangeable with Cat, Bird and Rabbit, respectively. This does not mean that the models in this paper are applicable to an actual Cat–Bird–Rabbit system.

2. The models

2.1. The basic model

As described in the previous section, we start with a basic model. This model is found in Holt (1977), which after rescaling becomes

$$\frac{dB}{dt} = r_B B(1-B) - BC, \tag{1}$$

$$\frac{dR}{dt} = r_R R(1-R) - \gamma RC, \tag{2}$$

$$\frac{dC}{dt} = (aB + bR)C - C, \tag{3}$$

where B, R and C are the rescaled variables for birds, rabbits and cats, respectively; r_B and r_R are the per capita intrinsic growth rates when rare for birds and rabbits, respectively; γ is the relative attack rate of cats on rabbits compared to birds; and a and b describe the cats' numerical response on birds and rabbits, respectively, combining predation rates and conversion efficiencies. Time has been scaled according to the average lifetime of cats; bird and rabbit densities have been scaled according to their respective carrying capacities; and cat density has been scaled such that the attack rate of cats on birds is unity.

This model was chosen for its relative simplicity and adaptability. Importantly for this paper, this model is the classic apparent competition model. All the other models in this paper are simple expansions of the basic model.

2.2. Holling type II functional response

Holling (1959) type II functional responses are frequently used to take into account that predation is limited by the time predators need to capture, kill and digest the prey. Incorporating a Holling type II functional response to the basic model gives

$$\frac{dB}{dt} = r_B B(1-B) - \frac{BC}{1+\alpha B+\beta R}, \tag{4}$$

$$\frac{dR}{dt} = r_R R(1-R) - \frac{\gamma RC}{1+\alpha B+\beta R}, \tag{5}$$

$$\frac{dC}{dt} = \left(\frac{aB+bR}{1+\alpha B+\beta R} - 1\right)C, \tag{6}$$

where α and β represent the scaled handling time for the cat on the bird and rabbit, respectively. Implicit in this formulation (and in fact all the other models) is that the predator acts based on random encounters with both prey, and cannot choose to focus on only one prey when both are present.

2.3. Predator interference

Predators are in competition for food. This mechanism can be incorporated into the basic model by using a Beddington–DeAngelis functional response (Beddington, 1975; DeAngelis et al., 1975), a functional response that uses a Holling time management argument by incorporating a term that factors in time the predator uses acting against other predators and consequently is not hunting. Such functional responses have been used in other hyperpredation models like Zhang et al. (2006). To isolate predator interference, we will assume that the predator has a zero handling time for both prey. This allows us to attribute any change in hyperpredation relative to the basic model to predator interference.

Using the same rescaling as the basic model, we get

$$\frac{dB}{dt} = r_B B(1-B) - \frac{BC}{1+hC}, \tag{7}$$

$$\frac{dR}{dt} = r_R R(1-R) - \gamma\frac{RC}{1+hC}, \tag{8}$$

$$\frac{dC}{dt} = \left(\frac{aB+bR}{1+hC} - 1\right)C, \tag{9}$$

where h is a scaled parameter based on time a cat wastes when encountering another cat when foraging.

2.4. Non-predatory competition among predators

Predators do not only compete for prey, but also for other resources like water, shelter and nesting sites. Consequently, this model includes a density dependent death term for the predator:

$$\frac{dB}{dt} = r_B B(1-B) - BC, \tag{10}$$

$$\frac{dR}{dt} = r_R R(1-R) - \gamma RC, \tag{11}$$

$$\frac{dC}{dt} = (aB+bR)C - C - \pi C^2, \tag{12}$$

where π is a scaled parameter that incorporates the strength of non-predatory competition among cats (classical intraspecific competition).

3. Steady state analysis

All our models have an equivalent set of seven steady states. The trivial (0,0,0), Bird only (1,0,0), Rabbit only (0,1,0) and Rabbit–Bird (1,1,0) steady states always exist no matter what parameter values are used. In addition to these, there are also Cat–Bird, Cat–Rabbit and Cat–Rabbit–Bird steady states, whose existence and value depend upon the parameter values. Although the actual details of each steady state for each model are given in the Appendix, a summary is given here.

Usually, the stability of steady states are found using the Routh–Hurwitz criteria. Computing the 3D Routh–Hurwitz criteria is not trivial. Two of the three conditions, namely a negative determinant and negative trace of the Jacobian are reasonably straightforward. However, the third condition is not. This can be bypassed in the basic, predator interference and non-predatory competition models by using the *qualitative stability criteria* (see May, 1973; Jeffries, 1974).

The qualitative stability criteria are a sequence of simple rules (see references above or Edelstein-Keshet, 2005, for details) based on the signs of the elements of the Jacobian (i.e. $+$, $0, -$), irrespective of their actual values. It is important to note that the qualitative stability criteria are stronger than the Routh–Hurwitz criteria. This means that if the qualitative stability criteria are satisfied, then the Routh–Hurwitz criteria must also be satisfied. In other words, qualitative stability implies stability. However, generally the reverse is not true.

Below are examples of the signed Jacobians to demonstrate qualitative stability, in this case for the basic model. Question marks signify that it is not absolutely clear whether the element is positive or negative when armed only with the fact that parameters (and non-zero variables) are strictly positive. In the Cat–Bird Jacobian matrix,

$$\begin{pmatrix} - & 0 & - \\ 0 & ? & 0 \\ + & + & 0 \end{pmatrix},$$

qualitative stability occurs when the middle element (the one that is a question mark) is negative. If the middle element is positive, then the determinant is positive, breaking one of the 3D Routh–Hurwitz criteria, and thus the Cat–Bird steady state cannot be stable. This means that not being qualitatively stable implies not being stable in this case. Hence stability and qualitative stability are equivalent for the Cat–Bird steady state. The same argument applies to the Cat–Rabbit steady state. For the Cat–Rabbit–Bird steady state,

$$\begin{pmatrix} - & 0 & - \\ 0 & - & - \\ + & + & 0 \end{pmatrix},$$

the Jacobian is always qualitatively stable and thus stable (when the steady state exists). The predator interference and non-predatory competition models have essentially the same Jacobians and thus qualitative stability conditions; the only difference is the bottom-right element is negative instead of zero.

All three of these models have the same overall structure, with equivalent existence and stability conditions. In particular, there is exactly one stable steady state for any given parameter set and consequently the long term dynamics are known for all but trivial initial conditions (Fig. A1 in Appendix). Using this knowledge, we can analytically find the hyperpredation effect for these models as there is no ambiguity of the long term results. However, the analytic solutions break down at $h=0$ for the interference model. Using the fact that the limit as h goes to zero is the same as the basic model; analytic solutions from the basic model were used in the interference model at $h=0$.

For the Holling type II model, the qualitative stability criteria are not useful for all steady states with cats present. For example, the Jacobian for the Cat–Bird steady state has too many elements whose sign are unknown:

$$\begin{pmatrix} ? & + & - \\ 0 & ? & 0 \\ + & ? & 0 \end{pmatrix}.$$

For the Cat–Rabbit–Bird steady state, the Jacobian,

$$\begin{pmatrix} ? & + & - \\ + & ? & - \\ ? & ? & 0 \end{pmatrix},$$

can never satisfy the qualitative stability criteria. A reason is the top-middle and middle-left elements are positive, which signifies a (short term) mutualistic relationship between birds and rabbits.

This is to be expected given that Holling type II functional responses are well known for non-trivial changes of stability; most notably, changes caused by Hopf bifurcations that lead to (stable) periodic solutions. This can happen prior to the rabbit invasion in the Cat–Bird system and in the full Cat–Rabbit–Bird system. Because of the complexity of deriving the stability conditions without the qualitative stability shortcut, the stability conditions for the Cat–Rabbit–Bird steady state have not been found. This is not important given that periodic solutions are known to exist for some parameter values, and consequently numerical solutions are acquired since analytical solutions are not possible for periodic solutions. However, except for the emergence of periodic solutions, the system still exhibits the same pattern as the other models (Fig. A2 in Appendix).

4. Hyperpredation measure

In this section, we develop some ground rules on measuring hyperpredation and comment on numerical and graphic methods. The measure of hyperpredation chosen for this paper is the long term reduction in the native prey (bird) following the arrival of the introduced prey (rabbit) relative to the pre-invasion native prey density as a percentage. This means that the hyperpredation measure of 100% is the extinction of the bird, and 0% means that bird densities are unchanged following rabbit introduction, most likely from a failed rabbit invasion. Negative values indicate an increase in the native prey population, i.e. hypopredation.

Other measures were considered, particularly the long term increase in predators and predation pressure. Although hyperpredation is the increase in predation pressure, this is not particularly tangible or observable as it is a rather abstract concept. The increase in predators are the observable cause and the decrease in native prey is the observable symptom. Likewise, native prey and probably to a lesser extent, native predators are usually the focus of conservation efforts and consequently these measures are likely to be of great interest to conservationists. Because of this, the reduction of native prey following rabbit introduction (as a percentage) has been chosen for particular focus, although the increase of predators is still of interest and was measured throughout for comparison and clarity.

To conform with other models based on the classical Macquarie Island Cat–Rabbit–Bird system (Courchamp et al., 1999, 2000; Zhang et al., 2006), the initial condition will be based on the Cat–Bird steady state of the model of interest with the addition of a small perturbation to represent the introduction of rabbits. This means that birds and cats have approached the Cat–Bird steady state prior to the introduction of rabbits. With respect to the model, parameters must therefore take values where a Cat–Bird steady state can exist when rabbits are absent (i.e. $a-\alpha>1$ for the Holling type II model, $a>1$ for all other models). In the Holling type II model, the Cat–Bird subsystem can be cyclic in the absence of rabbits. For simplicity, parameter values have been chosen such that no periodic solutions occur in the Cat–Bird system.

Even though periodic oscillations are excluded in the pre-invasion Cat–Bird system, they can still arise in the full Cat–Rabbit–Bird system. To deal with this, the system is run numerically for a long time period and all transients are discarded. From what remains, which is assumed to be the long term dynamics, we find the maximum and minimum of the variables of interest. We take these values to get minimum and maximum values of hyperpredation respectively. For stable steady states, the maximum and minimum values are the same (up to numerical error). For periodic solutions, the maximum and minimum values are distinct. This is only an issue in the Holling type II model since the other models do not have periodic solutions. Other measures such as the time average of the periodic solution were considered. However, the maximum hyperpredation is of more interest since if it is large, the bird population is at risk of (stochastic) extinction.

In some contour plots (Figs. 6a and 7a), '1%' and '99%' contour lines are used as approximations for '0%' and '100%' contour lines respectively. Likewise, Fig. 3c uses a '−99%' contour line to approximate the '−100%' contour line. This is because small numerical errors blur the boundaries of these clear cut regions of rabbit and bird (and cat in the case of Fig. 3c) extinction. It also reduces the 'waviness' that occurred in these contour lines, which are still prominent in Figs. 3c and 5.

5. Results

We begin with some fundamental results from the basic model. Then we will explore what effects the introduction of a Holling type II functional response, predator interference and non-predatory competition have on hyperpredation. The analysis focuses on the introduced parameters of bird and rabbit handling times (α and β), predator interference (h) and non-predator competition (π) together with differing choices of the apparent competition parameters (r_B, r_R, γ).

5.1. The basic model

The basic model is the classic apparent competition model from Holt (1977). In this model, there are two distinct cases: birds are the stronger apparent competitor ($\gamma r_b > r_r$) and rabbits are the stronger apparent competitor ($\gamma r_b < r_r$). The stronger apparent competitor is the one that can survive under the greater number of predators, and thus can never be driven to extinction by a predator population maintained by the other prey (Fig. A1 in Appendix). Fig. 2 demonstrates that if rabbits are a much weaker apparent competitor (i.e. $\log(\gamma) \gg 0$), rabbits will not invade and thus hyperpredation will not occur. Likewise, if rabbits are a much stronger apparent competitor (i.e. $\log(\gamma) \ll 0$), rabbits will invade, driving the predator density up which in turn drives birds to extinction. In between, both rabbits and birds will coexist with some reduction in bird densities. From this we can infer that, for this model, a successful invasion will always cause some sort of hyperpredation effect.

Many discussions on hyperpredation consider only the introduction of a stronger apparent competitor, so much so that some define hyperpredation as asymmetric (Whelan et al., 2003) or unilateral (Courchamp et al., 1999) apparent competition.

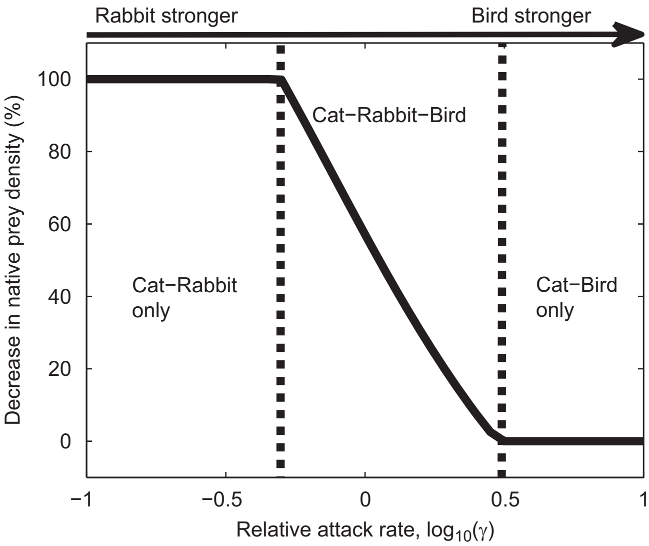


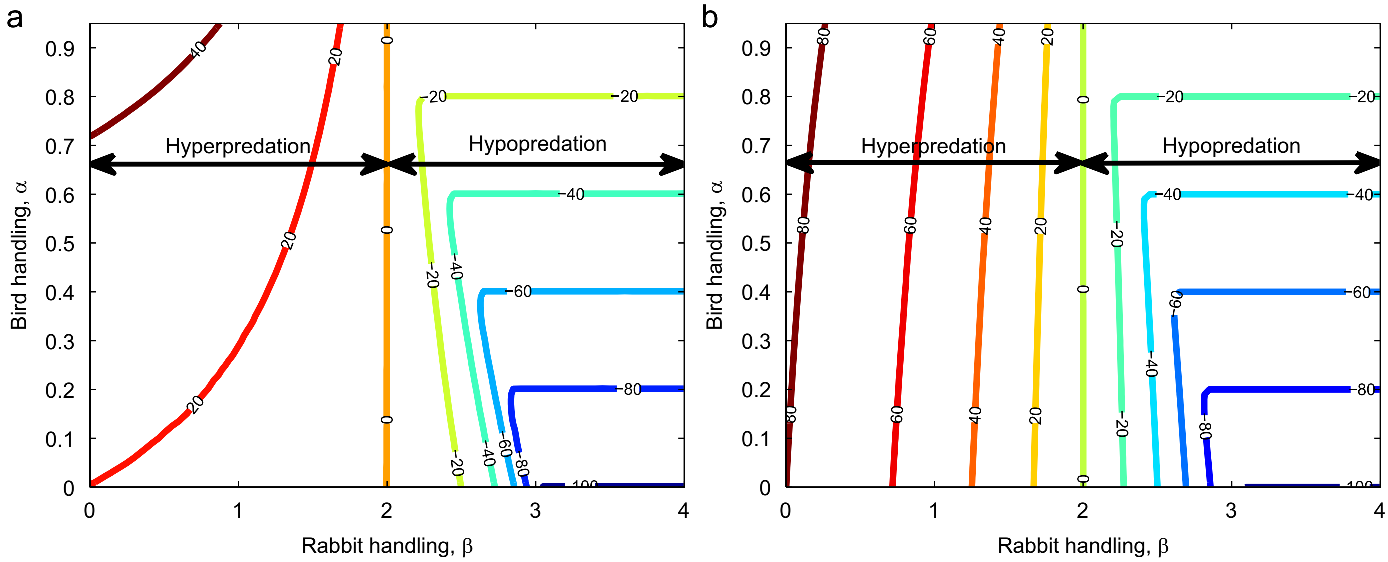
Fig. 2. Basic model: hyperpredation (native prey decrease) as a function of the relative attack rate $\log(\gamma)$ where $r_B=2$, $r_R=2$, $a=1.5$ and $b=2$.

However, it is of note that the successful invasion of a weaker apparent competitor (which occurs when $r_R > \gamma r_B(1-1/a)$ for the basic model) can still cause a significant reduction in the native prey population. It just cannot lead to the extinction of the native prey when considered in isolation. On top of this, hyperpredation can theoretically be the result of apparent predation (Fig. 1), although not in the basic model.

The same conditions for determining the stronger apparent competitor (the relative size of γr_b and r_r) apply in the predator interference, non-predatory competition models. On top of this, these conditions apply in the Holling model when the introduced prey is not poisoned prey, i.e when $b > \beta$. When the introduced prey is poisoned prey, the indirect effect of shared predation changes from apparent competition to apparent predation. In this case, the apparent prey (by model assumption, rabbits) suffers from the same negative indirect effect as apparent competition, with an equivalent dependence on the apparent competition parameters for survival. However, the apparent predators (in this case, birds) do not suffer from apparent competition. Instead, they benefit from reduced predation pressure as cats waste effort on the poisoned prey. Hence, the relative strength of 'apparent competitors' under apparent predation determines when the rabbits can successfully invade.

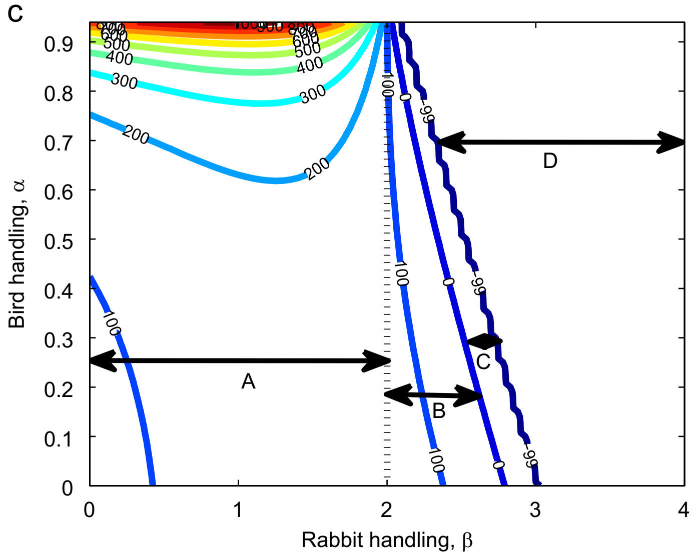
5.2. Holling type II functional response and hypopredation

Fig. 3a and b are contour plots of hyperpredation (native prey decrease) as a function of the handling times (α and β) where the stronger apparent competitor is the bird and rabbit, respectively. When $\beta < b = 2$, we have that increasing the rabbit handling time (β) decreases hyperpredation whereas increasing the bird handling time (α) increases hyperpredation (the left hand side of Fig. 3a and b). When $\beta > b = 2$ (the right hand side of Fig. 3a and b), all contours have become negative. This means that we have negative hyperpredation or hypopredation, the increase in bird density following rabbit introduction. Since both Fig. 3a and



Bird is stronger apparent competitor

Rabbit is stronger apparent competitor



Increase in predator

Fig. 3. Holling model: (a) and (b) Contour plots of hyperpredation (reduction in native prey) as a function of handling times of the bird (α) and rabbit (β). (c) uses the same parameter values of (b) but shows the increase in predator (%). Four qualitatively different regions A–D can be distinguished, which are illustrated in Fig. 4 by time profiles. The equivalent figure for (a) is very similar to (c) and thus has been omitted. For (a), r_B=3, r_R=2, whereas for (b) and (c), r_B=2, r_R=3. Other parameters: a=2, b=2 and $\gamma=1$.

b have qualitatively similar results, this suggests that which prey is the strongest apparent competitor does not change the pattern.

Fig. 3c plots the increase in predator density that corresponds to Fig. 3b. Region A is the region that corresponds with the hyperpredation in Fig. 3a and b and demonstrates a large increase in the predator population. There are three different outcomes for the predator within the region of hypopredation in Fig. 3a and b; the increase (region B), decrease (region C) and extinction (region D) of the cat population. All four of these regions in Fig. 3c have a sample time profile in Fig. 4 demonstrating changes following an invasion of rabbits.

Why do we have these results? To explain this, let us call α and β the (time) costs of predation on birds and rabbits, respectively, and let us call a and b the (growth) benefit from predation on birds and rabbits, respectively. Firstly, we assumed that cats derive profit (benefit minus cost) when preying upon birds only, otherwise there would not be any Cat–Bird steady state in the absence of rabbits. Following the introduction of rabbits, additional profit is available provided $\beta < b$. This would increase cat numbers, which in turn would increase predation on birds. This increase (hyperpredation) depends on the strength of the profit on the rabbits ($b-\beta$).

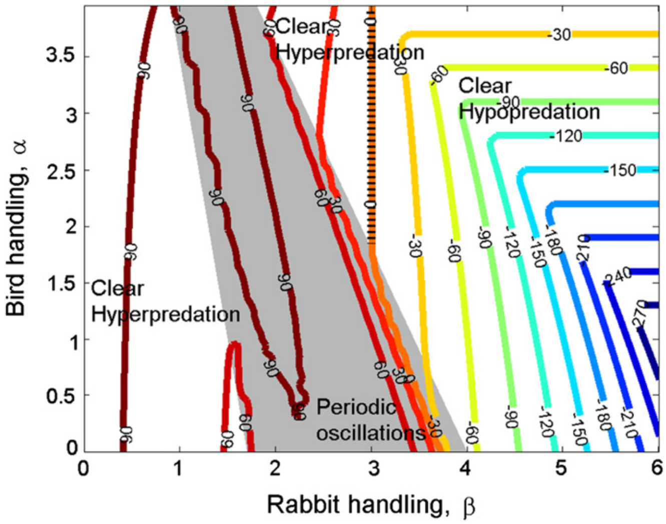
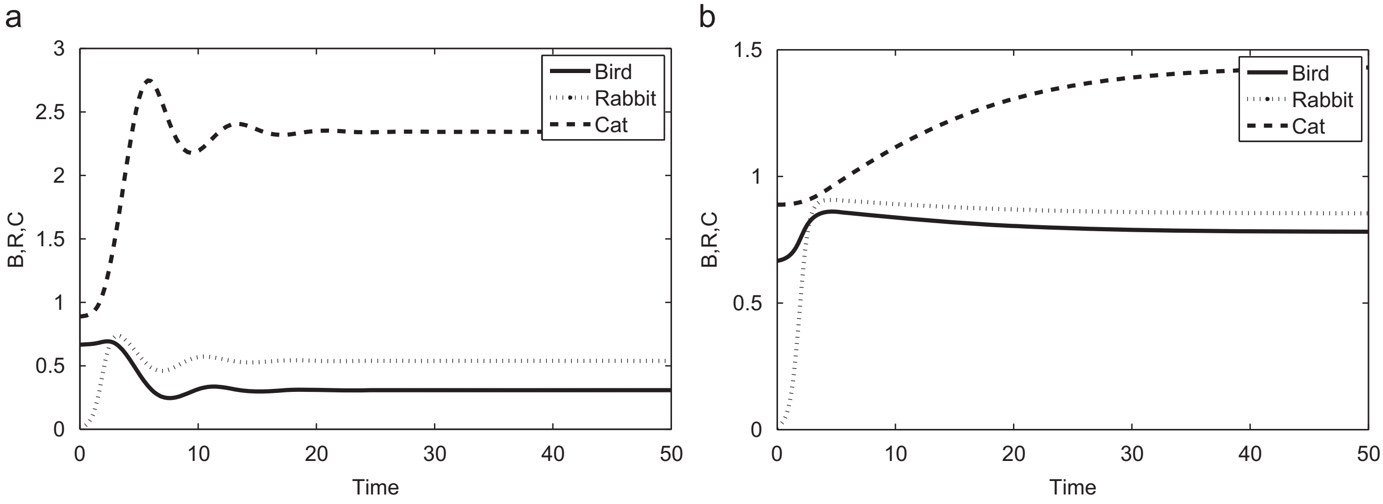
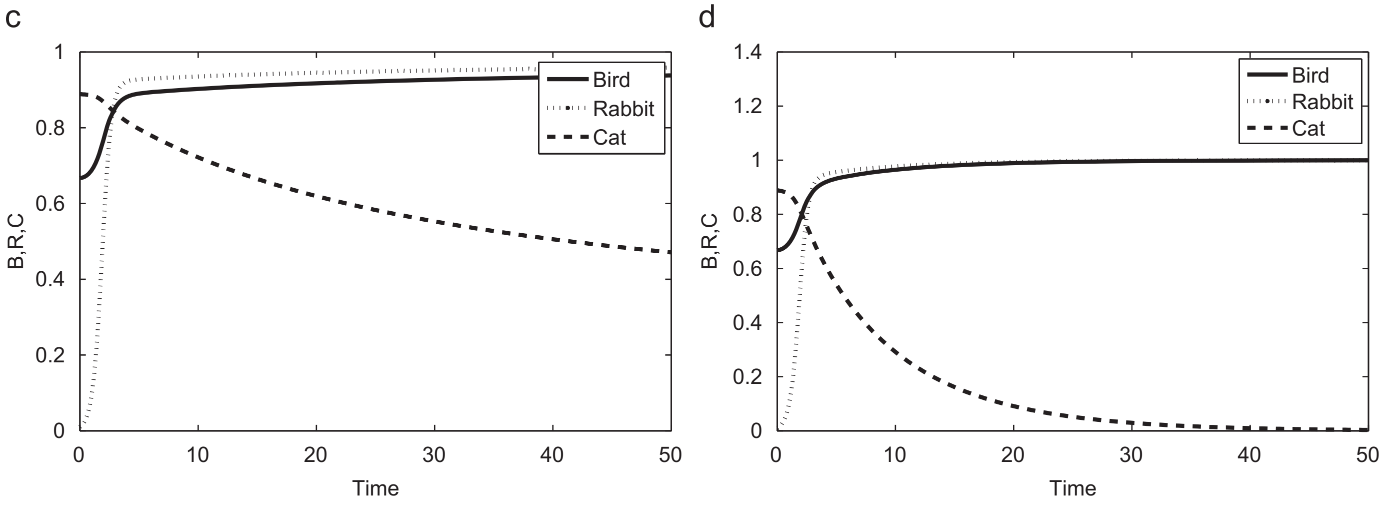


Fig. 5. Holling model in a parameter region where oscillations occur (grey area): hyperpredation patterns are 'clouded' by periodic solutions in the Holling model caused by Hopf bifurcations. The maximum hyperpredation values are shown. Parameter values: $r_B=2$, $r_R=3$, $a=5$, $b=3$ and $\gamma=1$.



Hyperpredation (↓ *Bird,*↑ *Cat*)

Hypopredation (*with* ↑ *Bird,* ↑ *Cat*)



Hypopredation (*with* ↑ *Bird,* ↓ *Cat*)

Hypopredation (*with* ↑ *Bird, Cat extinction*)

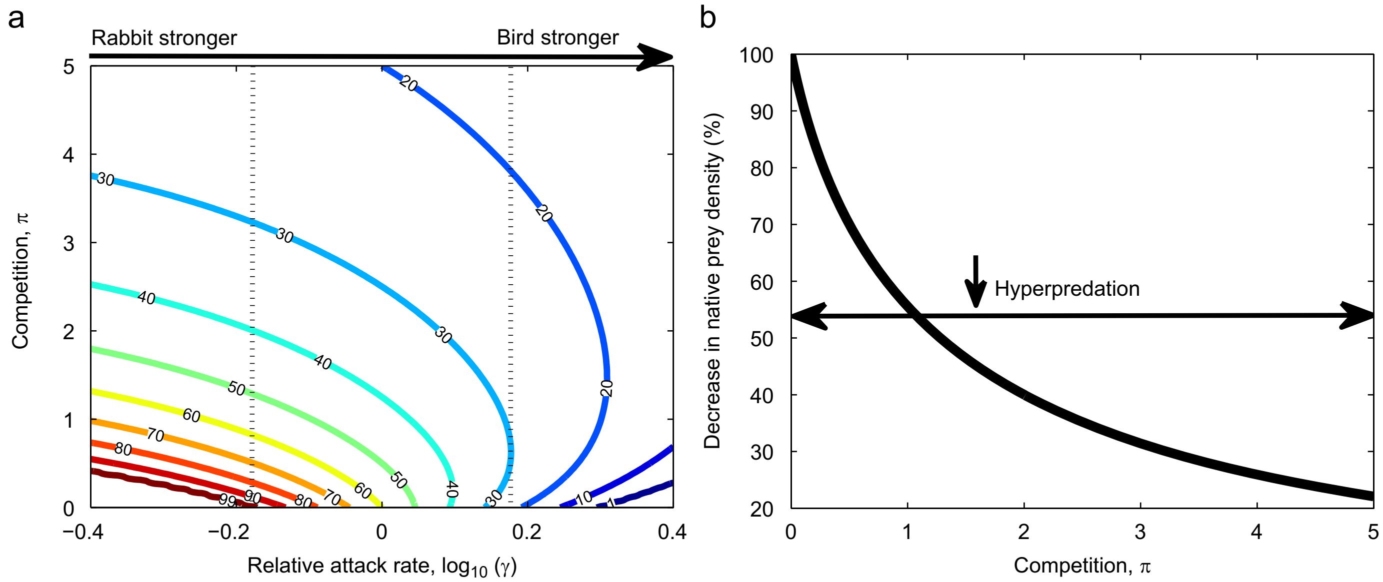
Fig. 4. Time profiles of the Holling model that correspond to the regions within Fig. 3c. (a) demonstrates a decrease in birds, hyperpredation. (b)–(d) demonstrate an increase in birds, hypopredation, with an increase, decrease and extinction in cats, respectively. For (a) $\beta=1$, (b) $\beta=2.2$, (c) $\beta=2.45$ and (d) $\beta=3$. Other parameters: $\alpha=0.5$, $r_B=2$, $r_R=3$, $a=2$, $b=2$ and $\gamma=1$.

Likewise, suppose that α is large (but small enough for the Cat–Bird steady state to exist); then before the rabbit invasion, the birds are near carrying capacity and there are a few cats (see Appendix A.4, the Cat–Bird steady state). Following a rabbit invasion, the cat population will increase substantially, which greatly increases hyperpredation (provided $\beta < b$). If α is small, so the bird population is small and the cat population is large; then although the cat population will increase and hyperpredation will occur following a rabbit invasion, the increase in the cat population will not be proportionally as large, and thus the increase in predation pressure would be less.

At $\beta = b$ we have that there is additional food for the cat, which increases the cat population. However, the total predation pressure on the birds is unchanged as the increase in cats is perfectly counterbalanced by the proportion of time each predator spends handling rabbits (see Appendix A.4.1). By continuity, when β is a little larger than b, we have both hypopredation and an increase in predator following a rabbit invasion (region B in Fig. 3c). But why is there this increase in the predators?

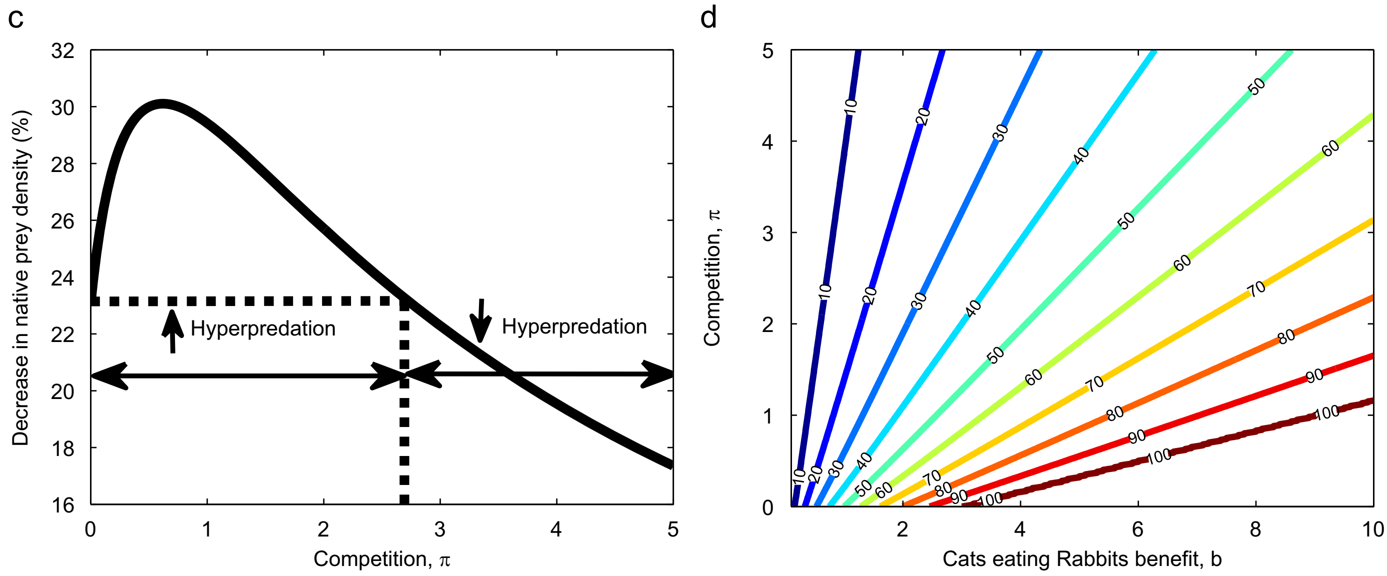
When β is a little larger than b (i.e. preying upon rabbits gives the predator a negative profit or a loss), even though predators are spending more time handling rabbits than there is growth benefit in preying upon rabbits, predator numbers increase following a rabbit invasion. This is because even though there is less predation on birds, there is more predation overall following the invasion. Alternatively, one can argue that even though preying upon rabbits has a higher time cost than nutritional benefit, hunting rabbits as well as birds will reduce the proportion of time wasted by the predator when searching for prey. Remember that while the predator is searching it is not getting any food benefit.

When β becomes significantly larger than b, the additional predation on rabbits following invasion does not make up for the decline in predation on birds. This results in a reduction in total predation rate and thus the predator population will decrease.



Contour across apparent competition scale

Rabbit is stronger apparent competitor



Bird is stronger apparent competitor

Non-predatory competition is 'linear' in strength

Fig. 6. Non-predatory competition model: (a) contour plot of hyperpredation (reduction in native prey (%)) as a function of relative attack rate ($\log(\gamma)$) and non-predatory competition (π), where r_B=2, r_R=2, a=2 and b=3. (b) and (c) follow along the vertical dotted lines in (a) at $\gamma = 2/3$ and $\gamma = 1.5$, respectively. (d) Contour plot of hyperpredation (reduction in native prey) as a function of b and non-predatory competition π where r_B=2, r_R=3, $\gamma = 1$ and a=2.

Here, the balance between high rabbit handling times and reduced search times for the predator has shifted; the high handling time is not fully compensated by the reduced time spent searching for prey. When β is so large that $(a-\alpha)+(b-\beta)\leq 1$, then the predator cannot survive even when the prey are at carrying capacity. This is because the overall growth rate from predation for the cats, when preying upon both birds and rabbits, cannot make up for the natural death rate. In other words, trying to catch rabbits that cats randomly encounter will drive the cats to extinction.

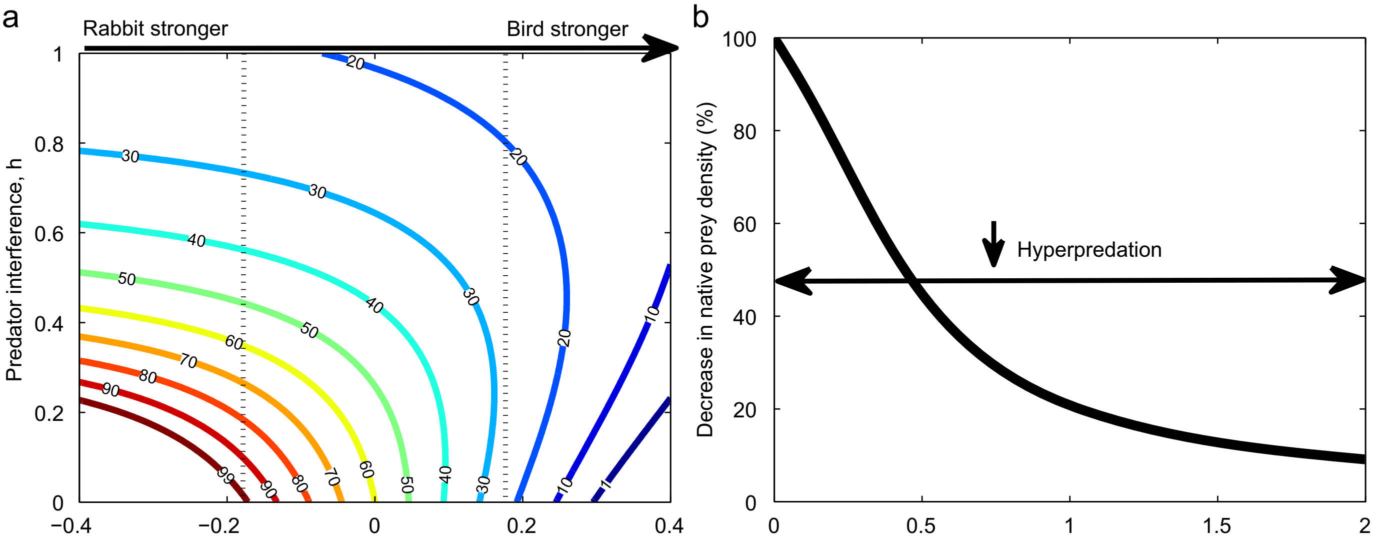
In this scenario of hypopredation, the introduced prey is 'poisoned prey' for the predator. This is a reference to a 'poisoned pawn' in chess, where the act of capturing a pawn ultimately results in a position considerably worse for the player than if the pawn is left alone. This is particularly apt when the predator dies out because of a strategy that involves preying upon poisoned prey.

Increasing a and b can lead to periodic solutions (Fig. A2 in Appendix), as expected from Holling type II functional responses. Fig. 5 shows how oscillatory dynamics affect hyper-/hypopredation. The grey region corresponds to periodic solutions with large amplitudes. This behaviour clouds the trends in hyperpredation, although Fig. 5 demonstrates the same hyper-/hypopredation effect outside the grey region as those found in Fig. 3. In the periodic region, the maximum hyperpredation can exceed 90%. Such values could lead to the extinction of the native prey via stochastic processes.

5.3. Predator interference and non-predatory competition

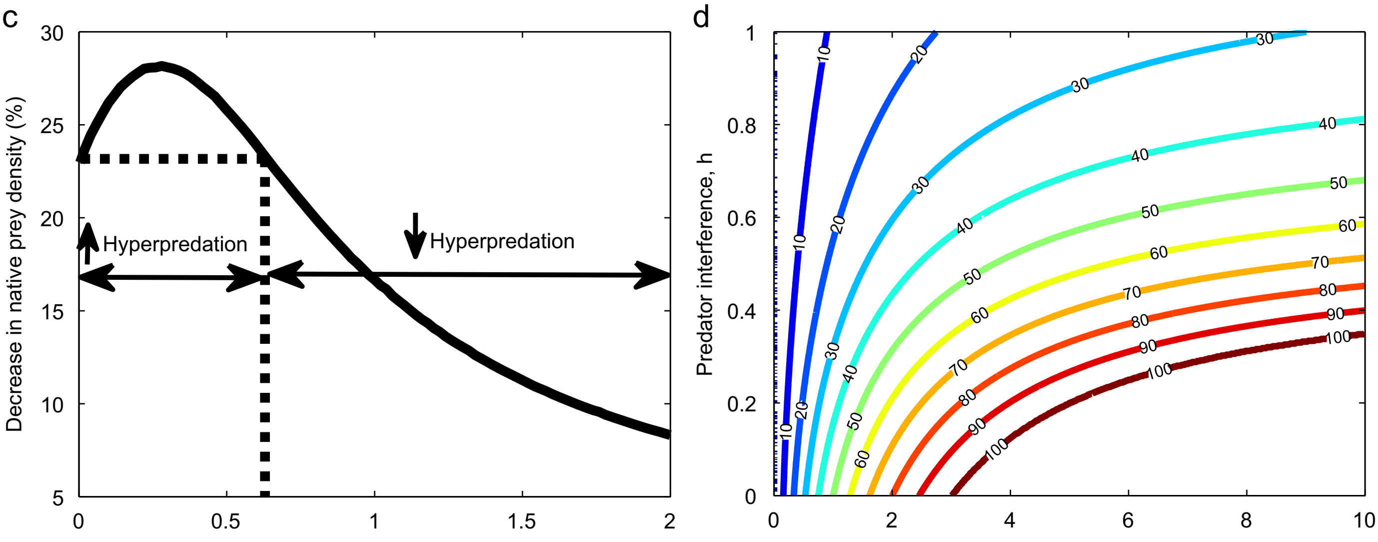
Figs. 6 and 7 demonstrate that both non-predatory competition and predator interference have similar results when compared with the basic model. Taking advantage that the basic model is exactly the same as the non-predatory competition and predator interference models when the parameters π and h are set to zero; we can simply compare results for $\pi, h>0$ with the case $\pi, h=0$.

When rabbits are the stronger apparent competitor, i.e. on the left hand side of Figs. 6a and 7a, the contours (and hence hyperpredation) decrease as non-predatory competition (π) or



Contour across apparent competition scale

Rabbit is stronger apparent competitor



Bird is stronger apparent competitor

Predator interference is 'quadratic' in strength

Fig. 7. Predator interference model. (a) Contour plot of hyperpredation (reduction in native prey (%)) as a function of relative attack rate ($\log(\gamma)$) and predator interference (h), where $r_B=2$, $r_R=2$, $a=2$ and $b=3$. (b) and (c) follow along the vertical dotted lines in (a) at $\gamma=2/3$ and $\gamma=1.5$, respectively. (d) Contour plot of hyperpredation as a function of b and predator interference. Other parameters as in Fig. 6.

predator interference (h) increase. This is demonstrated more clearly in Figs. 6b and 7b, where hyperpredation monotonically decreases as π or h increase, and thus hyperpredation is lower for all π, $h > 0$ than in the basic model (π,$h = 0$), where severe or very near severe hyperpredation occurs.

When birds are a significantly stronger apparent competitor, i.e. on the right hand side ($\log(\gamma) \gtrsim 0.1$) of Figs. 6a and 7a, the contours first increase with small π or h, and only start to decrease when π or h are sufficiently large. This is demonstrated in Figs. 6c and 7c, where hyperpredation increases for small π,h until hyperpredation reaches a maximum around $\pi = 0.6$ or $h=0.3$, beyond which hyperpredation starts to decline. Around $\pi = 2.7$ or $h=0.6$, hyperpredation is at the same level as that of the basic model. The reduction in hyperpredation continues beyond these points.

What explains these results? In general, one would assume that increasing negative effects on predators would decrease the growth from additional food sources and consequently reduce hyperpredation. This does not seem consistent with the anomaly of the increased hyperpredation when the birds are the stronger apparent competitor. However, this can be explained.

When the rabbit is the weaker apparent competitor, it is possible that the birds can sustain a large enough population of predators such that rabbits could not survive, or at least keep rabbit levels low, provided birds are suitably nutritious. However, with $\pi > 0$, there are less predators present before rabbit invasion than when compared to the basic model ($\pi = 0$). With a smaller predator population, (larger) invasions of rabbits are possible. However, with this (larger) invasion, the cat has a larger food source, which allows the cat to increase its population size. This increases predation pressure on the birds and thus increases hyperpredation. The same argument can be used for predator interference by replacing π with h.

This argument has omitted the counteracting effect of decreased growth from food sources for the predation mentioned earlier. However, the point is the relative strength of these two effects; when the rabbits cannot invade or have difficulty invading, the increase in hyperpredation from the (larger) invasion of rabbits has a much stronger effect. Also, this argument is only valid in scenarios where the invading prey is a weaker apparent competitor that has difficult invading; if it is the stronger apparent competitor, rabbits will always invade without difficulty.

We have established that both predator interference and non-predatory competition have similar effects on hyperpredation. However, there is a significant quantitative difference between the results of the two models, namely in the strength of hyperpredation. In Fig. 6a, all contour lines except for the '0%' contour eventually arc back to the left for large enough π. This implies that scenarios where the native prey were extinct in the basic model ($\pi = 0$) can exhibit any hyperpredation value except '0%' just by increasing π by the right amount. This means that the native prey can be saved from extinction. Fig. 7a demonstrates the same pattern except the 'arcing back' becomes more pronounced as h increases, i.e. the contours become more horizontal.

This comparison between Figs. 6a and 7a is like a comparison between a 'linear' function of π and a 'quadratic' function of h. This 'linear–quadratic' relationship is much clearer when comparing Figs. 6d and 7d. The contours in Fig. 6d are straight lines, whereas the contours look like quadratic curves in Fig. 7d. A possible explanation for this could be the nature of predation pressure, which is the product of the functional response and predator density. For the non-predatory competition model, π limits predator growth (by increasing predator mortality), whereas predator interference limits the functional response (by restricting hunting time) on top of limiting predator growth (again by restricting hunting time). This two-fold effect seems sufficient to explain the relative strength of π and h in limiting hyperpredation. However, this 'linear–quadratic' relationship could also just be an artefact based on the (per capita) linear nature of π, whereas h is hyperbolic in nature.

6. Discussion

We have found that the saturation of the predator's functional response can lead to a reduction of hyperpredation or even cause hypopredation when compared to the original linear functional response used in the basic model. We also found that competition and interference among predators usually decreases hyperpredation (when compared to the basic model); however, there can be an increase in hyperpredation when the native prey is the stronger apparent competitor. Previous works on hyperpredation have not taken these factors into account. Likewise, previous work on shared predation have rarely demonstrated apparent predation.

It is important to notice that hypopredation is beneficial to native prey whereas hyperpredation is not (Fig. 4a). In the Holling type II functional response model, we found that hypopredation occurs exactly when the rabbit handling time cost (β) is greater than the rabbit eating benefit (b), a condition called *poisoned prey*. This is a reference to the term 'poisoned pawn' from chess, where taking a pawn leaves the taker in a worse position in the long run. We found that hypopredation can lead to three fates for the generalist predator depending on the size of the loss (negative profit) when eating rabbits, i.e. the difference between rabbit handling time cost and rabbit eating benefit. Firstly, when this loss is small, predator numbers increase, although to a smaller degree than in scenarios of hyperpredation (Fig. 4b). This increase occurs because it is better to eat mildly bad food than spending more time searching for food and not eating. Secondly, for intermediate losses, the invasion of rabbits will cause a reduction in predator numbers (Fig. 4c). This reduction occurs because reducing the time spent searching for prey is not enough to compensate for the time spent handling rabbits. Lastly, when the loss is large, the invasion of rabbits leads to the extinction of the predator (Fig. 4d). Here, the predator spends so much of its time handling the introduced prey without getting much nutritional benefit that the predator starves to death.

The existence of hypopredation and poisoned prey stands in marked contrast to hyperpredation. Under hyperpredation, the native prey is under threat. Hypopredation caused by poisoned prey is beneficial for the native prey, but the predator is likely to be under threat. In many ecological systems, the native prey and predators are usually the focus of conservation efforts. Consequently, whether hyperpredation or hypopredation occurs and their strength are of great interest to conservationists. In the Macquarie Island Cat–Rabbit–Bird system (Courchamp et al., 1999, 2000; Zhang et al., 2006), it is the native prey that is the focus of conservation actions, with various control actions being taken against cats and rabbits. For example, cats have been successfully eradicated from Macquarie Island in the 1990s, whereas rabbits have been infected with myxomatosis (Bergstrom et al., 2009). In the Eagle–Pig–Fox system in the Californian Channel Islands, there is a conflict of interest between the native prey, the critically endangered Island Fox (*Urocyon littoralis*), and the predator, the protected Golden Eagle (*Aquila chrysaetos*) (Roemer et al., 2001; Courchamp et al., 2003). In this system, the ideal scenario would be that the non-native Feral Pigs (*Sus scrofa*) also present on the island are a mildly poisoned prey. In this case, an increase in both island fox and golden eagle numbers would occur. Although this is a hypothetical scenario, there could be systems with parameter values where hypopredation occurs due to poisoned prey, particularly given that Holling type II functional responses are considered to be ubiquitous in nature.

In comparison with the apparent mutualism found in Abrams and Matsuda (1996), the hypopredation in this paper only requires a Holling type II functional response; additional density dependence in the predator is not necessary for the native prey to benefit. Given this, hypopredation via apparent predation should exist in their model (Abrams and Matsuda, 1996). The parameter values where apparent predation should occur were dismissed because the predators calorific intake would decrease (in the short term) if they added the invading prey to their diets. However, we have shown that a mildly poisoned prey can benefit the predator in the long run.

There seems to be a lack of literature around the $(+,-)$ indirect interaction under shared predation, named apparent predation or sometimes indirect antagonism (Huang and Sih, 1990), apparent exploitation (Whelan et al., 2003) or contramensualism (Arthur and Mitchell, 1989). Holt (1983) found short-term apparent predation based on the analysis of isoclines. Likewise, Abrams (1987), Holt and Lawton (1994) and Whelan et al. (2003) state that short-term apparent predation can occur. In contrast, it is long-term, equilibrium-based apparent predation (where birds are the apparent predator) that causes hypopredation in this paper.

Although not found in this paper, there could be scenarios where the native prey are the apparent prey, resulting in hyperpredation via apparent predation and not apparent competition. This could happen in the Holling model by symmetry; if we changed the initial condition from a Cat–Bird steady state to say a Rabbit–Bird steady state with a cat invasion and birds acting as poisoned prey ($\alpha > a$). However, doing so would mean that the model would no longer follow the Cat–Rabbit–Bird scenario of Macquarie Island.

The invasion of rabbits can also cause Cat–Rabbit–Bird oscillations that can cloud the patterns of hyper-/hypopredation. These oscillations can be extreme, possibly resulting in stochastic extinctions of one or more species. In particular, the native prey is vulnerable when maximum hyperpredation is high. Previously, oscillations have not been considered as affecting hyperpredation, even if the models used should exhibit them; for example, the model in Zhang et al. (2006) should contain a region (in parameter space) of stable oscillations much like the Holling model in this paper. By contrast, Courchamp et al. (1999) omitted oscillations so that the model analysis would not be too complex. Abrams et al. (1998) focused on oscillating populations, in particular populations that oscillate in the one predator–one prey subsystem (whereas in this paper, the Cat–Bird steady state is stable); however, they used the time average to demonstrate that apparent predation can occur. As already mentioned in the methods section, using the time average hides a possible danger of large oscillations. We believe that the extrema of oscillations may be of great interest to conservationists, especially those who focus on systems that have small populations like on many isolated islands. The occurrence of oscillations is important since it could (i) result in the stochastic extinction of an endangered native species, or (ii) be helpful in eradicating pest species. Hence, the onset of large-amplitude cycles can be seen as a ‘double-edged sword’ (Oliveira and Hilker, 2010).

The results in the predator interference and non-predatory competition models are very similar. This is no surprise given that both restrict the growth in predators. When the native prey is the weaker apparent competitor, these restrictions to predator growth reduce hyperpredation. However, if the native prey is the stronger apparent competitor, then the restricted predator allows for (larger) invasions of the introduced prey, which in turn increases hyperpredation. The reason for this increase is that a generalist predator can act as an immune system for isolated islands, protecting the island from invasion. The level of protection is based on the size of the predator population maintained by native prey. Adding some competition or interference between predators reduces the predator population, weakening the immune system and thus reducing the protection from invasion, and can allow an invasion of rabbits if the native prey is the stronger apparent competitor. In turn, the numbers of predators increase from this larger food source which leads to an increase in hyperpredation.

Between predator interference and non-predatory competition, the former has the stronger effect on hyperpredation since it both restricts predator numbers and the functional response whereas the latter only restricts predator numbers. The context of this is that high interference or competition among predators allows for many more potential invaders; invaders that could have detrimental effects on the native prey, by causing hyperpredation, and on the rest of the ecosystem.

The discussion on predator interference is based on a simplification of the Beddington–DeAngelis functional response model. This simplification was done by setting prey handling times to zero; allowing us to separate the consequences of predator interference from its combination with prey handling times. We do not expect that a full Beddington–DeAngelis functional response would lead to significantly different results to those of the predator interference model once the properties of the Holling type II model like hypopredation have been taken into account. In particular, we suspect a full Beddington–DeAngelis functional response can either result in apparent competition or apparent predation, depending on whether the alternative prey is a poisoned prey. This contrasts with Abrams and Matsuda (1996), where combining a Holling type model with a non-predatory competition model leads to apparent mutualism.

Such a Beddington–DeAngelis functional response has already been put forward, namely in the pure apparent competition model by Zhang et al. (2006). However this and other models (Courchamp et al., 1999, 2000, 2003; Roemer et al., 2001, 2002) have largely overlooked the limitations of hyperpredation or the existence of hypopredation because of a focus on demonstrating hyperpredation and its application to control strategies.

The work in this paper is based on deterministic models and stability analysis. This ignores important factors like the stochasticity of real biological systems. Likewise, the speed of convergence to steady state and exact time trajectories have not been considered, although time profiles were used to establish how long transient dynamics last. This does limit the direct application of these results on control of invasive species, but the necessary time trajectories are easy to obtain numerically.

There are many other factors that could be considered to limit or increase hyperpredation. For example, spatial and temporal factors are likely to influence hyperpredation, especially if there are spatial or temporal obstacles separating the native and introduced prey or if refuges exist. Such obstacles could include difficult or impassible terrain or seasonal inactivity or migration that separate the prey and/or predators. Investigations of co-invading rabbits and cats in a spatially extended model have already been done (Gaucel et al., 2005; Gaucel and Pontier, 2005). They demonstrate that local and global extinctions of the native birds can occur. Likewise, habitat partitioning can encourage apparent competitors to coexist where they would not in a homogeneous environment (Holt, 1984).

In the models in this paper, the predator is assumed to be opportunistic, preying on whatever it can find. We have shown that this is not a good strategy to employ for a Holling type II functional response if one of the prey either has little nutritional benefit or a large handling time as this will lead to a large decline of predator numbers up to and including extinction. It is clear that predators could have different predation strategies than that of the opportunist, especially with respect to prey switching. Many existing hyperpredation models incorporate some sort of prey switching (Courchamp et al., 1999, 2000; Roemer et al., 2001, 2002; Zhang et al., 2006), although again most choose the predator as opportunistic. There is also a variety of prey switching strategies in shared predation modelling that go beyond an opportunistic predator (many listed in Harmon and Andow, 2004).

Some methods of prey switching could lead to hypopredation: for example, if the predator focused only on the prey that can support the larger predator population. Although this is not likely to be the optimal strategy, it is a better strategy when predator numbers decline in the Holling type II model. In this case, if the bird can sustain the larger population of predators, the alternative prey is ignored and hyperpredation does not occur. However, if the rabbit can sustain a larger population, the bird is then ignored and hypopredation occurs. Hence, with this predation strategy, hyperpredation will not occur.

When there is a decline in predators following the introduction of the poisoned prey, it is better to ignore the poisoned prey. One would expect that the predator would evolve to ignore the poisoned prey, probably via some adaptive dynamics argument. This probably means that the use of a pure two-prey Holling type II functional response for all time is unrealistic.

This discussion in prey switching is actually a necessity for cats on Macquarie Island. This is due to the temporal and spatial factors discussed earlier. On the island, many birds are migratory and many areas of the island are devoid of birds (Taylor, 1979). The near temporal and spatial uniformity of rabbits on the island following the invasion allows cats to survive at times and in places where birds are scarce (Courchamp et al., 2000). Similarly, temporal effects have already been considered in the Eagle–Pig–Fox system (Roemer et al., 2001). From these arguments, it is clear that the strategy of prey switching is key to hyperpredation, and is well worth further investigation.

In this paper, we have investigated a number of mechanisms (predator interference, non-predatory competition and predator saturation) that diminish hyperpredation effects. That is, a native prey is less severely affected by the invasion of an alternative prey in the presence of a shared predator. In fact, there is a scenario where the invasion of an alternative prey actually benefit the native prey. This case is best described as hypopredation via apparent predation, caused by poisoned prey. This has fundamental implications for the understanding of ecological communities and simple food web models. In particular, the food web module of shared predation may come in many forms, such as apparent competition, apparent predation and apparent mutualism (Fig. 1). The management of biological invasions and ecological restoration programmes should be aware of the diverse consequences of the establishment (or eradication) of alternative prey species. In particular, this calls for a holistic view of control methods that take into account all species interacting rather than only the target species.

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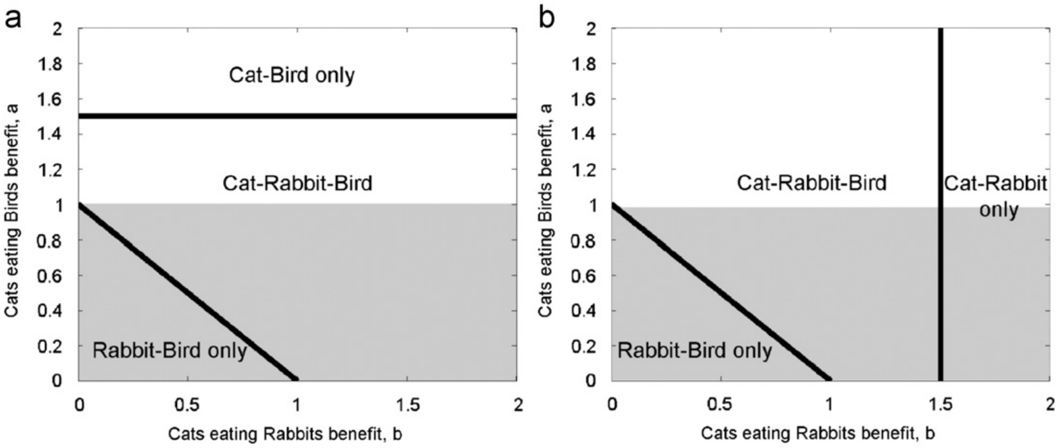
Appendix A. Steady states

As discussed in the stability analysis section of the paper, the steady states of all the models except the Holling type II model can be qualitatively stable (May, 1973; Jeffries, 1974). For the Holling type II model, this is not the case, and stability is not easy to determine. Consequently, here we will give the steady states of the basic, predator interference and non-predatory competition models and their stability conditions with no further justification. For the Holling type II model, more detail is required.

In all four models, the steady states (0,0,0), (1,0,0) and (0,1,0) are unstable and so will not be approached for all strictly positive initial conditions (i.e. $B,R,C > 0$).

A.1. Basic model steady states analysis

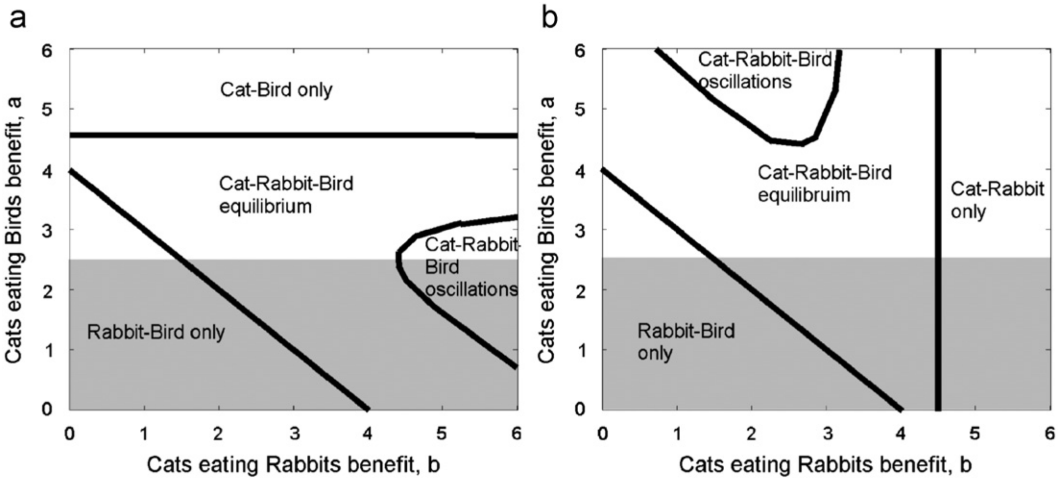
- (1,1,0). This always exists, and is stable when $a+b<1$.
- $(1/a, 0, r_B(1-1/a))$. This exists when $a>1$, and is stable when $r_R < \gamma r_B(1-1/a)$.
- $(0, 1/b, (r_R/\gamma)(1-1/b))$. This exists when $b>1$, and is stable when $r_B < (r_R/\gamma)(1-1/b)$.
- $((r_B b\gamma - r_R(b-1))/(r_R a + r_B b\gamma), (r_R a - \gamma r_B(a-1))/(r_R a + r_B b\gamma), r_B r_R(a+b-1)/(r_R a + r_B b\gamma))$. This exists when $a+b>1$, $r_B > (r_R/\gamma)(1-1/b)$ and $r_R > \gamma r_B(1-1/a)$, and is always stable.



Bird is the stronger apparent competitar

Rabbit is the stronger apparent competitar

Fig. A1. Regions of stability in parameter space for the basic model. Assuming the Cat–Bird steady state exists as an initial condition (with a small rabbit perturbation), we must have $a>1$ (white region). The grey region is where there is no valid Cat–Bird steady state. Notice that the stronger apparent competitor will never be driven to extinction. The predator interference and non-predatory competition models have the same qualitative properties. For (a), $r_B=3$, $r_R=2$ and $\gamma=1$, whereas for (b), $r_B=2$, $r_R=3$ and $\gamma=1$.



Bird is the stronger apparent competitar *Rabbit is the stronger apparent competitar*

Fig. A2. Regions of stability in parameter space for the Holling type II model. The saturating functional response adds an oscillatory region which has been approximated based on contour plots. Assuming the Cat–Bird steady state exists as an initial condition (with a small rabbit perturbation), we must have $a-\alpha>1$ (white region). The grey region is where there is no valid Cat–Bird steady state. Notice that the stronger apparent competitor will never be driven to extinction. For (a), $r_B=3$, $r_R=2$, whereas for (b), $r_B=2$, $r_R=3$. Other parameters: $\gamma=1$, $\alpha=1.5$ and $\beta=1.5$.

A.2. Non-predatory competition

- (1,1,0). This always exists, and is stable when $a+b<1$.
- $((\pi r_B+1)/(r_B\pi+a),0,r_B(a-1)/(r_B\pi+a))$. This exists when $a>1$, and is stable when $r_R<\gamma r_B(a-1)/(r_B\pi+a)$.
- $(0,(\pi r_R+\gamma)/(r_R\pi+\gamma b),r_R(b-1)/(r_R\pi+\gamma b))$. This exists when $b>1$, and is stable when $r_B<r_R(b-1)/(r_R\pi+\gamma b)$.
- $((\pi r_B r_R+b\gamma r_B-r_R(b-1))/(r_Ra+\pi r_B r_R+\gamma r_B b),(\pi r_B r_R+ar_R-\gamma r_B(a-1))/(r_Ra+\pi r_B r_R+\gamma r_B b),r_B r_R(a+b-1)/(r_Ra+\pi r_B r_R+\gamma r_B b))$. This exists when $a+b>1$, $r_B>r_R(b-1)/(r_R\pi+\gamma b)$ and $r_R>\gamma r_B(a-1)/(r_B\pi+a)$, and is always stable.

A.3. Predator interference

- (1,1,0). This always exists, and is stable when $a+b<1$.
- $((1+hC^*)/a,0,C^*)$, where
  $$C^*=\frac{-\left(\frac{a}{r_B}+h(2-a)\right)+\sqrt{\left(\frac{a}{r_B}+h(2-a)\right)^2+4h^2(a-1)}}{2h^2}.$$
  This exists when $a>1$, and is stable when $r_R<\gamma C^*/(1+hC^*)$.
- $(0,(1+hC^*)/b,C^*)$, where
  $$C^*=\frac{-\left(\frac{\gamma b}{r_R}+h(2-b)\right)+\sqrt{\left(\frac{\gamma b}{r_R}+h(2-b)\right)^2+4h^2(b-1)}}{2h^2}.$$
  This exists when $b>1$, and is stable when $r_B<C^*/(1+hC^*)$.
- $(1-C^*/r_B(1+hC^*),1-\gamma C^*/r_R(1+hC^*),C^*)$, where $C^*=(-P+\sqrt{P^2+4h^2(a+b-1)})/2h^2$ and $P=((r_Ra+\gamma r_Bb)/r_Br_R\ -h(a+b-2))$. This exists when $a+b>1$, $r_B>C^*/(1+hC^*)$ and $r_R>\gamma C^*/(1+hC^*)$, and is always stable.

A.4. Holling type II model

As mentioned in Section 3, for the Holling type II model, the qualitative stability criteria (see May, 1973; Jeffries, 1974) are not a short cut for the 3D Routh–Hurwitz criteria if the predator is present. Without the qualitative stability criteria, the full 3D Routh–Hurwitz stability criteria are required. However, this is not straightforward.

The argument used for the stability of Cat–Bird and Cat–Rabbit steady states is to reduce the system to the Cat–Bird ($R=0$) and Cat–Rabbit ($B=0$) plane. The stability of these are comparatively easy to compute via 2D Routh–Hurwitz conditions as they are the usual Holling type II predator–prey model. In particular, this model is well known for Hopf bifurcation induced periodic solutions when a or b is large, leading to the *paradox of enrichment*. These 2D results can be substituted back into the full 3D Holling model since the Jacobian has only one term in the dR/dt or dB/dt row, i.e. growth/decay in R or B is determined by this term.

Stability conditions of the Cat–Rabbit–Bird steady state are complicated and have been omitted, but all other steady states are unstable when this steady state exists. However, Cat–Rabbit–Bird periodic solutions do exist (Fig. A2) suggesting the Cat–Rabbit–Bird steady state can be unstable via a Hopf bifurcation.

- (1,1,0). This always exists, and is stable when $(a-\alpha)+(b-\beta)<1$.
- $(1/(a-\alpha),0,r_Ba(a-\alpha-1)/(a-\alpha)^2)$. This exists when $a-\alpha>1$, and is stable when $r_R<\gamma C^*/aB^*=\gamma r_B(1-1/(a-\alpha))$ and $r_B(1-2B^*)-C^*/(aB^*)^2<0$. There is a Hopf bifurcation at $r_B(1-2B^*)=C^*/(aB^*)^2$.
- $(0,1/(b-\beta),r_Rb(b-\beta-1)/\gamma(b-\beta)^2)$. This exists when $b-\beta>1$, and is stable when $r_B<C^*/bR^*=(r_R/\gamma)(1-1/(b-\beta))$ and $r_R(1-2R^*)-\gamma C^*/(bR^*)^2<0$. There is a Hopf bifurcation at $r_R(1-2R^*)=\gamma C^*/(bR^*)^2$.
- $(B^*,R^*,r_B(1-B^*)(aB^*+bR^*))$, where $B^*=(r_R(1-(b-\beta))+\gamma r_B(b-\beta))/\ (r_R(a-\alpha)+\gamma r_B(b-\beta))$ and $R^*=(\gamma r_B(1-(a-\alpha))+r_R(a-\alpha)/r_R(a-\alpha)+\gamma r_B(b-\beta))$. This exists when $(a-\alpha)+(b-\beta)>1$, $B^*>0$ and $R^*>0$. Stability is unknown but coexistent periodic orbits can occur.

A.4.1. The Cat–Rabbit–Bird steady state when $\beta=b$

Substituting $\beta=b$ into the expression for B^* gives $B^*=1/(a-\alpha)$, which is the same value as the Cat–Bird steady state. This means that the bird population is unchanged following a rabbit invasion and thus there is no hyperpredation.

Likewise, substituting $B^*=1/(a-\alpha)$ into C^* gives

$$C^*=r_B\left(1-\frac{1}{a-\alpha}\right)\left(\frac{a}{a-\alpha}+bR^*\right)$$

After some rearrangement we get

$$C^* = \frac{r_B a(a-\alpha-1)}{(a-\alpha)^2}\left(1+\frac{bR^*(a-\alpha)}{a}\right) = \frac{r_B a(a-\alpha-1)}{(a-\alpha)^2}\left(1+\frac{bR^*}{aB^*}\right)$$

Notice that the first part of the right hand side is exactly the cat population of the Cat–Bird steady state. Consequently, we have an increase in the number of cats following the invasion of rabbits, which depends on the relative total nutritional benefit of preying upon rabbits and birds.

Given these pieces of information, it is possible to demonstrate that the predation pressure upon birds is nevertheless unchanged by the invasion of rabbit; however, that is unnecessary since we have already shown that the bird population is unchanged.

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