

Search biases, frequency-dependent predation and species co-existence

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ABSTRACT

Search biases – behaviours that intentionally or unintentionally affect a forager's encounter probability with its resources – can have profound ecological and evolutionary effects. Courchamp *et al.* (2000) introduced a model of asymmetric apparent competition (hyperpredation) that incorporated a search bias influenced by the frequency of prey. We extend their model and assess the effects of a frequency-dependent search bias on the direct and indirect effects among a predator and two prey. We derive lines of equal harvest for the predator. These lines give all combinations of the abundances of the two prey such that the predator has the same harvest rate. (The predator's zero net growth isocline is the equal harvest rate line that just meets the predator's subsistence demand for energy.) All equal harvest rate lines have similar shapes, and all have regions of both positive and negative slope within the state space of prey densities. When they have a positive slope, one prey decreases the predator's harvest rate and total fitness. This leads to an indirect interaction between the prey types that mimics exploitation (+, –). Under this 'apparent exploitation', one prey indirectly harms the second, while the second indirectly benefits the first. At other prey densities when the predator's line of equal harvest rate has a negative slope, the prey interact indirectly through apparent competition (Holt, 1977, 1983). Our model provides an extension of Martin's (1988a,b) verbal model, in which nest predators, through density-dependent foraging and search images, select for nest site diversification among co-occurring bird species. Our model shows when Martin's hypothesis may and may not apply.

Keywords: direct and indirect interactions, frequency-dependent predation, nest predation, search bias, songbird communities, species co-existence, species interactions.

INTRODUCTION

How a forager searches for its resources impacts the forager, its resources, their populations and the community in which they reside. Search behaviour provides the link among these individual, population and community processes. Several search behaviours have

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been proposed, including search image (Tinbergen, 1960), area-restricted search (Smith, 1974a,b), micropatch partitioning (Brown and Mitchell, 1989; Schmidt and Brown, 1996) and directed search (Schmidt, 1998). Each of these behaviours results in what we will refer to, generically, as a 'search bias'. A search bias occurs when a forager's encounter probabilities for different foods change intentionally or unintentionally with the frequency or density of the foods. Other mechanisms besides search behaviour can also generate search biases. These include learning or training (McNair, 1980; Shettleworth *et al.*, 1993), neophobia (Greenberg, 1983, 1984, 1990, 1992) and predator avoidance (Brown, 1992; Brown and Morgan, 1995).

Search biases influence the direct effects of the predator on its prey species, but they may also result in a variety of indirect effects among the prey species (Holt, 1977, 1983; Holt and Kotler, 1987; Abrams, 1999). For instance, Holt (1977) showed how, through a numerical response of a shared predator species, an increase in abundance of one prey species can lead to a decrease in abundance of a second prey species. Later, Holt and Kotler (1987) found that, depending on the foraging rules used by a consumer, indirect effects among two (or more) prey species sharing one (or more) predator species may be (+, +), (-, +), (+, -) or (-, -). There is clearly a wide spectrum of possible interactions among prey species sharing common predator species, and which manifest will be strongly influenced by search biases.

Search biases have ecological and evolutionary consequences. They influence a consumer's diet choice (Pulliam, 1974; Holt and Kotler, 1987), functional response (Holling, 1965; McNair, 1980; Nunney, 1980) and habitat selection (Brown, 1992; Morgan and Brown, 1996). Search biases may also influence the co-existence of resource species (Hubbell, 1980), the stability of consumer-resource dynamics (McNair, 1980; Sih, 1984) and frequency-dependent diet selection (Krebs, 1983; Greenwood, 1984; Allen, 1988; Sherratt and Harvey, 1993).

Courchamp *et al.* (2000) proposed a model of hyperpredation or asymmetric apparent competition (Holt, 1977) that incorporates a search bias and in which predation is frequency-dependent. Their model is related to a family of switching models (Jacobs, 1977; Tansky, 1978; Teramoto *et al.*, 1979) analysed by Holt (1983), who showed that, for these models, predators display suboptimal behaviour. Courchamp *et al.* (2000) found that the predator's relative encounter rate with its prey changes with the relative frequency of the prey species. In their model, search bias reflects a superior ability to detect (or to capture) one prey species relative to the second prey species. Numerical analysis of this model demonstrated that the search bias in favour of one prey species can lead to the extinction of the second prey species.

Here we extend the model of Courchamp *et al.* (2000). In our model, we envision a predator that preys upon two prey types (which may or may not be different species), each of which occurs in a separate microhabitat. The predator's efficiency is greater, and its foraging costs lower, in one of the microhabitats, leading to a search bias in favour of prey residing there. In our analysis, we first assess the general effects of the three co-occurring species on each other. We then focus on the predator's isoclines of equal harvest rate (the zero net growth isocline, where the predator's harvest rate just matches needs, is one of these lines). The lines of equal harvest rate give the combinations of prey densities over which a predator has the same harvest rate. Our analysis indicates that the indirect effects (due to the shared predator species) between the two prey species depend upon their relative densities. At certain densities, a marginal increase in the population density of one prey species

increases the survival of (decreases the harvest on) the second prey species, but an increase in the population of the second prey species decreases survival of the first (= ‘apparent exploitation’). At other densities, marginal increases in the population density of either prey species decreases survival of the other (= ‘apparent competition’). We relate our analysis to current models of species co-existence, in particular the verbal model of Martin (1988a,b). This model suggests that shared predators of nesting songbird species will: (1) over evolutionary time, select for nest site diversification, and (2) over ecological time-scales, influence the likelihood for different songbird species to co-exist. Our model suggests that shared predators may either enhance or limit species co-existence, depending upon the relative densities of prey species.

THE MODEL

Courchamp and co-workers’ (2000) model ‘predicts that an introduced prey species, well adapted to high predation pressure could induce the extinction of an indigenous prey, through the sudden increased population size of an introduced predator’ (p. 154). They examine the population dynamics of a highly asymmetric apparent competition to determine conditions under which an introduced prey (such as rabbits on islands) can indirectly drive an indigenous prey extinct via the presence of a shared predator (such as feral cats).

Our extension of their model is motivated by nest predators of forest and grassland songbirds. Martin (1988a,b) proposed that nest predators, by focusing attention on a microhabitat dense with nests, may promote the co-existence of bird species that nest in different microhabitats. For us, Courchamp *et al.* (2000) provide a conceptual starting point for our search-bias model, and Martin (1988a,b) provides a biological context for examining how the model’s frequency-dependent predation rates on the prey may serve as a mechanism of co-existence. The modelling applies more generally to the question of when and how search biases can be expected to promote or inhibit the co-existence of prey species.

We envision a habitat that has two or more microhabitats. Following Martin (1988a,b, 1993a,b), imagine a forest divided into ground, shrub, sub-canopy and canopy strata, with each stratum constituting a separate microhabitat. Similarly, imagine a grassland that is comprised of forb/grass and shrub strata, again with each stratum constituting a separate microhabitat. Next, we envision a prey species that can nest in two of the microhabitats (say ground and shrub strata in a forest habitat, or ground and shrub strata in a grassland). (Alternatively, one can imagine two or more prey species, each of which nests in a different microhabitat.) Finally, we envision a predator that forages in each of the microhabitats in which the prey species places its nests, but we assume that the predator has different efficiencies and costs of foraging in the two microhabitats such that it is more effective in one than the other (e.g. raccoons forage more efficiently and with reduced costs on the ground than in woody vegetation off the ground).

We formalize our conceptual scenario as follows. We consider a songbird species with two nest placement strategies occurring at densities G (ground) and S (shrub), respectively. The nests will be preyed upon by a predator (P) that can search in each stratum. The risk of predation (μ_i) for a nest will be influenced by a stratum-specific encounter rate (a_i) and the predator’s lethality (k_i), such that $\mu_i = (a_i/k_i)$. We imagine that the predator has stratum-specific search biases (α_i). Note that α_i weights the predator’s use of the different habitat strata, and it has at least two biological interpretations. First, it can, as stated, be

thought of as a search image; second, it can be thought of as a bias in habitat selection or use. Finally, we imagine that the predator converts only a fraction of prey biomass into predator offspring (e), and that it experiences a stratum-specific cost of foraging (γ_i), which may reflect an energetic cost or its own cost of predation, and a stratum-independent mortality rate (m). In the absence of predation, the songbird population will grow (at rate r_i) in each stratum to its carrying capacity (K_i). These variables are related by the following equations:

$$dG/dt = r_g G (1 - G/K_g) - [(\mu_g \alpha_g G)/(\alpha_g G + \alpha_s S)]PG \quad (1)$$

$$dS/dt = r_s S (1 - S/K_s) - [(\mu_s \alpha_s S)/(\alpha_g G + \alpha_s S)]PS \quad (2)$$

$$dP/dt = eP\{[(\mu_g \alpha_g G^2)/(\alpha_g G + \alpha_s S)] - [(\alpha_g G)/(\alpha_g G + \alpha_s S)]\gamma_g + [(\mu_s \alpha_s S^2)/(\alpha_g G + \alpha_s S)] - [(\alpha_s S)/(\alpha_g G + \alpha_s S)]\gamma_s\} - mP \quad (3)$$

where the subscripts g and s relate to ground and shrub, respectively. Note that, in these equations, predation is now related to both the density and the frequency of the two nesting strategies.

We can determine the effect of the shrub nests on the ground nests via the predator's functional response by taking the derivative of equation (1) with respect to the shrub nesting strategy:

$$[\alpha_s (\mu_g \alpha_g G)]PG/(\alpha_g G + \alpha_s S)^2 \geq 0 \quad (4)$$

Similarly, taking the derivative of equation (2) with respect to the ground nesting strategy shows the effect of the ground nesting strategy on the shrub nesting strategy:

$$[\alpha_g (\mu_s \alpha_s S)]PS/(\alpha_g G + \alpha_s S)^2 \geq 0 \quad (5)$$

Because equations (4) and (5) are always positive (in the non-trivial cases of P , G and $S > 0$), the model suggests that the presence of each nesting strategy has a positive direct effect on the other, a result consistent with Martin's (1988a,b) verbal model.

To see the effect of the predator species on either nesting strategy, we take the derivative of equations (1) and (2), respectively, with respect to P :

$$\begin{aligned} -(\mu_g \alpha_g G^2)/(\alpha_g G + \alpha_s S) &\leq 0 \\ -(\mu_s \alpha_s S^2)/(\alpha_g G + \alpha_s S) &\leq 0 \end{aligned} \quad (6)$$

Unsurprisingly, the direct effect of the predator is negative for both nesting strategies.

To determine the effect of the two nesting strategies on the predator species, we take the derivative of (3) with respect to G and S , respectively:

$$\begin{aligned} eP\alpha_g(\mu_g \alpha_g G^2 + 2\mu_g G \alpha_s S + \gamma_s \alpha_s S - \mu_s \alpha_s S^2 - \gamma_g \alpha_s S)/(\alpha_g G + \alpha_s S)^2 \\ eP\alpha_s(\mu_s \alpha_s S^2 + 2\mu_s S \alpha_g G + \gamma_g \alpha_g G - \mu_g \alpha_g G^2 - \gamma_s \alpha_g G)/(\alpha_g G + \alpha_s S)^2 \end{aligned} \quad (7)$$

Crucially, equations (7) may have both positive and negative regions. This means that, at certain prey densities, a prey type has a negative effect on its predator. Graphically, this can be depicted by a plot of the predator's equal harvest rate isoclines (which, when the predator's harvest rate just matches its needs, is its zero net growth isocline, or ZNGI, *sensu* Tilman, 1982). Mathematically, the equal harvest rate isoclines for the predator are found

by setting equation (3) equal to an arbitrary constant, k , and then solving for G in terms of S . This results in a quadratic equation with two solutions:

$$G = [(\gamma_g \alpha_g + [(m+k)\alpha_g]/e) \pm \{(\gamma_g \alpha_g + [(m+k)\alpha_g]/e)^2 - 4\mu_g \alpha_g [\mu_s \alpha_s S^2 - (\gamma_s \alpha_s + [(m+k)\alpha_s]/e)S]\}^{1/2}] / 2\mu_g \alpha_g \quad (8)$$

In contrast to typical isoclines with a negative slope everywhere (Tilman, 1982), the isoclines given by this equation are always humped (Fig. 1). The harvest rate isoclines have both positive and negative regions. In fact, these predator isoclines conform to the humped isocline in Holt (1983: figure 1E), in that they have two regions of positive slope separated by a region of negative slope.

We can fully characterize these isoclines with respect to intercepts and slopes by rearranging equation (3) into a form characterizing an ellipse:

$$[\mu_g \alpha_g G^2 - (\alpha_g \gamma_g + [(m+k)\alpha_g]/e)G] + [\mu_s \alpha_s S^2 - (\gamma_s \alpha_s + [(m+k)\alpha_s]/e)S] = 0 \quad (9)$$

and applying the implicit function theorem.

We can determine the G and S intercepts, \check{G} and \check{S} , of the predator's harvest rate isoclines by setting S (or G) = 0 in equation (9) and solving for G (or S):

$$\check{G} = (\gamma_g + [(m+k)/e]) / \mu_g$$

$$\check{S} = (\gamma_s + [(m+k)/e]) / \mu_s$$

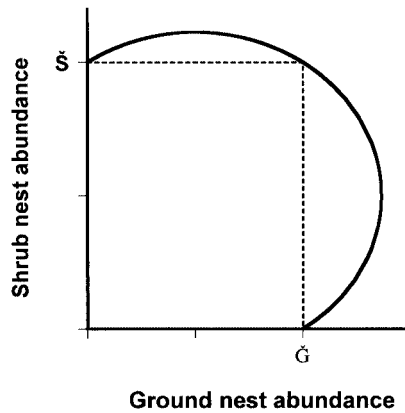


Fig. 1. Graphical analysis of the equal harvest rate isocline for a generalist predator feeding on two prey types in relation to their abundances. Solid line convex to horizontal axis represents the equal harvest rate isocline for a generalist predator that depredates both ground and shrub nests. When the equal harvest rate isocline has a positive slope, the two nest types interact indirectly via apparent exploitation [the signs of their interactions are (+, -)], and when it has a negative slope, via apparent competition [the signs of their interactions are (-, -)]. Ideally, the predator would like to adjust its foraging behaviour so that its equal harvest rate isocline resembles that of a switching predator, indicated by the horizontal dotted line at \check{S} and the vertical dotted line at \check{G} . This would represent an extension of the model that would correspond to the predator's foraging only incidentally on ground nests (where isocline is horizontal) or on shrub nests (where isocline is vertical), respectively (see Schmidt and Whelan, 1998). Parameter values for this figure are: $\alpha_g = 1.5$, $\alpha_s = 1$, $\mu_g = 0.12$, $\mu_s = 0.009$, $\gamma_g = 0.1$, $\gamma_s = 0.2$, $m = 0.01$, $e = 0.1$, $G = 0-30$, $S = 0-40$.

We can determine the slope of the predator's isoclines by implicitly differentiating (9) with respect to G :

$$\partial S/\partial G = \alpha_g \gamma_g + (m+k)\alpha_g/e - 2\mu_g \alpha_g G / [2\mu_s \alpha_s S - [\gamma_s \alpha_s + (m+k)\alpha_s]] \quad (10)$$

To determine the slope of the predator's isoclines in the vicinity of \tilde{G} , we set S in (10) equal to zero, substitute \tilde{G} ($[\gamma_g + (m/e)]/\mu_g$) for G , and simplify:

$$[\alpha_g(\gamma_g + [(m+k)/e])]/[\alpha_s(\gamma_s + [(m+k)/e])] > 0 \quad (11)$$

The slope of the harvest rate isoclines near \tilde{G} is > 0 because (11) is necessarily positive. Similarly, we can find the analogous expression to (11) for the slope in the vicinity of \tilde{S} . The slope of the isoclines near \tilde{S} is also positive.

At the intercepts, the isoclines' slope is positive. To determine where the slope of the isoclines switches from positive to negative (for $G > 0$, $S > 0$), we solved for when the numerator or denominator of equation (10) is positive or negative. The numerator is positive when $G < (\gamma_g + [(m+k)/e])/2\mu_g$ and negative when $G > (\gamma_g + [(m+k)/e])/2\mu_g$. The denominator is positive when $S > (\gamma_s + [(m+k)/e])/2\mu_s$ and negative when $S < (\gamma_s + [(m+k)/e])/2\mu_s$. Along the G -axis, $G = \tilde{G}/2$ is the switch point from positive to negative slope; $S = \tilde{S}/2$ is the switchpoint along the S -axis. Therefore, when $G < \tilde{G}/2$ and $S > \tilde{S}/2$, the slope of the isoclines is positive. When $G > \tilde{G}/2$ and $S > \tilde{S}/2$, the slope of the isoclines is negative. When $G > \tilde{G}/2$ and $S < \tilde{S}/2$, the slope of the isoclines is positive again.

In summary, there are two points along the predator's isocline where its slope switches sign. Along each axis, these points occur halfway between the origin and the respective intercepts (Fig. 1).

Holt (1983) analysed such humped harvest rate isoclines and suggested that, in the regions of prey densities where the slope of the isoclines is positive, the predator is, to some extent, 'suboptimal'. This is because where the slope of the isoclines is positive, total fitness of the predator declines with increasing abundance of one prey. In other words, at prey densities at which the slope of the isoclines is positive, the two prey species (nesting strategies in our scenario) interact indirectly via apparent exploitation [their signs of interaction are, respectively, (+, -)]. At prey densities at which the slope of the isoclines is zero, the prey do not interact. And at prey densities at which the slope of the isoclines is negative, the two prey species (nesting strategies) interact indirectly as apparent competitors [their signs of interaction are (-, -)].

From the perspective of Martin's model, adding frequency dependence to the predator's functional response increases the possible outcomes of shared predation on co-existing prey species. Shared predators can influence indirect interactions among co-occurring prey in a variety of ways (Holt and Kotler, 1987), enhancing co-existence under some circumstances and inhibiting co-existence under others (Ricklefs, 1989). In our case, the circumstances that cause those different outcomes are changes in the relative densities of the prey types:

- At lopsided frequencies of nests, the ground and shrub nest strategies interact via apparent exploitation. Increasing the density of the rarer ($< \frac{1}{2} \tilde{G}$ or $< \frac{1}{2} \tilde{S}$) nest strategy increases the survival of the common ($> \frac{1}{2} \tilde{G}$ or $> \frac{1}{2} \tilde{S}$) nest strategy. Increasing the density of the common nest strategy decreases the survival of the rarer nest strategy.
- At intermediate frequencies of nests, the ground and shrub nest strategies interact via apparent competition. Increased densities of either nest strategy decreases the survival of the other.

An empirical context

During the 1992–97 breeding seasons, C.J. Whelan and K.A. Schmidt intensively studied the demography and reproductive ecology of American robin and wood thrush in deciduous woodlands of the 660 ha Morton Arboretum (collectively called the East Woods, about 175 ha) and Hidden Lake Forest Preserve of DuPage County (about 75 ha). Both sites are located about 45 km west of Lake Michigan in the western suburbs of Chicago, IL. These woodlands have canopies dominated largely by *Acer saccharum*, *Quercus alba*, *Q. rubra* and *Fraxinus americana*, and an understory consisting of *Acer* saplings, understory trees (e.g. *Ostrya virginiana*) and native (*Viburnum* spp.) and non-native (*Lonicera maackii* and *Rhamnus cathartica*) shrubs. At these sites, raccoons and blue jays are by far the most dominant nest predators (Whelan *et al.*, 1994; Schmidt and Whelan, 1998, 1999a; Schmidt, 1999). Although various other small and medium-sized mammals are present, they depredate nests only occasionally.

To determine patterns of substrate use and nest predation on American robin and wood thrush, we located and monitored 40–90 nests of each species each breeding season. Plants commonly used for nesting included native trees (e.g. *Acer*, *Ostrya* and *Prunus*), native shrubs (*Viburnum* and *Crataegus*) and non-native shrubs (*Lonicera maackii* and *Rhamnus cathartica*). For each nest we recorded the height and substrate species, determined the date of nest initiation and, when a nest failed because of predation (>95% failed attempts), ascribed predation to large mammalian or avian predators based on disturbance to the nest and other evidence (tracks, fur, etc.). Predation rate was estimated as the daily mortality rate calculated according to the method of Mayfield (1975).

Results pertinent to the present model indicate shared predation and apparent competition between American robins and wood thrush nesting in the shrub layer (Fig. 2). Over the course of the study, the total number of robin and thrush nests increased in bush honeysuckle (*L. maackii*) and common buckthorn (*R. cathartica*) because of an increased use of those species by the robin (Schmidt and Whelan, 1999b). One consequence of the increased number of robin nests was an increase in the daily mortality on nests of wood thrush. Although nests of both species were located within a single vegetative stratum, the result clearly demonstrates a link (apparent competition) between the two species via nest predation.

We do not have comparable data for natural nests located in different vegetative strata (different nesting guilds, *sensu* Schmidt and Whelan, 1998), but Schmidt and Whelan (1998) demonstrated such a link experimentally. In their study, they used artificial nests baited with quail (*Coturnix japonica*) eggs that were accessible only to raccoons. The experiment consisted of three different nest treatments: Treatment 1 (control) consisted of 8 ground and 8 shrub nests within a plot for a total nest density of 7.1 nests · ha⁻¹ or 3.6 nests · ha⁻¹ for each stratum; Treatment 2 (high-density ground) contained 16 ground and 8 shrub nests; and Treatment 3 (high-density shrub) contained 8 ground and 16 shrub nests (see Schmidt and Whelan, 1998, for details). They found that a greater proportion of all nests were depredated in response to increasing the abundance of ground nests (17.2 vs 30.5%; $F_{1,68} = 7.55$, $P < 0.02$) and to increasing the abundance of shrub nests (17.2 vs 27.6%; $F_{1,68} = 4.78$, $P = 0.07$), indicating short-term apparent competition between nests in the different strata (Fig. 3). Furthermore, as can be seen in Fig. 3, increasing ground nest density increased shrub nest predation, and increasing shrub nest density increased ground nest predation. Together, the results imply that, at the nest densities used in the experiment,

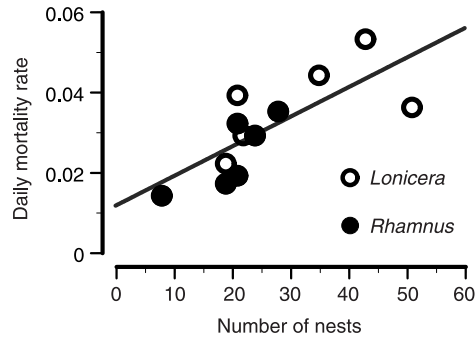


Fig. 2. Daily rates of mortality for wood thrush nests as a function of total American robin and wood thrush nests built in *Lonicera* and *Rhamnus* substrates. In this figure, the increase in total nest abundance was due to an increase in the number of American robins nesting in the two plant species (see Schmidt and Whelan, 1998). The positive slope indicates that as nest overlap in the shrub stratum provided by these two plant species increases, the proportion of wood thrush nests depredated increases, indicating apparent competition between the American robin and wood thrush.

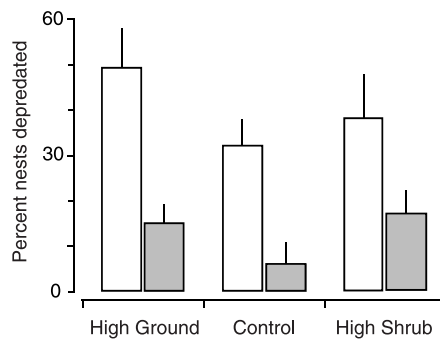


Fig. 3. Proportion of artificial ground (\square) and shrub (\blacksquare) nests depredated by frequency treatment. Increasing the abundance of ground nests (high ground) or shrub nests (high shrub) significantly increased the total number of nests depredated. In addition, the high ground treatment increased the proportion of shrub nests depredated, and the high shrub treatment increased the proportion of ground nests depredated.

the predator's isocline has a negative slope. What has yet to be established is whether, at lopsided nest densities, marginal increases in the density of the rare nest type will increase survival of the abundant nest type, which would be consistent with a positive slope to the predator's isocline at those nest densities.

DISCUSSION

Our model, a direct extension of the model of Courchamp *et al.* (2000), provides an interesting contrast to previous models. The model examines the effect of a predator on two prey species, each in a separate habitat. The predator has a search bias for prey in one habitat but also varies its predation intensity relative to the frequency of prey in the two habitats.

Although the search bias, α , increases the vulnerability of one of the prey species, the predator switches its use of the two habitats relative to prey frequency, which influences the predator's encounter probability with the two prey types. The presence of one prey influences the predator's encounter probability with the other and vice versa. The frequency-dependent foraging behaviour, manifested through the predator's functional response, can actually exacerbate the search bias indicated by α . In contrast, in classic diet choice models, prey co-occur within habitat patches, search is undirected, encounters with prey are random, and hence encounter probabilities are independent of food abundances. So long as all prey offer a sufficiently high energy to handling time ratio, two prey types will interact indirectly as apparent competitors (Holt, 1977). In classic habitat selection models, prey occur in separate habitats, and predators distribute themselves between the habitat types according to their reward within the different habitats following an ideal free distribution. In this case, at equilibrium population sizes, the presence of one prey in its own habitat has no effect on the equilibrium abundance of the other prey in its habitat – there is no indirect effect via a shared predator between prey species occupying separate habitats when predators follow the classic ideal free distribution. The difference in indirect effects between diet choice and habitat selection occurs because in the former, search is entirely undirected with respect to prey type, while in the latter, it is entirely directed towards one prey or the other. Because of the search bias in our model, search is neither entirely directed nor entirely undirected. Rather, search becomes more directed towards the prey with the higher relative abundance. As a consequence, the prey interact indirectly. Over some ranges of prey densities, the interaction between the prey types follows traditional apparent competition (Holt, 1977, 1983) and is $(-, -)$. Over other ranges of prey densities, the interaction becomes $(+, -)$, which we refer to as apparent exploitation.

In contrast to our emphasis on search bias, Courchamp *et al.* (2000) developed their model to address theoretically a problem of conservation concern: the extinction (or extirpation) of native species in the face of the introduction of both an exotic predator species and an exotic prey species. In their scenario, the exotic predator and prey have a long history of association through which the exotic prey species has evolved resistance to the exotic predator. In the three-species food web of their model, highly asymmetric apparent competition (hyperpredation) between the native and the exotic prey species leads to the decline and ultimate local extinction of the native species. In their analysis, Courchamp *et al.* (2000) used simulations to examine the population trajectories of each species under a variety of parameter values. They demonstrated that behavioural adjustments (adaptations) by the native prey to the exotic predator ameliorate more effectively the hyperpredation process than do life-history characteristics such as carrying capacity (K) or intrinsic growth rate (r).

A somewhat similar analysis to ours is that of Schmidt (1998), who proposed a model allowing for a partially directed search mode. In this case, the predator has visual access to two or more habitat types simultaneously (e.g. an insectivorous bird that can simultaneously search nearby branches, twigs and leaves for insect prey). In our model, prey are in separate habitats but are linked indirectly via the predator's response to their frequency distribution in those habitats. In Schmidt's (1998) model, prey experience either $(0, 0)$ or $(-, -)$ indirect effects, depending upon their relative densities in relation to search mode trajectories. This contrasts with the $(-, -)$ or $(+, -)$ interactions that arise from the search bias of our model.

Our model shows how a predator that develops search images and forages in a frequency-dependent manner can, over different ranges of nest densities, promote co-existence via apparent exploitation or inhibit co-existence via apparent competition. This arises because the equal harvest rate isocline of the predator, being humped, has both regions of positive slope and negative slope within the state space of prey densities. Holt (1977) discussed the significance of positively sloped predator isoclines, suggesting that such cases can lead to 'pathological' foraging behaviour. The pathology arises because inclusion of one prey type in the diet decreases the net fitness of the predator. Later, in an insightful analysis of the form of the predator isocline, Holt (1983) described the possibility that predator isoclines could be humped (which he then asserted suggests non-optimal predator foraging behaviour for the reason just mentioned), and he analysed the mechanisms that can lead to such isoclines. In general, those involve handling time and prey switching, or other constraints on foraging behaviour of the predator. Holt (1983) cited two empirical studies providing evidence for the existence of positively sloped predator equal harvest rate isoclines.

Apparent exploitation

In our model, at certain prey densities, an increase in the population density of one of the prey decreases the predator's harvest rate and hence its absolute fitness. The point at which the increase of this prey type hurts the predator is crucial. At this point, the predator's harvest isocline switches from having a negative to a positive slope (Fig. 1). In our example, at lopsided densities of the prey types, a marginal increase in the density of the rare nest type decreases the predator's total harvest rate, which, in turn, decreases the predator's fitness and, ultimately, its population size. As a consequence of the decreased harvest rate and population size of the predator, survival of the abundant nest type increases. On the other hand, a marginal increase in the density of the abundant nest type increases the predator's harvest rate, its fitness and its population size, causing a reduction in the survival of both nest types. In this region of prey densities, therefore, the signs of the prey's indirect interactions on each other are (+, -), indicating apparent exploitation (the signs of the interaction arise indirectly via the shared predator). At higher densities of both nest types, a marginal increase in either nest density increases total harvest, which leads to a positive numerical response of the predator. In this region of prey densities, the signs of the prey's indirect effects on each other are (-, -), which is Holt's (1977) apparent competition.

In this model, the prey on which the predator has a higher lethal encounter probability (μ) always benefits the predator. It is the prey on which the predator has a low μ that can actually reduce the predator's harvest rate. Increasing the abundance of the favourable prey serves the predator's interests twice and always enhances predator fitness. The predator harvests more of the favourable prey as a consequence of their greater availability, and its search bias further enhances encounters with this favourable prey. Increasing the abundance of the less favourable prey presents the predator with mixed results (sometimes increasing and sometimes decreasing predator fitness). While harvesting more of this prey as a consequence of its availability, the predator suffers, through its search bias, by having its attention diverted away from the favourable prey.

Apparent exploitation can arise through a variety of mechanisms. These mechanisms emerge from the perception abilities of the predator. The mere presence and location of prey may distract or redirect attention from seeking other, often more profitable prey.

Similarly, the addition of microhabitats may necessarily distract a predator and decrease its effectiveness in its preferred microhabitat. Through no fault of the predator, less desirable prey or microhabitats, as 'attention-grabbers', may impede the predator's overall success at finding and harvesting prey. [While it may appear implausible that natural selection would result in such apparently maladaptive search behaviour, any investigator who searches for subjects such as songbird nests is probably aware of the distracting properties of things like dead-leaf clusters suspended within nearby branches of vegetation (C.J. Whelan, personal observations).]

Other scenarios and models can also generate apparent exploitation. Consider random search on multiple prey types (e.g. multiple food type extension of Holling's disc equation). If the predator is constrained to be opportunistic and harvest all encountered prey, then the presence of food types with sufficiently low energy to handling time ratios will depress the predator's overall harvest rate. These unprofitable prey indirectly benefit all other prey types, while the profitable prey always indirectly hurt all prey types. Hence, unprofitable prey interact as indirect mutualists, profitable prey interact as apparent competitors, and pairs of profitable and unprofitable prey interact as apparent exploiters. When there is apparent exploitation, then the predator's equal harvest rate isocline is everywhere positively sloped.

Recognition time (Kotler and Mitchell, 1995), whereby the predator must expend additional time to discern the identity of an encountered prey item, can also produce apparent exploitation. With recognition time, a predator can save time by electing to forage opportunistically even if it means unintentionally consuming unprofitable food items. Increasing the abundance of unprofitable food items can hurt the predator either through increased consumption of these foods, or by encouraging the predator to now spend time identifying and rejecting them. Like the present model, models of recognition time can generate predator equal harvest rate isoclines that have regions of positive (apparent exploitation) and negative (apparent competition) slopes.

Aposematic coloration and mimicry by prey provide perhaps the clearest case of apparent exploitation. Here the unprofitable food (the aposematic model) goes out of its way to assist the predator in its diet choice. The model is free from predation and the predator does not waste time looking for and handling it. Along comes a mimic that exploits the predator's perceptions. Apparent exploitation ensues. As a highly profitable food the mimic may cause the predator to unintentionally consume models, and higher abundances of the models may benefit the mimic as the predators forego entirely this hard-to-distinguish class of prey. The model and mimic generate equal harvest rate isoclines that are everywhere positively sloped.

Application

Communities of songbirds are particularly appropriate systems in which to investigate direct and indirect effects of predation (Hoi and Winkler, 1994; Martin, 1996; Barber and Martin, 1997; Schmidt and Whelan, 1998). Both adult birds and their nests (eggs or nestlings) can fall prey to predators. In many cases, the resident songbird species share the same predator species (e.g. Cooper's hawk, *Accipiter cooperii*, preying on adult birds of many species; raccoons, *Procyon lotor*, preying on the nests of multiple species). Recognizing the potential role of predation in affecting species co-existence in songbird communities, Martin (1988a,b, 1993b) proposed a model of nest predation based on the concepts of

density-dependent predation and search images. Specifically, Martin proposed that if predators can form search images for nest site locations, and if their nest predation is positively density-dependent, then, over evolutionary time, predators will select for nest site diversification among birds. Over ecological time-scales, nesting bird species that possess diverse nest site locations will be more likely to co-exist (i.e. selective predation may act as an ecological sieve, influencing species co-existence).

Martin's model emphasized density-dependent predation, but once there is nest site diversification, then, in addition to density-dependent predation, there is also potential for frequency-dependent predation (Ricklefs, 1989; Schmidt and Whelan, 1999b; Reitsma and Whelan, 2000). Although both processes (density dependence coupled with search images versus frequency-dependent predation) may result in species diversification and influence co-existence in particular assemblages, they are not identical processes, as shown by our model. In our model, in accord with Holt and Kotler (1987), when prey species share predator species, interactions among the prey species can be $(-, -)$ or $(+, -)$. Our analysis supports the suggestion of Ricklefs (1989) that interactions of multiple prey species subject to shared predation may limit or decrease species diversification and co-existence under some circumstances, even while promoting co-existence under others.

Prospectus

The model invites at least two extensions. First, as formulated, the possible disjunct between prey value, e , and the predator's search bias creates a potential 'pathology' (Holt, 1977) in which the predator, in a suboptimal manner, unwittingly switches its attention to the less valuable habitat and prey (Holt, 1983). Second, the prey and predators may engage in a game in which the predators respond to the density and distribution of prey species, and the prey species adjust their habitat selection in response to both the predator's behaviours and proclivities and the strategies of co-occurring prey species.

From these considerations, a logical next step is to extend the present model to incorporate a game theoretic perspective (Schmidt and Whelan, 1999b; Reitsma and Whelan, 2000). To accomplish this, one would first consider a predator that can adjust its search biases or habitat preferences (α) to changes in the densities and distributions of prey types among the available habitats. Prey switching in response to the distribution of prey is sensible, but over-switching is not. In fact, a predator with perfect information should direct all of its activity towards the most favourable habitat. The perfectly informed predator would have habitat-specific preferences that would switch from $\alpha_1 = 1$ and $\alpha_2 = 0$ to $\alpha_1 = 0$ and $\alpha_2 = 1$ at appropriate densities of prey in each of two habitat types. Reality must be somewhere in between the case of fixed habitat preferences and that of perfect habitat preferences.

Furthermore, the prey may have latitude to respond to the abundance of predators, the abundance of other prey, the habitat strategy of the predators and the habitat selection of other prey. For this to happen, there must be uncertainty or variability in the opportunities afforded by the two habitats for the prey. Otherwise the prey should simply distribute themselves according to an ideal free distribution that balances their population growth rates, and which can be achieved behaviourally or by simply letting populations grow to equilibrium within each habitat.

These extensions of the theory would indicate the robustness of the humped equal harvest rate isocline and determine whether flexible predator and/or prey behaviour support

Martin's hypothesis for density-dependent nest predation promoting the co-existence of birds via their nesting strategies.

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