Evolutionary Ecology Research, 2004, **6**: 1063–1081

Do short-term behavioural responses of consumers in tri-trophic food chains persist at the population time-scale?

Vlastimil Křivan[1]* and Etienne Sirot[2]

[1]*Department of Theoretical Biology, Institute of Entomology, Academy of Sciences of the Czech Republic, Branišovská 31, 370 05 České Budejovic, Czech Republic and*
[2]*Biologie Evolutive, LAUBS, Université de Bretagne Sud, Campus de Tohannic, BP 573, 56017 Vannes, France*

ABSTRACT

We present a theoretical study of individual response to the feeding efficiency–predation risk trade-off in tri-trophic food chains where consumers (the species at the intermediate trophic level) choose their activity level to maximize their fitness. We derive the optimal level of foraging activity as a function of resource abundance and predation risk, and we study the long-term effects of these behavioural traits on population dynamics. We compare different models of population dynamics and we show that long-term predictions depend heavily on the model description. In particular, linear functional responses lead to maximal foraging activity of consumers at the population equilibrium, while Holling type II functional responses can lead to moderate or low levels of consumer activity at the population equilibrium.

Keywords: adaptive foraging, anti-predator behaviour, feeding efficiency–predation risk trade-off, food chain, population dynamics, trait-mediated indirect interactions, trophic cascade.

INTRODUCTION

It has been observed that in tri-trophic food chains consisting of resources, consumers and predators, consumers often adjust their activity level (e.g. the speed of movement, use of safe habitats, level of vigilance) in response to the density of predators and/or the density of resources (for reviews, see Lima, 1998a,b; Bolker *et al.*, 2003; Werner and Peacor, 2003; Schmitz *et al.*, 2004). For example, it is well documented that consumers respond to predator presence by reducing their foraging activity (e.g. Milinski and Heller, 1978; Sih, 1980, 1986, 1987; Cerri and Fraser, 1983; Lima and Dill, 1990; Werner, 1992; Werner and Anholt, 1993; Beckerman *et al.*, 1997; Schmitz, 1998; Lima and Bednekoff, 1999; Peacor and Werner, 2001; Bolker *et al.*, 2003; Werner and Peacor, 2003). The effect of resources on

---

* Author to whom all correspondence should be addressed. e-mail: krivan@entu.cas.cz

consumer foraging activity is less clear. In the majority of experiments (reviewed in Werner and Anholt, 1993), consumer activity decreased with increased resources. However, some research has suggested the opposite pattern (Gilliam and Fraser, 1987; Holbrook and Schmitt, 1988).

As behavioural traits are observed on a short-term time-scale, the question arises as to whether they persist on a longer population time-scale, or if they attenuate without influencing population dynamics and food web structure. Many recent theoretical studies have predicted that adaptive behavioural traits influence population dynamics (reviewed in Bolker *et al.*, 2003). However, most of these studies have focused mainly on the effects of adaptive diet selection in food webs comprising one-predator/two-prey and/or two-predators/one-prey community module(s) (Tansky, 1978; Teramoto *et al.*, 1979; Holt, 1984; Gleeson and Wilson, 1986; Abrams and Matsuda, 1993; Fryxell and Lundberg, 1994, 1997; Křivan, 1996, 1997, 1998, 2003; Křivan and Sikder, 1999; van Baalen *et al.*, 2001; Grand, 2002; Křivan and Eisner, 2003; Křivan and Schmitz, 2003). A general conclusion from these studies is that adaptive foraging weakens exploitative and/or apparent competition (Holt, 1977), which allows for species survival when compared with a similar food web without adaptive behaviour. These studies support the idea that animal behaviour has a strong influence on food web dynamics and food web structure – that is, it does not attenuate at the longer population time-scales.

Abrams (1984) considered a linear food chain where the intermediate species (consumers) optimizes the amount of time spent foraging. He explored two particular cases: Case I considers the Lotka-Volterra model in which the cost of foraging increases quadratically with time, while the resource intake rate increases linearly. Case II assumes that the resource intake rate levels off as consumer foraging time continues to increase, while the cost of foraging increases linearly with time. Based on these assumptions, Abrams showed that at the population equilibrium there exists an optimal intermediate foraging time that maximizes consumer fitness. Once again, this result supports the idea that short-term behavioural traits persist at the longer population time-scales. However, two points should be clarified: What is the mechanism that promotes these behavioural effects to influence population dynamics, as there is no apparent competition in food chains? Second, does Abrams' conclusions also hold for models where costs and benefits scale at the same order (e.g. linearly), or are derived from more mechanistic principles?

MODELS

We consider a tri-trophic food chain consisting of resources R, consumers C and predators P. Population dynamics are described by the following general model

$$\begin{aligned}
\frac{\mathrm{d}R}{\mathrm{d}t} &= rR\left(1-\frac{R}{K}\right) - f_R(u, R)C \\
\frac{\mathrm{d}C}{\mathrm{d}t} &= e_C f_R(u, R)C - f_C(u, C)P - m_C C \qquad (1) \\
\frac{\mathrm{d}P}{\mathrm{d}t} &= (e_P f_C(u, C) - m_P)P
\end{aligned}$$

where r and K are classical demographic parameters for the resource, f_R and f_C are functional responses, e_C and e_P are the efficiency constants that describe how food is transformed into new individuals, and m_C and m_P are per capita mortality rates of consumers and predators, respectively. Parameter u represents the consumer activity level, which can have several meanings depending on the particular system under study. For example, it can be the proportion of time devoted to foraging, or the proportion of time an animal spends in the food patch. Throughout the rest of the article, we will assume that the consumer activity level is normalized between 0 and 1, and both functional responses are an increasing function of the consumer activity level. This is because very active foragers find more prey, but are also more exposed to predators.

Together with model (1) we assume that consumers choose their activity level so as to maximize fitness. In this article, we assume that consumer fitness (W) is measured as the per capita population growth rate:

$$W = \frac{1}{C}\frac{\mathrm{d}C}{\mathrm{d}t} = e_C f_R(u, R) - f_C(u, C)\frac{P}{C} - m_C \to \max_u$$

Thus, for each fixed set of population densities we can compute the optimal consumer strategy:

(i) If consumer fitness W is an increasing (decreasing) function of the consumer activity level, then consumer activity should be at its maximal [$u = 1$ (minimal; $u = 0$)] level.
(ii) If consumer fitness W has a maximum at some intermediate consumer activity level u^* ($0 \le u^* \le 1$), then the consumer level of activity should be intermediate and given by u^*.

The necessary (derivative of the fitness function equals to zero) and sufficient (second derivative of the fitness function is negative) conditions for this to happen are:

$$e_C \frac{\partial f_R}{\partial u}(u^*, R) - \frac{\partial f_C}{\partial u}(u^*, C)\frac{P}{C} = 0 \quad \text{and} \quad e_C \frac{\partial^2 f_R}{\partial u^2}(u^*, R) - \frac{\partial^2 f_C}{\partial u^2}(u^*, C)\frac{P}{C} < 0$$

Providing that population dynamics settle at an equilibrium, we can compute the consumer activity level at this population equilibrium. This approach allows us to determine the long-term effects of adaptive consumer behaviour on population dynamics. The population equilibrium is located on the consumer isocline, which is given by the following equation ($W = 0$):

$$\frac{P}{C} = \frac{e_C f_R - m_C}{f_C}$$

By substituting this expression in conditions (i)–(ii) above, we obtain the following possibilities for the foragers' activity level at the population equilibrium:

(A) If

$$\frac{e_C f_R - m_C}{e_C f_C} < \frac{\partial f_R}{\partial u} \Big/ \frac{\partial f_C}{\partial u}$$

for all u's between 0 and 1, then at the equilibrium consumer activity will be at its maximum ($u = 1$). If the opposite inequality holds, then at the population equilibrium consumer activity will be at its minimum ($u = 0$).

(B) If

$$\frac{e_C f_R - m_C}{e_C f_C} = \frac{\partial f_R}{\partial u} \Big/ \frac{\partial f_C}{\partial u}$$

for some $u = u^*$ ($0 \le u^* \le 1$), then at the population equilibrium consumer activity will be at an optimal intermediate level ($u = u^*$).

In what follows, we use the above conditions to study the long-term evolution of the consumer activity level at population equilibrium for some population models widely used in the ecological literature.

The Lotka-Volterra model

Here we assume that functional responses in model (1) are linear with respect to densities, which corresponds to the following Lotka-Volterra model:

$$\begin{aligned}
\frac{\mathrm{d}R}{\mathrm{d}t} &= rR\left(1 - \frac{R}{K}\right) - \lambda_R(u)CR \\
\frac{\mathrm{d}C}{\mathrm{d}t} &= (e_C\lambda_R(u)R - \lambda_C(u)P - m_C)C \qquad (2) \\
\frac{\mathrm{d}P}{\mathrm{d}t} &= (e_P\lambda_C(u)C - m_P)P
\end{aligned}$$

where the consumer activity level u influences the encounter rate of consumers with resources (λ_R) and the encounter rate of predators with consumers (λ_C). Several functional dependencies of the encounter rate on the activity level have been considered in the literature (Yapp, 1955; Skellam, 1958; Werner and Anholt, 1993). In what follows, we will consider two particular dependencies.

The linear case

Here we assume that the encounter rate of consumers with resources is a linear function of consumer activity:

$$\lambda_R(u) = u\lambda_{RC} \qquad (3)$$

Control parameter u can be the proportion of time the consumer is actively searching for resources in a homogeneous environment, or it can be the proportion of time the consumer spends in the feeding patch if food is spatially distributed (in which case $1 - u$ is the proportion of time the consumer spends in a refuge).

Equation (3) implies that consumers do not feed while they are inactive (one-patch model) or when they are in the refuge (two-patch model). Similarly, we assume that consumers suffer a basic encounter rate with predators while inactive (or while in the refuge), denoted by λ_{PC}. While active (or while outside the refuge), the encounter rate with predators increases linearly:

$$\lambda_C(u) = u\lambda_{CP} + \lambda_{PC} \tag{4}$$

Because

$$\frac{e_C f_R - m_C}{e_C f_C} = \frac{e_C u \lambda_{RC} R - m_C}{e_C(\lambda_{PC} + u\lambda_{CP})C} < \frac{\lambda_{RC} R}{\lambda_{CP} C} = \frac{\partial f_R}{\partial u} \Big/ \frac{\partial f_C}{\partial u}$$

for every consumer activity level $0 \le u \le 1$, then condition (A) holds. This implies that at the population equilibrium, the consumer activity level will be maximal (i.e. $u = 1$). To understand this somewhat paradoxical result, we follow the dynamics of the system in the resource–predator phase space (see Fig. 1). There are two lines in Fig. 1. The first line ('equal fitness' line; dashed line) is the line along which the derivative of consumer fitness is equal to zero:

$$P = \frac{e_C \lambda_{RC}}{\lambda_{CP}} R$$

Above this line it is more profitable for consumers to be inactive because predation risk is high when compared with resource level, while below this line it is better to be maximally active.

The second line is the consumer isocline (dotted line in Fig. 1). It is given by:

$$P = \frac{e_C \lambda_{RC}}{\lambda_{CP} + \lambda_{PC}} R - \frac{m_C}{\lambda_{CP} + \lambda_{PC}} \tag{5}$$

This line clearly describes the cascading effect because equilibrial resource and predator densities are linearly proportional. An increase in predator equilibrial density is followed

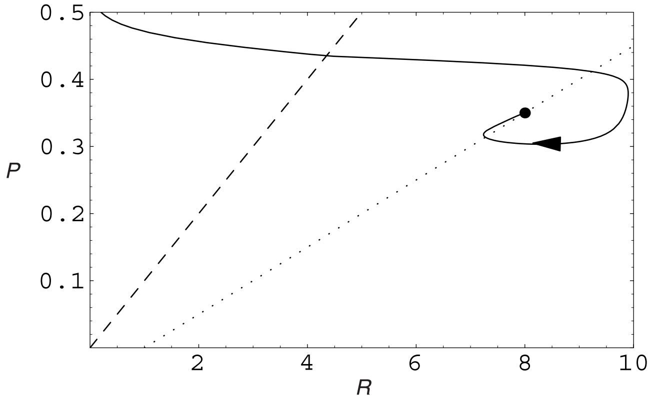

Fig. 1. Population dynamics of model (2) with linear dependencies of encounter rates (3) and (4) on the consumer activity level. The equal fitness line (dashed line) separates the part of the phase space where consumers feed at the maximal speed ($u = 1$; lower triangular region) from the part of the phase space where they are inactive ($u = 0$; upper triangular region). Parameters: $K = 10$, $r = 1$, $\lambda_{RC} = 1$, $\lambda_{CP} = 1$, $\lambda_{PC} = 1$, $e_C = 0.1$, $e_P = 0.05$, $m_C = 0.1$, $m_P = 0.02$.

by an increase in the resource equilibrial density. Note that this isocline lies in the lower triangular part of the resource–predator phase space where consumer activity is maximal. Thus, along the isocline we cannot simultaneously have rare prey and abundant predators. This is why consumers are predicted to display maximal activity at equilibrium.

Figure 1 shows a typical trajectory of model (2). Above the equal fitness line, consumers do not feed at all and resource density increases. The trajectory enters the region where it pays consumers to feed on resources and the trajectory converges to the corresponding equilibrium of the food chain.

Thus, the model predicts that although consumers switch their activity level between 0 and 1 as resource and predator densities change, these behavioural effects attenuate on the population time-scale, and at the population equilibrium consumers will maximize their activity level. In what follows, we explore the consequences of a non-linear dependency of encounter rates on consumer activity levels.

The Yapp model

Yapp (1955; see also Skellam, 1958; Werner and Anholt, 1993) derived mechanistically a formula for the encounter rate of a searching predator with a moving consumer. This formula assumes that individuals move on a two-dimensional plane and the direction of predator movement is randomly and uniformly distributed with respect to prey movement direction:

$$Z = 2rN\sqrt{v^2 + u^2}$$

Here Z is the encounter rate of a prey individual with the predator, r is the perceptual radius of the predator, N is the predator density, and v and u are average foraging speeds of the predator and prey, respectively. In what follows, we re-scale this formula as

$$\lambda_C(u) = \frac{Z}{N} = \sqrt{\lambda_{CP}u^2 + \lambda_{PC}v^2}$$

where u and v are the activity levels of consumers and predators, respectively. Once again, for simplicity we set $v = 1$ as our analysis focuses on the consumer activity level rather than on the predator activity level. We assume that resources are immobile, which implies that the search rate of consumers for resources is given by formula (3).

Because

$$\frac{e_C f_R - m_C}{e_C f_C} = \frac{e_C u \lambda_{RC} R - m_C}{e_C C\sqrt{\lambda_{PC} + \lambda_{CP}u^2}} < \frac{\lambda_{RC} R\sqrt{\lambda_{PC} + \lambda_{CP}u^2}}{u\lambda_{CP} C} = \frac{\partial f_R}{\partial u} \Big/ \frac{\partial f_C}{\partial u}$$

for every consumer activity level ($0 \le u \le 1$), condition (A) holds. This implies that at the population equilibrium, the consumer activity level is again maximal ($u = 1$).

We now show why this is so. The optimal consumer activity level as a function of resource and predator densities (Appendix 1) is:

$$u^*(R, P) = \begin{cases} \dfrac{e_C \lambda_{RC} R\sqrt{\lambda_{PC}}}{\sqrt{\lambda_{CP}(P^2\lambda_{CP} - e_C^2\lambda_{RC}^2 R^2)}} & \text{if } P > \dfrac{e_C \lambda_{RC} R}{\lambda_{CP}}\sqrt{\lambda_{PC} + \lambda_{CP}} \\ 1 & \text{if } P \le \dfrac{e_C \lambda_{RC} R}{\lambda_{CP}}\sqrt{\lambda_{PC} + \lambda_{CP}} \end{cases} \qquad (6)$$

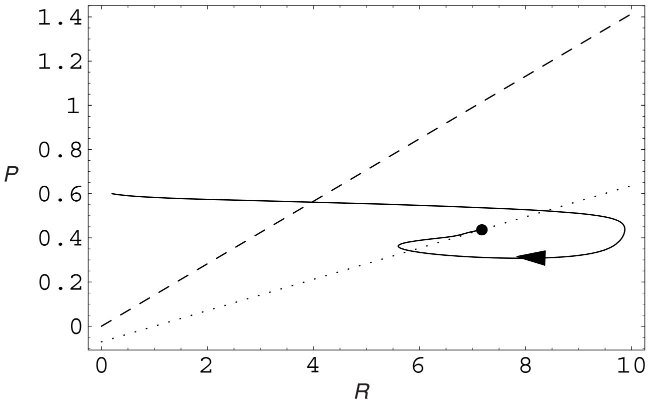

Fig. 2. Population dynamics of model (2) with the optimal consumer behaviour (6) (Yapp model). Below the dashed line the consumer optimal activity level is maximal ($u = 1$), while above this line it is intermediate. Parameters: $K = 10$, $r = 1$, $\lambda_{RC} = 1$, $\lambda_{CP} = 1$, $\lambda_{PC} = 1$, $e_C = 0.1$, $e_P = 0.05$, $m_C = 0.1$, $m_P = 0.02$.

Thus, if predator densities are low (below the dashed line in Fig. 2), it pays for consumers to forage at maximum speed ($u = 1$) because their fitness increases with activity level. Similar to the linear case, we observe that the consumer isocline (dotted line in Fig. 2) is always in the lower triangular part of the resource–predator phase space. Thus, once again, at the population equilibrium we observe a cascading effect (i.e. the linear relation between predator and resource densities) expressed as

$$P = \frac{e_C \lambda_{RC}}{\sqrt{\lambda_{CP} + \lambda_{PC}}} R - \frac{m_C}{\sqrt{\lambda_{CP} + \lambda_{PC}}} \tag{7}$$

which causes the population equilibrium to be in that part of the phase space where consumer activity level is maximal.

Abrams model

Abrams (1984) considered a model where the encounter rate of consumers with resources is a linear function of the consumer activity level, while the encounter rate of predators with consumers increases quadratically with consumer activity. Thus, $\lambda_R(u)$ is given by formula (3) and $\lambda_C(u) = \lambda_{CP} u^2$. Because

$$\frac{e_C f_R - m_C}{e_C f_C} = \frac{e_C \lambda_{RC} R u - m_C}{e_C \lambda_{CP} C u^2} = \frac{\lambda_{RC} R}{2uC\lambda_{CP}} = \frac{\partial f_R}{\partial u} \Big/ \frac{\partial f_C}{\partial u}$$

holds for

$$u^* = \frac{2m_C}{e_C R \lambda_{RC}}$$

it follows that at the population equilibrium the consumer activity will be intermediate (provided $0 < u^* < 1$). This is in agreement with Abrams' conclusion but it does not agree with our previous model, despite the fact that the encounter rate of consumers with predators increases with consumer activity in an accelerating manner in both cases. In Abrams' model, the consumer isocline intersects with the line (in the resource–predator phase space) along which the derivative of consumer fitness ($\partial W/\partial u$) equals zero, which is the necessary condition for optimality. For Yapp's model these two lines never intersect, which excludes the possibility of an intermediate consumer activity level at the population equilibrium.

The optimal consumer activity level as a function of resource and predator densities is given by:

$$u^*(R, P) = \begin{cases} \dfrac{e_C \lambda_{RC} R}{2\lambda_{CP} P} & \text{if } P > \dfrac{e_C \lambda_{RC} R}{2\lambda_{CP}} \\ 1 & \text{if } P \le \dfrac{e_C \lambda_{RC} R}{2\lambda_{CP}} \end{cases} \tag{8}$$

In contrast to the previous two models, the linear relation between the equilibrium resource and predator density (i.e. the linear cascading effect) is lost because in the present case this relation is curvilinear and is given by

$$e_C \lambda_{RC} \frac{e_C \lambda_{RC} R}{2\lambda_{CP} P} R - \lambda_{CP} \left(\frac{e_C \lambda_{RC} R}{2\lambda_{CP} P} \right)^2 P - m_C = 0$$

for $P > (e_C \lambda_{RC} R)/(2\lambda_{CP})$ (dotted line in Fig. 3). Thus, for this model we still observe a cascading effect, but the relation between predators and resources is non-linear. Because of this non-linearity, the equal fitness line intersects with the consumer isocline, which leads to the intermediate consumer activity level at the population equilibrium.

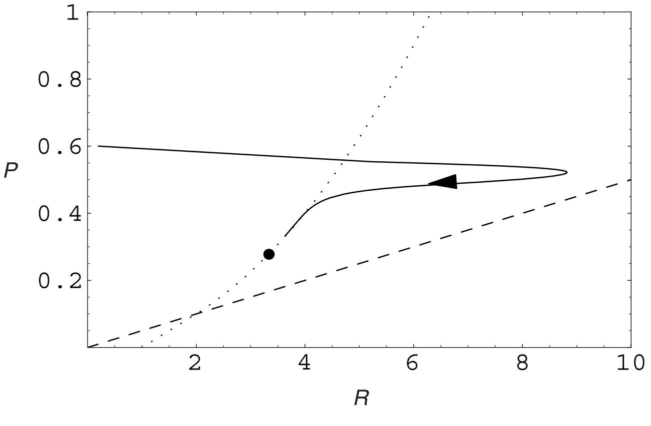

Fig. 3. Population dynamics of model (2) with the optimal consumer behaviour (8) (Abrams' model). Below the dashed line the consumer optimal activity level is maximal ($u = 1$), while above this line it is intermediate. Parameters: $K = 10$, $r = 1$, $\lambda_{RC} = 1$, $\lambda_{CP} = 1$, $\lambda_{PC} = 1$, $e_C = 0.1$, $e_P = 0.05$, $m_C = 0.1$, $m_P = 0.02$.

Holling type II functional response

Here we consider a food chain with the Holling type II functional response and linear dependency of encounter rates on the consumer activity level. We will consider two types of environment: patchy environments and homogeneous environments. We remark that such a distinction does not make sense in the case of the Lotka-Volterra population dynamics because both situations lead to the same model (2). However, when handling times are positive, the two types of environments lead to different models.

Patchy environment

Here we assume that besides the foraging patch with resources there exists a refuge without resources where consumers are protected from predation. In this setting, the parameter u represents the proportion of time an average consumer spends in the foraging patch. On average, the consumer density in the foraging patch is uC. Then, the corresponding population dynamics in the food patch is described by the following model:

$$\begin{aligned}
\frac{\mathrm{d}R}{\mathrm{d}t} &= rR(1 - R/K) - \frac{\lambda_R R u C}{1 + \lambda_R h_R R} \\
\frac{\mathrm{d}C}{\mathrm{d}t} &= \left(e_C \frac{\lambda_R R u}{1 + \lambda_R h_R R} - \frac{\lambda_C u P}{1 + \lambda_C h_C u C} - m_C\right) C \\
\frac{\mathrm{d}P}{\mathrm{d}t} &= \left(e_P \frac{\lambda_C u C}{1 + \lambda_C u h_C C} - m_P\right) P
\end{aligned} \tag{9}$$

Because

$$\frac{e_C f_R - m_C}{e_C f_C} = \frac{(1 + C h_C u \lambda_C)(e_C \lambda_R R u - m_C(1 + h_R \lambda_R R))}{e_C \lambda_C C u (1 + h_R R \lambda_R)} < \frac{\lambda_R R (1 + C h_C u \lambda_C)^2}{C \lambda_C (1 + h_R R \lambda_R)} = \frac{\partial f_R}{\partial u} \Big/ \frac{\partial f_C}{\partial u}$$

for every consumer activity level, it follows from (A) that at the population equilibrium consumers should spend all their time in the foraging patch.

The optimal consumer strategy is (Appendix 2):

$$u^* = \begin{cases} 1 & \text{if } P < \dfrac{e_C \lambda_R R (1 + h_C \lambda_C C)}{\lambda_C + h_R \lambda_C \lambda_R R} \\ 0 & \text{if } P \geq \dfrac{e_C \lambda_R R (1 + h_C \lambda_C C)}{\lambda_C + h_R \lambda_C \lambda_R R} \end{cases} \tag{10}$$

Once again we see that for low predator densities the consumer should be maximally active, while they should be inactive for high predator densities. However, the consumer optimal strategy also depends on the consumer density due to positive handling times. It is a straightforward exercise to show that the consumer isocline is always in the part of the resource–consumer–predator three-dimensional phase space where consumer activity is at its maximum. This is shown in Fig. 4 for a fixed equilibrial consumer density. Figure 4 shows that, despite the fact that the cascading effect is partly lost, because at the population equilibrium the consumer isocline depends not only on resource and predator density but also on the consumer density, the consumer isocline (computed at the predator equilibrium density) is below the dashed line. It is thus again in the part of the resource–predator phase space where consumer activity should be at its maximum.

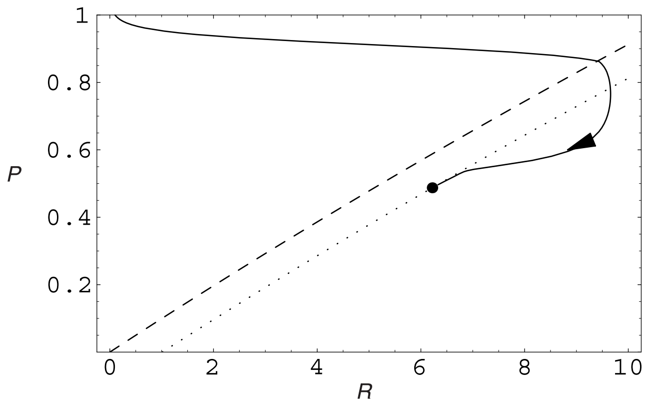

Fig. 4. Population dynamics of model (9) with the optimal consumer behaviour (10) (patchy environment). Below the dashed line the consumer optimal activity level is maximal ($u = 1$), while above this line it is intermediate. Parameters: $K = 10$, $r = 1$, $\lambda_{RC} = 1$, $\lambda_{CP} = 1$, $\lambda_{PC} = 1$, $e_C = 0.1$, $e_P = 0.05$, $m_C = 0.1$, $m_P = 0.02$.

Homogeneous environment

Here we assume a homogeneous environment where consumers are always exposed to predation. At any moment, they may reduce their activity level, which will lower both their feeding efficiency and the probability of being spotted by a predator. The population dynamics is now described by the following model:

$$\begin{aligned}
\frac{\mathrm{d}R}{\mathrm{d}t} &= rR(1 - R/K) - \frac{\lambda_R(u)RC}{1 + \lambda_R(u)h_R R} \\
\frac{\mathrm{d}C}{\mathrm{d}t} &= \left(e_C \frac{\lambda_R(u)R}{1 + \lambda_R(u)h_R R} - \frac{\lambda_C(u)P}{1 + \lambda_C(u)h_C C} - m_C\right) C \qquad (11) \\
\frac{\mathrm{d}P}{\mathrm{d}t} &= \left(e_P \frac{\lambda_C(u)C}{1 + \lambda_C(u)h_C C} - m_P\right) P
\end{aligned}$$

We assume that encounter rates are linear functions of the consumer activity level and they are given by formulas (3) and (4).

Because condition (B) holds for

$$u^* = \frac{h_R m_C + C e_C h_C \lambda_{PC} + \dfrac{\sqrt{e_C(m_C\lambda_{CP} + R\lambda_{PC}\lambda_{RC}(e_C - h_R m_C))(h_R R(1 + C h_C \lambda_{PC})\lambda_{RC} - C h_C \lambda_{CP})}}{\sqrt{R\lambda_{CP}\lambda_{RC}}}}{h_R(e_C - h_R m_C)R\lambda_{RC} - C e_C h_C \lambda_{CP}} \qquad (12)$$

it follows that at the population equilibrium, the consumer activity can be intermediate (provided $0 < u^* < 1$).

To study population dynamics, the optimal consumer strategy is computed explicitly in Appendix 3 as a function of population densities. The optimal consumer strategy depends not only on resource and predator densities, but also on its own density. In fact, because of this dependence on its own density, the classical linear cascading effect (5) is partly lost.

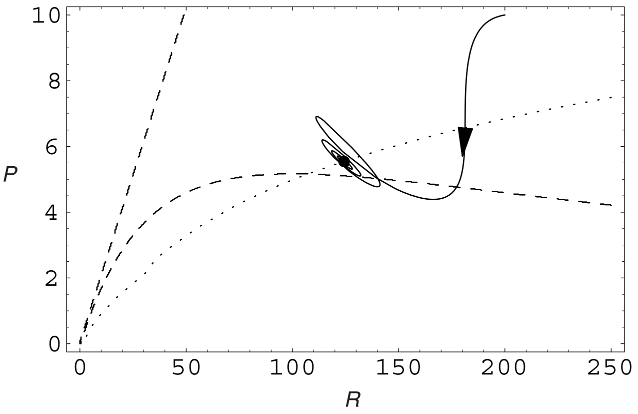

Fig. 5. Population dynamics of model (11) with the optimal consumer behaviour. Between the two dashed lines the consumer optimal activity level is intermediate and given by (12). Below the lower dashed line consumer activity is maximal ($u = 1$), while above the upper dashed line consumers are inactive ($u = 0$). Parameters: $K = 200$, $r = 2$, $\lambda_{RC} = 1$, $\lambda_{CP} = 0.5$, $\lambda_{PC} = 0.5$, $e_C = 0.1$, $e_P = 0.6$, $h_R = 0.01$, $h_C = 0.01$, $m_C = 0.1$ $m_P = 1$.

In the region in Fig. 5 between the two dashed lines, consumer activity level is intermediate. Because the population equilibrium which is located on the consumer isocline is in this part of the phase space, the consumer activity level at this equilibrium is intermediate too.

Figure 6 shows dependency of the stable interior equilibrium on the resource carrying capacity. The left-hand panels assume that consumers are non-adaptive and their activity is at maximum ($u = 1$). We observe the classical increase in the abundance of trophic levels across a resource productivity gradient (Oksanen *et al.*, 1981). When all three species co-exist, higher resource productivity leads to higher resource and predator densities without influencing consumer densities. This is the classical trophical cascading effect. The right-hand panels show the same model providing that consumers are adaptive. For low resource carrying capacities, it pays for consumers to forage with maximum activity. As predator density increases, foragers start to decrease their foraging activity, which results in an increase in consumer abundance. In fact, decreased resource intake by consumers is overcompensated for by decreased predation mortality due to the non-linear effects. Thus, for high carrying capacities for resources, intermediate or even low levels of foraging activity are predicted at population equilibrium. We note that the resulting population dynamics may converge to a stable equilibrium level (as shown in Fig. 6), or that they may fluctuate either regularly or irregularly due to the paradox of enrichment (Hastings and Powell, 1991).

DISCUSSION

Recent empirical work (for reviews, see Lima, 1998a,b; Werner and Peacor, 2003) has shown that consumers adjust their feeding effort adaptively to changing predation risk and resource levels. However, most of these empirical studies are short-term experiments that do not allow us to predict the effect of such behavioural traits on population dynamics and food web topology. There are two possibilities: either these behavioural traits attenuate in

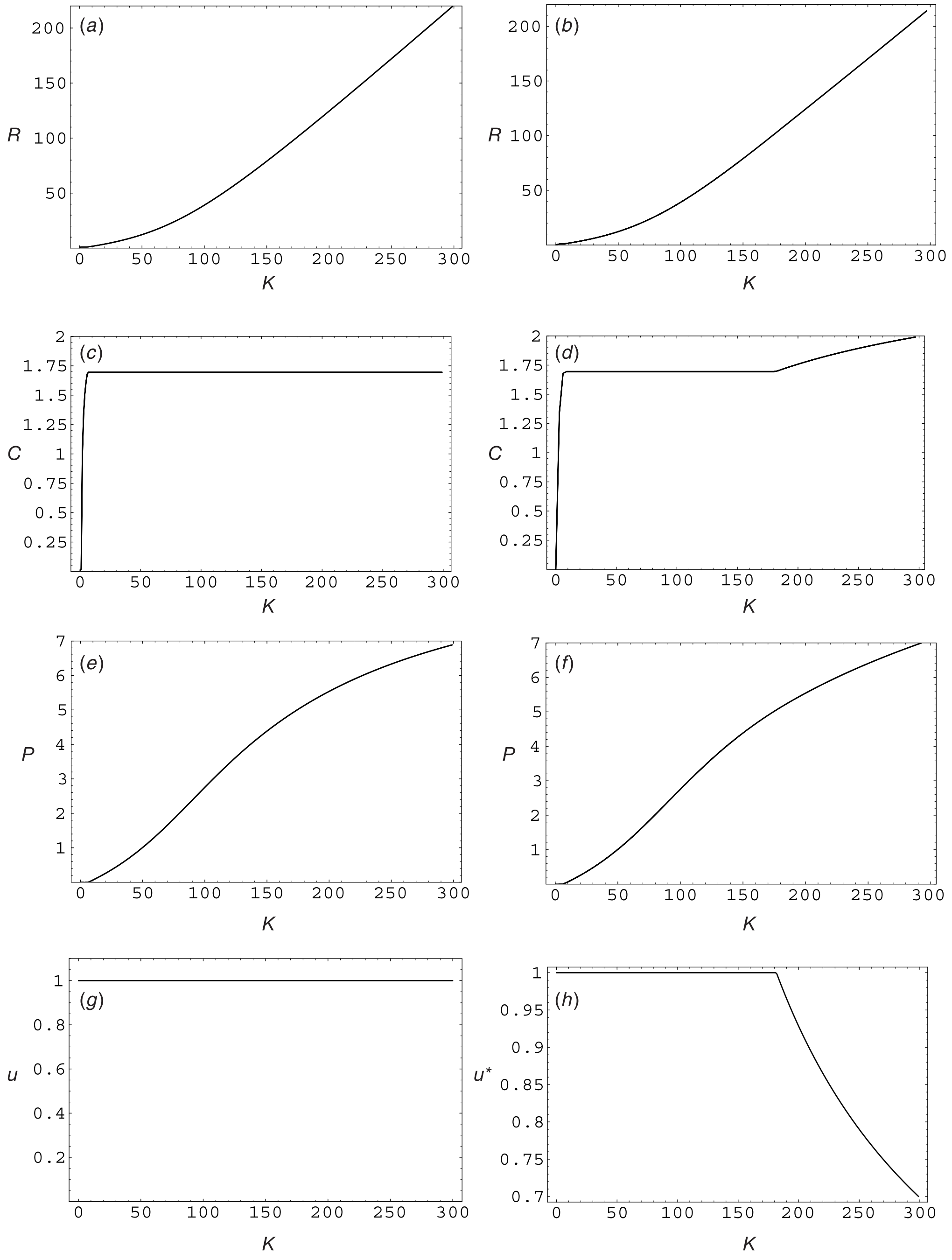

Fig. 6. The dependence of population equilibrium densities of model (11) on the resource carrying capacity. The left-hand panels assume inflexible consumers that forage at maximum speed ($u = 1$). The right-hand panels assume adaptive foragers that follow a strategy that maximizes their fitness. Parameters: $r = 2$, $h_C = 0.01$, $h_R = 0.01$, $\lambda_{RC} = 1$, $\lambda_{CP} = 0.5$, $\lambda_{PC} = 0.5$, $e_C = 0.1$, $e_P = 0.6$, $m_C = 0.1$, $m_P = 1$.

time and produce little or no effect on longer time-scales (population, evolutionary), or they are preserved on longer time-scales and influence food web dynamics. At present, this issue is not resolved satisfactorily, because there is no empirical evidence.

Recent theoretical work (for a review, see Bolker *et al.*, 2003) on the effect of adaptive foraging on predator–prey population dynamics showed that adaptivity makes apparent competition (Holt, 1977) weaker, which leads to higher species persistence. Most of the food webs considered in these studies comprised a two-resource/one-consumer community module (Holt, 1995), where apparent competition is a strong driving force. Thus, the general prediction from these studies is that animal behaviour has important population dynamical consequences. In other words, short-term animal behaviour does not attenuate at a longer, population dynamical time-scale. Similarly, Abrams (1984) showed that in food chains where consumers trade-off foraging risk with resource intake, the consumer activity level at the population equilibrium is intermediate. Once again, this suggests that short-term animal behaviour has important consequences for population dynamics. However, Abrams assumed that the predation risk and foraging benefits scale differently. In particular, he assumed that either predation risk increases quadratically as a function of foraging activity while the resource consumption rate increases linearly, or the resource consumption rate levels off while the predation risk increases linearly. Thus, it is unclear if Abrams' conclusion holds also in cases where both predation risk and foraging rate scale the same with consumer activity level, or when these functions are more mechanistically derived.

A general condition for consumer activity to be intermediate at the population equilibrium is that the consumer isocline intersects with that part of the species density phase space where the short-term optimal consumer activity level (i.e. the activity level predicted for a fixed population density) is intermediate. To investigate the likelihood of this situation, we considered a series of models with increasing complexity.

For the Lotka-Volterra type model we considered two possibilities. The first model assumed that predation risk and foraging rate increase linearly with increased consumer activity. The second model used a more mechanistically derived relation between consumer activity and predation risk (Yapp, 1955; Skellam, 1958), which implies that the consumer foraging rate will increase linearly with increasing consumer activity, but the predation risk increases with predation risk in an accelerating way. Both these models predict that at the population equilibrium, consumer activity should be at its maximum.

The first model considers type I functional responses and assumes that the encounter rate between consumers and predators increases linearly with consumer activity. It predicts that consumers will switch from maximum activity to total inactivity, depending on the resource–predator balance. Consumers will be inactive when predators are abundant and resources are scarce. Otherwise, they will accept that foraging represents a certain risk of predation, which increases with resource density. In accordance with this prediction, experimental work shows that one can increase foragers' tolerance to predation risk by increasing food abundance (Abrahams and Dill, 1989). However, these behavioural effects attenuate at a longer population time-scale because at the population equilibrium consumer activity is at its maximum.

Qualitatively similar results hold for the second model, where we introduce a more realistic link between consumer activity and exposure to predators. The only difference is that, for intermediate predator and resource abundance, consumers will display intermediate activity. However, at the population equilibrium, we will again observe maximal activity for consumers. Thus, our models predict that if consumers modulate their activity as a response to resource availability and predation threat, this is unlikely to have an influence on the equilibrium population densities in food chains.

We next considered two models with the Holling type II functional response, which gives a more realistic measure of foraging success. This led to separate models for the case where consumers can lower predation risk by reducing their foraging activity on the food patch (homogeneous environment), and the case where consumers avoid predators by occupying a refuge (heterogeneous environment). In the case of heterogeneous environments, predictions agree with those of the first models. For fixed population densities, consumers will use the refuge when prey are scarce and predators are numerous. These results support the conclusions of many experimental studies (Werner *et al.*, 1983; Kotler *et al.*, 1993; Lagos *et al.*, 1995; Abramsky *et al.*, 1996; Downes and Shine, 1998). However, at the population equilibrium consumers spend all their time in the feeding area, which corresponds to maximal consumer activity.

In the case of homogeneous environments, predictions are different from the previous three models because at the population equilibrium consumer activity can be intermediate (Fig. 6). This particular conclusion comes from the non-linearities in the Holling type II functional response. At very high resource levels, decreasing the level of activity has very little effect on feeding rate, but significantly decreases predation risk. Thus, animals prefer to be less active. Since this effect only appears for high densities of resources, it will be observed at the population equilibrium when resource carrying capacity is high (see Fig. 6). Thus, if the environment is very productive, consumers are expected to display only moderate activity at the population equilibrium. This is a major difference from the previous models, which may also explain some contradictory results with respect to consumer behaviour under predation risk (Lima and Dill, 1990).

In general, our models predict that for fixed population densities, consumer activity should be high when resource density is high when compared with predator density, while consumers should be inactive when predator density is high when compared with resource density. For some intermediate predator and resource densities, consumer activity can be intermediate, which depends on the particular model. The trophic cascading effect in food chains with linear functional responses predicts that predator and consumer equilibrial densities are positively correlated (Oksanen *et al.*, 1981). Thus, it is impossible in a food chain to have a high equilibrial predator density and low equilibrial resource density, or vice versa. An increase in resources due to enrichment leads directly to a proportional increase in predator density. Thus, the cascading effect predicts that at the population equilibrium, resources will always be high when compared with predator equilibrium density, which is the condition under which consumer activity should be maximal. Thus it is the cascading effect which diminishes the short-term behavioural effects at the population time-scale. However, the linear relation (cascading effect) between resources and predators can be weakened by various non-linearities. This happens in our model with the Holling type II functional response, where at the population equilibrium we do not observe the classical trophic cascade, because the relation between predator and resource densities is non-linear. Similarly, in Abrams' (1984) model, the relation between resources and predator densities is also non-linear, which is the cause of the observed intermediate consumer activity at the population equilibrium.

We have shown that indirect interactions in food webs may either promote or dilute the effect of observed short-term foraging behaviours on a longer, population time-scale. While apparent competition in community modules with more resources is an important driving force promoting a short-term effect on the population time-scale, the linear relation between predator and resource population densities (cascading effect) seems to dilute short-term behavioural effects on a longer, population time-scale. Thus, experimental ecologists should consider these indirect effects carefully, to predict population dynamical consequences of short-term experiments.

ACKNOWLEDGEMENTS

We thank Sebastian Diehl, Yoh Iwasa and Chris Steer for helpful comments. This work was supported by the NATO Collaborative Linkage Grant 979213. V.K. was supported by the Institute of Entomology (AV ČR Z5007907, K6005114) and GA ČR (201/03/0091).

REFERENCES

Abrahams, M. and Dill, L. 1989. A determination of the energetic equivalence of the risk of predation. *Ecology*, **70**: 999–1007.

Abrams, P.A. 1984. Foraging time optimization and interactions in food webs. *Am. Nat.*, **124**: 80–96.

Abrams, P. and Matsuda, H. 1993. Effects of adaptive predatory and anti-predator behaviour in a two-prey-one-predator system. *Evol. Ecol.*, **7**: 312–326.

Abramsky, Z., Strauss, E., Subach, A., Kotler, B. and Riechman, A. 1996. The effect of barn owls (*Tyto alba*) on the activity and microhabitat selection of *Gerbillus allenbyi* and *G. pyramidum. Oecologia*, **105**: 313–319.

Beckerman, A.P., Uriarte, M. and Schmitz, O.J. 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Ecology*, **94**: 10735–10738.

Bolker, B., Holyoak, M., Křivan, V., Rowe, L. and Schmitz, O.J. 2003. Connecting theoretical and empirical studies of trait-mediated interactions. *Ecology*, **84**: 1101–1114.

Cerri, R.D. and Fraser, D.F. 1983. Predation and risk in foraging minnows: balancing conflicting demands. *Am. Nat.*, **121**: 552–561.

Downes, S. and Shine, R. 1998. Heat, safety or solitude? Using habitat selection experiments to identify a lizard's priority. *Anim. Behav.*, **55**: 1387–1396.

Fryxell, J.M. and Lundberg, P. 1994. Diet choice and predator–prey dynamics. *Evol. Ecol.*, **8**: 407–421.

Fryxell, J.M. and Lundberg, P. 1997. *Individual Behavior and Community Dynamics*. London: Chapman & Hall.

Gilliam, J.F. and Fraser, D.F. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology*, **68**: 1856–1862.

Gleeson, S.R. and Wilson, D.S. 1986. Equilibrium diet: optimal foraging and prey coexistence. *Oikos*, **46**: 139–144.

Grand, T. 2002. Foraging–predation risk trade-offs, habitat selection, and the coexistence of competitors. *Am. Nat.*, **159**: 106–112.

Hastings, A. and Powell, T. 1991. Chaos in a three-species food chain. *Ecology*, **72**: 896–903.

Holbrook, S.J. and Schmitt, R.J. 1988. The combined effects of predation risk and food reward on patch selection. *Ecology*, **69**: 125–134.

Holt, R.D. 1977. Predation, apparent competition, and the structure of prey communities. *Theor. Pop. Biol.*, **12**: 197–229.

Holt, R.D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *Am. Nat.*, **124**: 377–406.

Holt, R.D. 1995. Community modules In *Multitrophic Interactions in Terrestrial Systems* (A.C. Gange and V.K. Brown, eds.), pp. 333–350. Oxford: Blackwell Scientific.

Kotler, B., Brown, J., Slotow, J., Goodfriend, W. and Strauss, M. 1993. The influence of snakes on the foraging behavior of gerbils. *Oikos*, **67**: 309–316.

Křivan, V. 1996. Optimal foraging and predator–prey dynamics. *Theor. Pop. Biol.*, **49**: 265–290.

Křivan, V. 1997. Dynamic ideal free distribution: effects of optimal patch choice on predator–prey dynamics. *Am. Nat.*, **149**: 164–178.

Křivan, V. 1998. Effects of optimal antipredator behavior of prey on predator–prey dynamics: role of refuges. *Theor. Pop. Biol.*, **53**: 131–142.

Křivan, V. 2003. Competitive coexistence caused by adaptive predators. *Evol. Ecol. Res.*, **5**: 1163–1182.

Křivan, V. and Eisner, J. 2003. Optimal foraging and predator–prey dynamics, III. *Theor. Pop. Biol.*, **63**: 269–279.

Křivan, V. and Schmitz, O.J. 2003. Adaptive foraging and flexible food web topology. *Evol. Ecol. Res.*, **5**: 623–652.

Křivan, V. and Sikder, A. 1999. Optimal foraging and predator–prey dynamics, II. *Theor. Pop. Biol.*, **55**: 111–126.

Lagos, V., Contreras, L., Meserve, P., Gutierrez, J. and Jaksic, F. 1995. Effects of predation risk on space use by small mammals: a field experiment with a neotropical rodent. *Oikos*, **74**: 259–264.

Lima, S.L. 1998a. Nonlethal effects in the ecology of predator–prey interactions. *Bioscience*, **48**: 25–34.

Lima, S.L. 1998b. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Stress and Behavior*, **27**: 215–290.

Lima, S.L. and Bednekoff, P.A. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *Am. Nat.*, **153**: 649–659.

Lima, S.L. and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, **68**: 619–640.

Milinski, M. and Heller, R. 1978. Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.). *Nature*, **275**: 642–644.

Oksanen, L., Fretwell, S.D., Arruda, J. and Niemelä, P. 1981. Exploitation ecosystems in gradients of primary productivity. *Am. Nat.*, **118**: 240–261.

Peacor, S.D. and Werner, E.E. 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. *Proc. Natl. Acad. Sci. USA*, **98**: 3904–3908.

Schmitz, O.J. 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. *Am. Nat.*, **151**: 327–342.

Schmitz, O.J., Křivan, V. and Ovadia, O. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol. Lett.*, **7**: 153–163.

Sih, A. 1980. Optimal behavior: can foragers balance two conflicting demands? *Science*, **210**: 1041–1043.

Sih, A. 1986. Antipredator responses and the perception of danger by mosquito larvae. *Ecology*, **67**: 434–441.

Sih, A. 1987. Prey refuges and predator–prey stability. *Theor. Pop. Biol.*, **31**: 1–12.

Skellam, J.G. 1958. The mathematical foundations underlying the use of line transects in animal ecology. *Biometrics*, **14**: 385–400.

Tansky, M. 1978. Switching effect in a prey–predator system. *J. Theor. Biol.*, **70**: 263–271.

Teramoto, E., Kawasaki, K. and Shigesada, N. 1979. Switching effect of predation on competitive prey species. *J. Theor. Biol.*, **79**: 303–315.

Van Baalen, M., Křivan, V., van Rijn, P.C.J. and Sabelis, M. 2001. Alternative food, switching predators, and the persistence of predator–prey systems. *Am. Nat.*, **157**: 512–524.

Werner, E.E. 1992. Individual behavior and higher-order species interactions. *Am. Nat.*, **140**: S5–S32.

Werner, E.E. and Anholt, B.R. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *Am. Nat.*, **142**: 242–272.

Werner, E.E. and Peacor, S.D. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology*, **84**: 1083–1100.

Werner, E., Gilliam, J., Hall, D. and Mittelbach, G. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, **64**: 1540–1548.

Yapp, W.B. 1955. The theory of line transects. *Bird Study*, **3**: 93–104.

APPENDIX 1: THE OPTIMAL CONSUMER STRATEGY FOR THE LOTKA-VOLTERRA MODEL WHEN THE ENCOUNTER RATE WITH RESOURCES IS A NON-LINEAR FUNCTION OF ACTIVITY

The derivative of the fitness function $1/C\mathrm{d}C/\mathrm{d}t$ is:

$$e_C R\lambda_{RC} - \frac{u\lambda_{CP}P}{\sqrt{\lambda_{CP}u^2 + \lambda_{PC}}}$$

At the point of local maxima, the derivative equals 0, which gives

$$u = \frac{e_C\lambda_{RC}R\sqrt{\lambda_{PC}}}{\sqrt{\lambda_{CP}(P^2\lambda_{CP} - e_C^2\lambda_{RC}^2R^2)}}$$

The second derivative of the fitness function is:

$$-\frac{P\lambda_{CP}\lambda_{PC}}{(u^2\lambda_{CP} + \lambda_{PC})^{3/2}}$$

Thus, provided u is between 0 and 1, it is the point where the fitness function maximizes. This is so, provided predation risk is high enough, i.e. $P > e_C\lambda_{RC}R/\lambda_{CP}\sqrt{\lambda_{PC} + \lambda_{CP}}$. For smaller predator densities, the fitness function is maximized when $u = 1$.

APPENDIX 2: THE OPTIMAL CONSUMER STRATEGY FOR THE PATCH MODEL (9)

The derivative of the consumer fitness with respect to consumer activity is:

$$\frac{e_C R(1 + Ch_C u\lambda_C)^2\lambda_R - P(\lambda_C + h_R R\lambda_C\lambda_R)}{(1 + Ch_C u\lambda_C)^2(1 + h_R R\lambda_R)}$$

Solving for a local extremum on the interval [0, 1] gives one candidate solution:

$$u = \frac{\sqrt{P(1 + h_R R\lambda_R)}}{\sqrt{e_C R\lambda_R Ch_C}\sqrt{\lambda_C}} - \frac{1}{Ch_C\lambda_C}$$

However, the second derivative at this point is positive, which implies that the fitness function attains its local minimum. Consequently, on the interval [0, 1] the consumer fitness function achieves its maximum either at 0 or at 1. Trivial algebra shows that the maximum is given by formula (10).

APPENDIX 3: THE OPTIMAL CONSUMER STRATEGY FOR MODEL (11)

The derivative of the consumer fitness with respect to consumer activity is:

$$\frac{e_C R(1 + Ch_C(u\lambda_{CP} + \lambda_{PC}))^2\lambda_{RC} - P\lambda_{CP}(1 + h_R Ru\lambda_{RC})^2}{(1 + Ch_C(u\lambda_{CP} + \lambda_{CP}))^2(1 + h_R Ru\lambda_{RC})^2}$$

Solving for a local extremum on the interval [0, 1] gives one candidate solution:

$$u = \frac{\sqrt{P\lambda_{CP}} - \sqrt{e_C R\lambda_{RC}}(1 + Ch_C\lambda_{PC})}{Ch_C\lambda_{CP}\sqrt{e_C R\lambda_{RC}} - h_R\lambda_{RC}R\sqrt{P\lambda_{CP}}}$$

The second derivative at this point is:

$$-\frac{2R^{3/2}\lambda_{CP}^{3/2}(Ch_C\sqrt{e_C\lambda_{CP}} - h_R\sqrt{PR\lambda_{RC}})^4\lambda_{RC}^{3/2}}{\sqrt{e_C}P(h_R R(1 + Ch_C\lambda_{PC})\lambda_{RC} - Ch_C\lambda_{CP})^3}$$

Provided

$$h_R R(1 + Ch_C\lambda_{PC})\lambda_{RC} - Ch_C\lambda_{CP} < 0$$

then the consumer fitness achieves its local minimum at the above point and it maximizes either at 0 or at 1, which gives

$$u^*(R, C, P) = \begin{cases} 1 & \text{if } P < \dfrac{e_C R(1 + Ch_C\lambda_{PC})(1 + Ch_C(\lambda_{CP} + \lambda_{PC}))\lambda_{RC}}{\lambda_{CP} + h_R R\lambda_{CP}\lambda_{RC}} \\[2ex] 0 & \text{if } P > \dfrac{e_C R(1 + Ch_C\lambda_{PC})(1 + Ch_C(\lambda_{CP} + \lambda_{PC}))\lambda_{RC}}{\lambda_{CP} + h_R R\lambda_{CP}\lambda_{RC}} \end{cases}$$

If

$$h_R R(1 + Ch_C\lambda_{PC})\lambda_{RC} - Ch_C\lambda_{CP} > 0$$

then the consumer fitness achieves at the candidate point its maxima, provided the point is between 0 and 1. This leads to

$$u^*(R, C, P) = \begin{cases} \dfrac{\sqrt{P\lambda_{CP}} - \sqrt{e_C R \lambda_{RC}}(1 + Ch_C\lambda_{PC})}{Ch_C\lambda_{CP}\sqrt{e_C R\lambda_{RC}} - h_R\lambda_{RC}R\sqrt{P\lambda_{CP}}} & \text{if} \quad \dfrac{e_C R(1 + Ch_C(\lambda_{CP} + \lambda_{PC}))^2\lambda_{RC}}{\lambda_{CP}(1 + h_R R\lambda_{RC})^2} \leq \\ & P \leq \quad \dfrac{e_C R(1 + Ch_C\lambda_{PC})^2\lambda_{RC}}{\lambda_{CP}} \\ 0 & \text{if } P > \dfrac{e_C R(1 + Ch_C\lambda_{PC})^2\lambda_{RC}}{\lambda_{CP}} \\ 1 & \text{if } P < \dfrac{e_C R(1 + Ch_C(\lambda_{CP} + \lambda_{PC}))^2\lambda_{RC}}{\lambda_{CP}(1 + h_R R\lambda_{RC})^2} \end{cases}$$