

Thermal games: frequency-dependent models of thermal adaptation

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Summary

1. Most models of thermal adaptation ignore biotic interactions, and those that do consider biotic interactions assume that competitors or predators cannot respond to adaptation by the focal species. Nevertheless, real biotic interactions involve responsive entities, which can be more accurately modelled using evolutionary game theory.
2. We present a two-part analysis of a thermal game between prey and predators. First, we model a game in which prey choose patches on the basis of operative temperature and predation risk, whereas predators choose patches on the basis of prey density. Second, we consider how this thermal game influences the evolution of the prey's thermal physiology.
3. The solution of the thermal game is an evolutionarily stable Nash equilibrium in which prey divide their time equally among a range of thermal patches while predators bias their hunting efforts toward warmer patches, even though they derive no thermoregulatory benefit from doing so. Furthermore, the optimal range of temperatures selected by prey and predators increases as the lethality of predators increases.
4. This thermal game potentially influences the evolution of the prey's thermal physiology. When predators are less lethal, prey should thermoregulate over a narrower range of temperatures, resulting in selection for thermal specialization of physiological performance. But when predators are very lethal, prey should thermoregulate over a broad range of temperatures; in this case, prey pay no fitness cost for being thermal generalists.
5. Evolutionary game theory provides a powerful tool for generating hypotheses about the effects of biotic interactions on evolution in heterogeneous environments.

Key-words: game theory, Nash equilibrium, performance breadth, temperature, thermal performance curve, thermal optimum, thermoregulation

Introduction

Mathematical models have played an increasingly prominent role in the study of thermal adaptation (reviewed by Angilletta *et al.* 2006; Angilletta 2009). The current theory focuses on four widespread phenomena: (i) the behavioural regulation of temperature (Huey & Slatkin 1976); (ii) the thermal sensitivity of performance (Lynch & Gabriel 1987; Gilchrist 1995); (iii) the thermal acclimation of physiology (Gabriel & Lynch 1992; Gabriel 1999); and (iv) the thermal plasticity of the life history (Berrigan & Charnov 1994; Yampolsky & Scheiner 1996). These models formalize hypotheses about costs and benefits to determine the optimal phenotypes in specific thermal environments. By doing so, the models generate quantitative predictions that thermal biologists can evaluate through comparative and experimental studies.

Despite the proliferation of evolutionary models, many phenomena in thermal biology remain poorly understood (Angilletta 2009). For example, researchers recently questioned the ability of Huey and Slatkin's (1976) model of optimal thermoregulation to explain the behaviour of lizards (Blouin-Demers & Nadeau 2005). Similarly, observed patterns of thermal sensitivity often deviate from predicted patterns (Angilletta *et al.* 2002). Finally, the thermal plasticity of size at maturity continues to puzzle life historians (Angilletta & Dunham 2003; Angilletta *et al.* 2004). The mismatches between theoretical predictions and empirical observations call into question the simplifying assumptions that permeate current models of thermal adaptation. In particular, these models assume that genotypes evolve in a biotic vacuum, where interactions with other genotypes do not occur. Yet the interactions among organisms – be they competitors, predators or prey – certainly impose costs that influence thermal adaptation. Unfortunately, such costs were placed on the 'back

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burner' of theoretical development and have only recently moved from this position (e.g. see Hughes & Grand 2000).

Meanwhile, a growing body of empirical evidence confirms the influence of biotic interactions on thermal adaptation. The seminal work of Magnuson *et al.* (1979) revealed that conspecifics partition thermal resources in a manner that resembles the partitioning of nutritional resources. In the presence of competitors, an individual may either monopolize or abandon preferred microclimates (e.g. see Regal 1971; Beitinger & Magnuson 1975; Medvick *et al.* 1981). Likewise, predators alter the behaviours of organisms seeking to balance the costs and benefits of thermoregulation. Shuttling animals would more likely encounter ambush predators or attract actively foraging predators. Terrestrial ectotherms spend less time basking when their perception of risk increases (Downes 2001; Polo *et al.* 2005), and aquatic ectotherms avoid thermally favourable waters when they contain predators or their chemical cues (Lampert 1989; Loose & Dawidowicz 1994; Gerald & Spezzano 2005). Clearly, interactions such as competition and predation should become part of our theory of thermal adaptation.

In this article, we generate novel insights about adaptation to thermal heterogeneity by modelling an ecological interaction between predators and prey. We start by considering the adaptation of thermoregulatory behaviour in prey with a fixed thermal physiology. Then, we move on to consider the coadaptation of thermoregulatory behaviour and thermal physiology. Both of these traits have been modelled previously without an explicit consideration of ecological interactions (Huey & Slatkin 1976; Gilchrist 1995). Existing models could be used to predict the evolutionary impact of competition or predation (see Huey & Slatkin 1976), but this approach treats competitors, predators, and prey as inert features of the environment (Lima 2002). Alternatively we model the coevolution of predators and prey as an evolutionary game (Maynard Smith 1982), in which the fitness of a particular genotype depends on the strategies adopted by other genotypes (i.e. frequency-dependent selection). As we will show, an evolutionary game predicts qualitatively different selective pressures than traditional models of thermal adaptation.

A thermal game between predators and prey

In this section, we develop a game model of thermoregulation under predation risk. The current model of optimal thermoregulation describes the strategy that maximizes net energetic gain in a heterogeneous environment (Huey & Slatkin 1976). According to this model, effective thermoregulation enhances an organism's energetic gain, but imposes an energetic cost associated with travelling between patches. The optimal strategy of thermoregulation would maximize the net energetic benefit. This strategy does not depend on the presence of other organisms. In contrast, we model the optimal thermoregulation of individuals when (i) prey must simultaneously gain energy and avoid predators, and (ii) predators can respond to the behaviour of prey. The first condition acknowledges that many animals experience

habitat-specific risks, and these risks can impose a trade-off between thermoregulation and survival. The second condition acknowledges that predators are not 'black boxes', imposing a fixed predation risk; rather, predators can forage adaptively for resources just as their prey do. By allowing predators to behave adaptively, our model becomes a thermal game.

To link thermal heterogeneity of the environment to the rate of energetic gain, we rely on the concept of a thermal performance curve (Huey & Stevenson 1979). This curve describes the relationship between an organism's temperature and its physiological performance. A typical performance curve has a mode and a breadth. The mode reflects the body temperature that maximizes performance (the thermal optimum). The breadth reflects the range of body temperatures that enables some degree of performance (the performance breadth). In our case, the performance consists of the rate of energetic gain (Joules/time). For a given performance curve, we can rank patches in a thermally heterogeneous environment based on an organism's physiological performance, with superior patches offering operative temperatures closer to the thermal optimum. The qualitative behaviour of the model does not depend on whether poor patches are warmer or cooler than the thermal optimum, as long as we can rank all patches by their impact on performance. Therefore, our hypothetical environment consists of patches that are equal to or colder than the thermal optimum. Thus warm patches enhance the rate of energetic gain relative to cold patches. In the discussion, we touch on the evolutionary consequences of patches that are hotter than the thermal optimum.

We investigate the thermal game by solving for the Nash equilibrium strategies of thermoregulating prey and their predators. The Nash equilibrium consists of the pair of prey and predator strategies such that if all individuals use their respective Nash strategies, no individual could improve its fitness by using an alternative strategy. We then show that this Nash equilibrium is dynamically stable to perturbations from the equilibrium. An evolutionary game differs from a traditional optimality model, where one uses a hypothetical fitness landscape to find the phenotype that maximizes the fitness of an organism (Maynard Smith 1978). In an evolutionary game, this process becomes more complex because the fitness landscape changes fluidly as phenotypes become more or less frequent within a population (hence the term frequency-dependent selection).

In our thermal game, each strategy consists of the time spent in microhabitats that differ in operative temperature (i.e. thermal patches). The fitness of a prey depends on its body temperature in a microhabitat as well as its risk of predation. The fitness of a predator depends only on its success at capturing prey. The thermal game resembles previously described predator-prey games in which prey select microhabitats on the basis of nutritional rather than thermal resources (e.g. Hugie & Dill 1994; Sih 1998; Alonzo 2002; Sih 2005; Abrams 2007). Importantly, our model differs from or extends previous models in several ways. First, we use different fitness functions than most models of predator-prey games. In other models, players instantaneously realize their energetic

benefits as fitness; consequently, fitness can be represented as the rate of reproduction minus the rate of predation (e.g. see Abrams *et al.* 2007). Instead, we assume that a prey must survive a finite period before realizing fitness from its energetic gain, as would be true for most organisms. Second, many games have been solved by assuming that prey seek to minimize the ratio of predation risk to energetic gain (Sih 1998; Rosenheim 2004). This rule applies most readily to cases in which each prey reproduces after obtaining a threshold energetic state and seeks to minimize its chance of dying before reproduction (Gilliam & Fraser 1987; Brown & Kotler 2004). Alternatively, we assume that prey seek to maximize the product of survivorship and fecundity as a function of their energetic gain over a finite period (Mitchell *et al.* 1990; Brown & Kotler 2004). Finally, we go beyond the classic game between predators and prey in two microhabitats to consider a game in many microhabitats, each defined by an operative temperature. Ultimately, this generalization enables us to investigate the coadaptation of thermoregulatory behaviour and thermal physiology in prey.

THE BASIC MODEL

We first consider the simple case of an environment that consists of two microhabitats, which differ in operative temperature (hereafter referred to as patches). A prey allocates t_1 and t_2 units of time to the warm and cool patches, respectively (Table 1). The sum of these allocations equals the time available during the active season, t_{\max} (i.e. $t_{\max} = t_1 + t_2$). Similarly, a predator allocates v_1 and v_2 units of time to the same patches (where, $v_{\max} = v_1 + v_2$). We wish to find the Nash equilibrium for the predators and prey, defined as the combination of t_1^* , t_2^* and v_1^* , v_2^* such that any individual (prey or predator) using a different time allocation cannot have higher fitness.

We define prey fitness (G) as the product of fecundity (F) and survivorship to maturity (S):

$$G = FS. \quad \text{eqn 1}$$

This function describes the fitness of a semelparous organism (Abrams 1991; Brown 1999), but it could also describe the fitness of an iteroparous organism if F is defined as survivor's fitness (Brown 1999), which is future fecundity discounted by survivorship. For simplicity, we will refer to F as fecundity.

Table 1. Definitions of mathematical symbols

Symbol	Definition
e_i	Rate of energetic gain by prey in patch i
t_i	Time spent by prey in patch i
v_i	Time spent by predator in patch i
u	Lethality of predators
π	Rate of conversion of consumed prey to predators
b	Breadth of prey's thermal performance curve
Ω	Scaling factor for prey's thermal performance curve
T_{opt}	Thermal optimum of prey

We assume that fecundity increases linearly or asymptotically as the energetic state of a prey (X) increases:

$$\frac{\partial F}{\partial X} > 0 \quad \text{eqn 2a}$$

and

$$\frac{\partial^2 F}{\partial X^2} > 0. \quad \text{eqn 2b}$$

The energetic state of a prey depends on its use of the thermal patches. If e_i equals the net rate of energetic gain in patch i , the energetic state becomes

$$X(t_1, t_2) = e_1 t_1 + e_2 t_2.$$

The probability that a prey survives to the end of the season declines exponentially over time, according to the duration of exposure to and the rate of predation in each patch (see Brown 1999). The rate of predation in patch i equals the predator's lethality (u) multiplied by the time the predator spends in this habitat (v_i); for simplicity, we assume that the predator achieves the same lethality in both habitats. Under this condition, the fitness of a prey (G) corresponds to

$$G(t_1, t_2, v_1, v_2) = F(e_1 t_1 + e_2 t_2) e^{-u(v_1 t_1 + v_2 t_2)}. \quad \text{eqn 3}$$

Although prey do not directly compete in this model, they can indirectly influence each other's fitness by affecting the behaviour of predators.

The fitness of a predator increases with the number of prey that it consumes, but does not depend directly on the operative temperature of its microhabitat. The latter assumption has two biological interpretations: the model describes either an ectothermic predator with a wide performance breadth or an endothermic predator with a wide thermoneutral zone. We also assume that each predator hunts within an exclusive territory; thus different predators do not simultaneously deplete prey within the same area. This assumption seems reasonable because many predators maintain territories. A predator hunts for prey by allocating time to each patch within its home range. Thus, the fitness of the predator (H) corresponds to

$$H(v_1, v_2, t_1, t_2, N) = \pi N (1 - e^{-u(t_1 v_1 + t_2 v_2)}), \quad \text{eqn 4}$$

where N equals the number of prey within a predator's home range at the beginning of the season, and π equals the efficiency with which a predator converts prey into offspring. Because predators maintain exclusive territories, each predator's fitness does not depend directly on the behaviours of its conspecifics.

FINDING THE NASH EQUILIBRIUM

For any given prey strategy, there is at least one corresponding predator strategy that is unbeatable in the sense that no other

predator strategy would yield greater fitness. We refer to this set of unbeatable strategies as the predators' set of 'best responses.' Likewise, for any strategy adopted by predators, there is at least one 'best response' strategy for prey. The intersection of the predator and prey best response sets yields a combination of strategies at which no individual predator or prey can achieve higher fitness by changing its strategy unilaterally. We refer to this intersection of best response sets as a behavioural Nash equilibrium. In this section we solve for the behavioural Nash equilibrium in the thermal game. Then, in the following section, we demonstrate that this behavioural equilibrium is dynamically stable.

We start by finding a predator's best response to the prey's strategy. For any pair of predator and prey strategies, a predator should attempt increase its allocation of time to whichever patch yields the higher rate of fitness gain ($\partial H/\partial v_i$), unless both patches confer equal rates for some combination of v_1 and v_2 . In other words, a predator should attempt to increase v_i (and decrease v_j) if

$$\frac{\partial H(v_1, v_2, t_1, t_2)}{\partial v_i} > \frac{\partial H(v_1, v_2, t_1, t_2)}{\partial v_j} \tag{eqn 5}$$

But if $v_i = v_{\max}$, then the predator cannot increase v_i , and its best response (\hat{v}_1, \hat{v}_2) is to allocate all of its time to patch i , and none of its time to patch j (i.e. $\hat{v}_i = v_{\max}$ and $\hat{v}_j = 0$). On the other hand, if $v_i < v_{\max}$, the predator should increase v_i until either $v_i = v_{\max}$, or the rates of fitness gain in the two patch types equal one another. In the latter case, the predator's best response (\hat{v}_1, \hat{v}_2) is given by:

$$\left. \frac{\partial H(v_1, v_2, t_1, t_2)}{\partial v_1} \right|_{i_1} = \left. \frac{\partial H(v_1, v_2, t_1, t_2)}{\partial v_2} \right|_{i_2} \tag{eqn 6}$$

For the predators' fitness function (see eqn 4), the patches confer equal rates of fitness gain if and only if the prey spend equal time in both patches:

$$t_1 = t_2. \tag{eqn 7}$$

Interestingly, this requirement does not depend on the behaviour of predators. Furthermore, if the prey allocates equal time to both patches, all predator strategies yield the same fitness. In this case, the joint behavioural equilibrium depends entirely on how the behaviour of predators influences the fitness of prey (see below).

To find a prey's best response (\hat{t}_1, \hat{t}_2) to the predators' strategy, we take the partial derivative of the prey's fitness with respect to the time spent in each patch. As with a predator, a prey should increase its allocation to whichever patch yields the higher rate of fitness gain ($\partial G/\partial t_i$), unless both patches confer equal rates for some combination of t_1 and t_2 . Thus, the prey should increase t_i and decrease t_j if

$$\frac{\partial G(t_1, t_2, v_1, v_2)}{\partial t_i} > \frac{\partial G(t_1, t_2, v_1, v_2)}{\partial t_j}, \tag{eqn 8}$$

as long as $t_i < t_{\max}$. If $t_i = t_{\max}$, a prey's equilibrium strategy consists of allocating all of its time to patch i . But if $t_i < t_{\max}$, a prey should increase t_i until the rates of fitness gain in the two patches equal one another:

$$\left. \frac{\partial G(t_1, t_2, v_1, v_2)}{\partial t_i} \right|_{i_{ji}} = \left. \frac{\partial G(t_1, t_2, v_1, v_2)}{\partial t_j} \right|_{i_j} \tag{eqn 9}$$

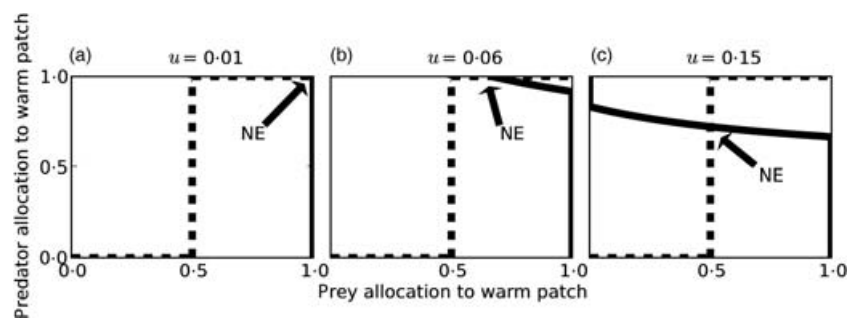
For the prey's fitness function (see eqn. 3), the patches confer equal rates of fitness gain if

$$e_1 - uv_1 \left[\frac{F}{\partial F/\partial X} \right]_{i_1} = e_2 - uv_2 \left[\frac{F}{\partial F/\partial X} \right]_{i_2} \tag{eqn 10}$$

Each side of eqn 10 represents the marginal value of time spent in a patch, defined as the rate of energetic gain minus the cost of predation. The cost of predation depends not only on the predator's behaviour, but also on the potential fitness that the prey would lose if consumed by a predator. This potential fitness, expressed in units of energy, equals the ratio of fecundity over the derivative of fecundity with respect to the energetic state (Brown *et al.* 2004). Obviously, this ratio depends on the behaviour of prey. A prey that allocates more time to the warm patch increases its energetic state (X), which in turn increases its predation cost (see eqns 2a and 2b). Consequently, a prey might equalize the two sides of eqn 10 by simply allocating time to whichever habitat yields the higher rate of fitness gain.

We can use eqn 7 to generate a curve illustrating how the best response of predators varies with the behaviour of prey, and then use eqn 10 to generate another curve that shows how the best response of prey varies with behaviour of predators. The intersection of these curves corresponds to the behavioural Nash equilibrium. Figure 1 shows how this joint behavioural equilibrium depends on the lethality of predators. At low

Fig. 1. The Nash equilibrium (NE) depends on the lethality of predators (u). The Nash equilibrium resides at the intersection of the best response curves of predators (dashed line) and prey (solid line). As the predator lethality increases, both prey and predators should spend less time in the warm patch. At relatively high predator lethality, the prey divides its time equally between the warm and cool patches, while the predator allocates more time to the warm patch.



lethality, both predators and prey should allocate all of their time to the warm patch (Fig. 1a). As predators become more lethal, prey should allocate some time to the cool patch, while predators still should hunt only in the warm patch (Fig. 1b). If predators become extremely lethal, prey should allocate equal time to the warm and cool patches, while predators should allocate the majority of their time to the warm patch (Fig. 1c).

BEHAVIOURAL DYNAMICS

Here we show that the joint behavioural Nash equilibrium in the thermal game described above is asymptotically stable. An equilibrium is said to be asymptotically stable if perturbations from the equilibrium decay over time, returning the system to the equilibrium. Such stability cannot in general be assumed for predator–prey games. Recent analyses of other predator–prey games involving patch choice have revealed cases in which the behavioural equilibrium is not asymptotically stable; in these cases, perturbations from the behavioural equilibrium increase over time, eventually settling into endless limit cycles in which the predators ‘chase’ the prey between patches (Schwinning & Rosenzweig 1990; Abrams 2007).

To investigate the stability of the behavioural equilibrium, we must write dynamic equations for the rates of change in the behaviours of predators and prey. In our model, an individual can move between patches frequently within its lifetime; thus, its behavioural strategy is a continuous variable denoting the amount or proportion of time spent in a particular patch. Abrams *et al.* (2007) referred to such models as ‘rapid’ models, to distinguish them from ‘slow’ models in which the rate of movement between patches is slow relative to demographic processes (see also the adaptive dynamics of behavioural strategies in Chapter 7 of Hofbauer & Sigmund 1998). These authors use the following expression for the time derivative of the behavioural strategy p , defined as the proportion of time spent in one of two patch types,

$$\frac{dp}{dt} = \sigma(p) \left(\frac{dW(p', p)}{dp} \Big|_{p'=p} \right) + \mu(p). \tag{eqn 11}$$

Here, $W(p', p)$ represents the fitness of a behaviourally deviant individual that uses strategy p' while the resident population uses strategy p , $\sigma(p)$ scales the rate of change, and $\mu(p)$ represents non-adaptive change. In some models, $\sigma(p)$ has been defined such that p can never attain the values of 0 or 1 (Abrams *et al.* 2007). We avoid such restrictions by letting σ be a constant. Also, we assume that all behavioural change is adaptive ($\mu(p) = 0$). Furthermore, recall that in our model, the fitness of an individual prey (predator) does not depend directly on the behaviour of other resident prey (predators), but does depend on the behaviour of resident predators (prey).

For our analysis, we define the variables p and q as the proportions of time allocated to the warm patch by the prey and predators, respectively (i.e., $p = t_1/t_{\max}$, and $q = v_1/v_{\max}$). Then, we can use eqn 11 to define the time derivatives for p and q , evaluated at (p', q') :

$$\frac{dp}{dt} = a \frac{\partial G(p, q)}{\partial p} \Big|_{p', q'} \tag{eqn 12a}$$

and

$$\frac{dq}{dt} = z \frac{\partial H(p, q, N)}{\partial q} \Big|_{p', q'}, \tag{eqn 12b}$$

where a and z scale the time dynamics of the behaviours of prey and predators, respectively.

To be asymptotically stable, a behavioural Nash equilibrium at which predators and prey allocate time to both warm and cool patches (Fig. 1c) must satisfy the following condition: the eigenvalues of the associated Jacobian matrix, evaluated at the equilibrium point (p^*, q^*) , must have negative real parts. The Jacobian matrix (J) for this system is defined as

$$J = \begin{bmatrix} \frac{\partial}{\partial p} \left(\frac{dp}{dt} \right) & \frac{\partial}{\partial q} \left(\frac{dp}{dt} \right) \\ \frac{\partial}{\partial p} \left(\frac{dq}{dt} \right) & \frac{\partial}{\partial q} \left(\frac{dq}{dt} \right) \end{bmatrix} \Big|_{(p^*, q^*)}. \tag{eqn 13}$$

The Routh-Hurwitz criteria (Kot 2001) states that the eigenvalues of J have negative real parts if the following two conditions are met:

$$-(J_{11} + J_{22}) > 0 \tag{eqn 14a}$$

and

$$(J_{11}J_{22} + J_{12}J_{21}) > 0, \tag{eqn 14b}$$

where J_{ij} denotes the element in the i th row and j th column of the Jacobian matrix. By examining the derivatives for each element J_{ij} , we confirmed that the joint behavioural equilibrium satisfies the Routh-Hurwitz criteria (see Appendix S1 in Supporting Information). Therefore, we can conclude that the behavioural equilibrium (p^*, q^*) is asymptotically stable. Numerical integration of the dynamical system described by eqns 12a and 12b also illustrates this stability; after being perturbed from the equilibrium, the system exhibits some oscillations, but these oscillations decay over time (Fig. 2).

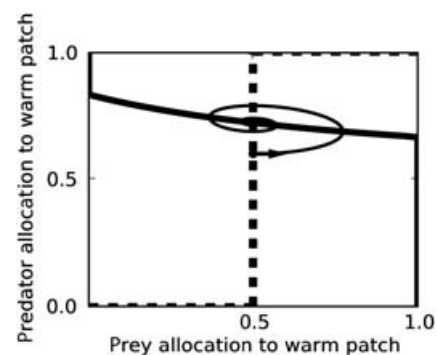


Fig. 2. Adaptive behavioural dynamics illustrate the asymptotic stability of the predator–prey behavioural Nash equilibrium. For the dynamics shown here, the lethality of predators was relatively high ($u = 0.15$), so the prey divide their time between the warm and cool patches.

Although we display only one solution in Fig. 2, numerous integrations yielded the same qualitative results.

GENERALIZING THE MODEL TO INCLUDE MANY MICROHABITATS

Because temperature varies continuously over space, real interactions between predators and prey occur in environments comprising more than two patches. Fortunately, we can generalize the model described in the previous section to characterize the Nash equilibrium in an environment with n patches. In this more general case, the fitness of prey and predators are, respectively,

$$G(t_1, \dots, t_n, v_1 \dots v_n) = F(X(t_1, \dots, t_n))e^{-u \sum_1^n t_i v_i} \quad \text{eqn 15a}$$

and

$$H(v_1, \dots, v_n, t_1, \dots, t_n, N) = N\pi \left(1 - e^{-u \sum_1^n t_i v_i} \right) \quad \text{eqn 15b}$$

The time constraints for prey and predators are

$$\sum_{i=1}^n t_i = t_{\max} \quad \text{eqn 17a}$$

and

$$\sum_{i=1}^n v_i = v_{\max} \quad \text{eqn 17b}$$

By ranking the n patches from warmest to coolest (i.e. $e_1 \geq e_2 \geq \dots \geq e_n$), we can continue the analysis we began for the case of two patches. We start by asking when the prey should allocate some portion of time to the third warmest patch. A prey should only allocate time to the third warmest patch if it already uses the two warmest patches equally; hence, the following condition must hold for a prey to allocate time to the third patch:

$$e_3 > e_2 - uv_2 \frac{F}{\partial F / \partial X} = e_1 - uv_1 \frac{F}{\partial F / \partial X} \quad \text{eqn 19}$$

This condition does not include a predation cost for the third patch because we already know that predators should not hunt in a patch that contains fewer prey than other patches (see eqn 3). If eqn 19 holds, the prey should shift equal amounts of time from the two warmer patches to the third patch. In doing so, the prey reduces its energetic state, and hence its predation costs for patches 1 and 2. If the reduction of predation costs converts the inequality to equality while t_3 is less than t_1 and t_2 , the Nash equilibrium strategy satisfies the following equality:

$$e_3 = e_2 - uv_2 \frac{F}{\partial F / \partial X} = e_1 - uv_1 \frac{F}{\partial F / \partial X} \quad \text{eqn 20}$$

The time allocations will satisfy the following condition:

$$t_1^* = t_2^* > t_3^* > 0 \quad \text{eqn 21a}$$

and

$$v_1^* > v_2^* \text{ and } v_3^* = 0. \quad \text{eqn 21b}$$

But if the inequality in eqn 19 holds even when t_3 equals t_1 and t_2 , then both predator and prey should allocate time to all three patches, and the marginal values of the three patches used by the prey satisfies

$$e_3 - uv_3 \frac{F}{\partial F / \partial X} = e_2 - uv_2 \frac{F}{\partial F / \partial X} = e_1 - uv_1 \frac{F}{\partial F / \partial X}, \quad \text{eqn 22}$$

while the time allocations satisfy

$$t_1^* = t_2^* = t_3^* > 0 \quad \text{eqn 23a}$$

and

$$v_1^* > v_2^* > v_3^* > 0. \quad \text{eqn 23b}$$

In this Nash equilibrium, both predators and prey divide their time among the three patches, with prey using patches equally and predators allocating more time to warmer patches.

We can repeatedly apply these steps to evaluate the conditions for the inclusion of the m th warmest patch if prey already use $m - 1$ patches. In general, the Nash equilibrium consists of prey using m patches equally and perhaps using the next warmest patch to a lesser degree, while predators use m patches and bias their time toward warmer patches. The range of patches used by predators and prey at the Nash equilibrium increases as the lethality of the predator increases (Fig. 3). In the presence of very lethal predators, prey should spread their time across a wide range of temperatures in an effort to reduce encounters with predators. In doing so, the prey suffer a reduction of fecundity. The predators should hunt in patches where they expect to find prey. Although predators receive the same energetic gain in all patches when prey are evenly distributed among patches, a Nash equilibrium occurs only when predators spend more time in patches that provide prey with greater energetic benefits.

How can we consider an environment that encompasses a continuous range of operative temperatures? For simplicity, we could divide this range into n discrete patches. As n becomes larger, the environment gets divided into smaller patches, each defined by a narrower range of temperatures. As n approaches infinity, the problem resembles the case of a continuous distribution of temperatures. In the case of a continuous distribution, we can consider not only the evolution of the prey's thermoregulatory behaviour, but also the evolution of its thermal sensitivity of energetic gain. With this in mind, we now turn to the problem of the coadaptation of behaviour and physiology.

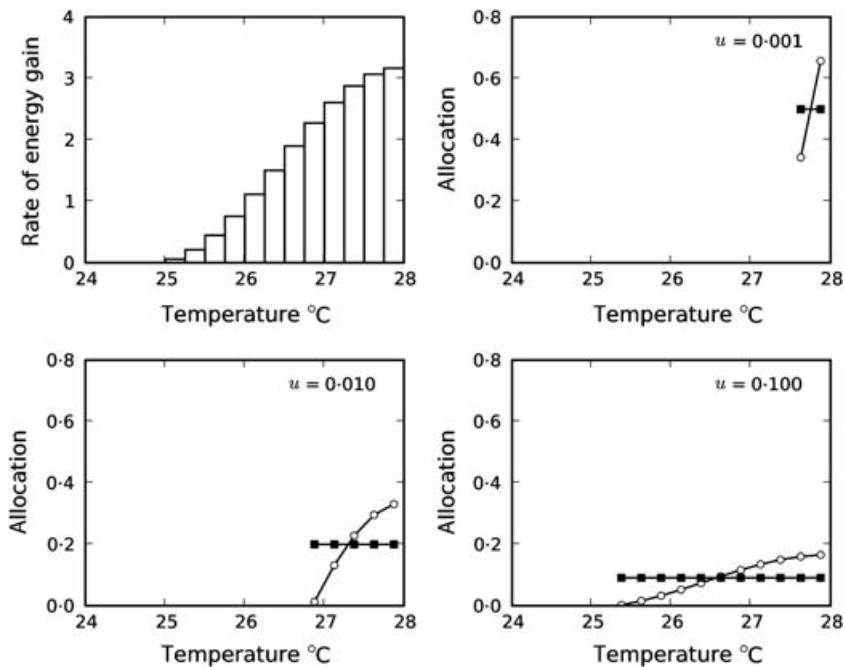


Fig. 3. (a) The relationship between body temperature and energetic gain for prey. Figures b, c and d show the effect of the predators' lethality (u) on the Nash equilibrium allocation of time to thermal patches by predators and prey. As lethality increases, prey (solid squares) should spread their time equally over a greater range of thermal patches; predators (open circles) should also increase their range of thermal patches, spending more time in patches that provide greater benefits to prey.

COADAPTATION OF BEHAVIOUR AND PHYSIOLOGY IN A THERMAL GAME

In this section, we show how a game between predators and prey can influence the evolution of a thermal physiology. The thermal sensitivity of energetic gain falls into the framework of a performance curve. Such curves relate an organism's body temperature to its rate of physiological performance (Huey & Steveson 1979). Performance curves vary within and among populations, and this variation presumably reflects some degree of physiological adaptation (Angilletta *et al.* 2002). Both theory and data suggest that tradeoffs constrain performance curves, leading to the evolution of thermal specialists or thermal generalists (Huey & Kingsolver 1989; Angilletta *et al.* 2003; Angilletta 2009). A specialist has a tall, narrow curve indicating excellent performance over a small range of temperatures, whereas a generalist possesses a short, broad curve indicating modest performance over a large range of temperatures. Here, we focus on how the interaction between predators and prey might influence evolution along this specialist-generalist continuum.

For mathematical convenience, we modelled the thermal sensitivity of energetic gain as a cosine probability density function, multiplied by a scaling factor:

$$f(T) = \frac{1}{2b} \left[1 + \cos\left(\frac{T - T_{\text{opt}}}{b} \pi\right) \right] \times \Omega, \quad \text{eqn 24}$$

where T_{opt} and b represent the thermal optimum and performance breadth, respectively. The scaling factor, Ω , converts the value of the cosine density to the appropriate magnitude and units (i.e., Joules/time). Because the integral of this function equals the constant, Ω , the evolution of the curve entails the desired trade off between specialization and

generalization. In other words, a small value of b yields the tall, narrow curve of a specialist, while a large value of b yields the short, broad curve of a generalist. We shall focus on the strength of selection acting on b .

Modelling the thermal environment as a continuous distribution of temperatures does not qualitatively alter the predictions derived in the previous section. A predator still hunts only in those patches where it expects the greatest success; thus, it should hunt across a range of patches only if it expects equal success across the entire range. Correspondingly, as in the case of n patches (Fig. 3), prey can still increase their survivorship (at the cost of reduced fecundity) by dividing their time equally over a range of patches, and thereby spread the predators' efforts over a greater area. One slight difference exists between the discrete and the continuous case. In the discrete case, prey were predicted to spend equal time in some number of warm patches and possibly spend less time in the next warmest patch (eqns 20 and 21a; Fig. 1); this result occurred because each patch received a finite allocation of time. But in the continuous case, prey choose a range of temperatures, and allocate the same time to all temperature in that range. The next warmest temperature is a single point, which cannot receive a finite allocation of time. Still, the prey's Nash equilibrium strategies in discrete and continuous environments are essentially the same; prey should select the range of temperatures that balances the risk of predation against the rate of energetic gain. This range always encompasses the thermal optimum of the performance curve. The question then becomes, how wide a range of temperatures should the prey use?

Our model yields a surprising prediction about the coadaptation of thermoregulatory behaviour and thermal physiology: lethal predators can reduce, or even eliminate selection for thermal specialists (Fig. 4). This prediction

Fig. 4. The optimal thermoregulatory behaviour and thermal physiology of prey depend on the lethality of predators (u). The dashed line depicts the use of thermal patches, and the solid line represents the thermal sensitivity of fecundity. At low lethality (left column), a thermal specialist ($b = 0.5$) achieves substantially higher fitness (G) than does a thermal generalist ($b = 1.0$). As predators become more lethal, the fitness of specialists and generalists become more similar (right column). This result occurs because fitness equals the product of the performance curve and the probability density function of body temperature; this product remains the same as long as the performance curve spans a narrower range of temperatures than the prey experience.

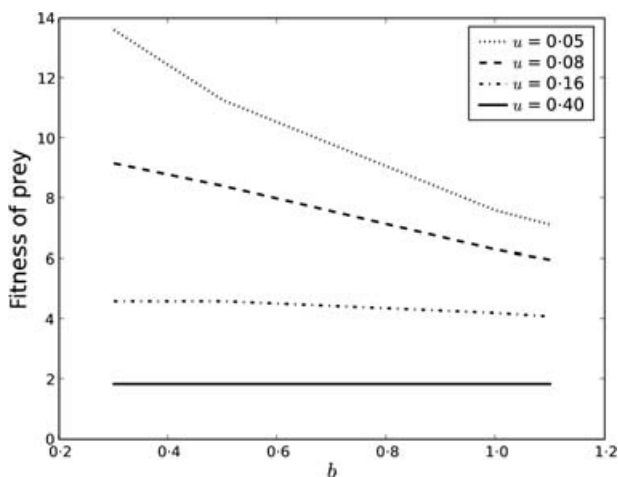
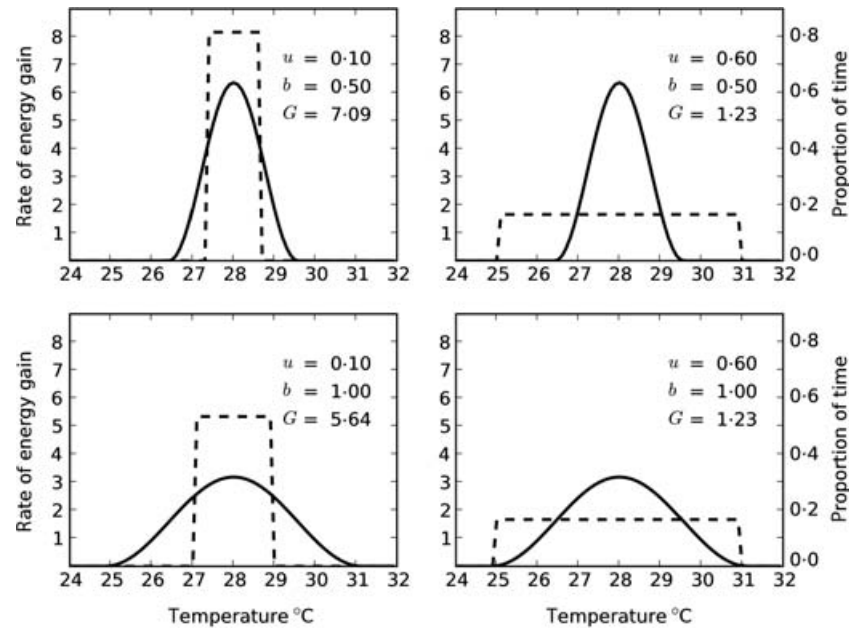


Fig. 5. Increasing the lethality of predators (u) reduces the intensity of selection for a narrow thermal breadth of performance (b).

follows from the results of the previous section. In the previous section, we showed that when predators are not too lethal, prey use a narrow range of thermal patches near their thermal optimum; this favours thermal specialists over generalists because specialists have the greater rate of energetic gain near their thermal optimum. But as predators become more lethal, prey use (equally) a wider range of thermal patches. If predator lethality is high enough, the range of temperatures used by prey can actually exceed the width of their thermal performance curve. As long as prey use a wider range of temperature than the width of their thermal performance curve, fecundity does not vary with the width of the curve (see Fig. 4). This result represents one end of a continuum in which increasingly lethal predators weaken selection of thermal physiology (Fig. 5). Though predator behaviour is not depicted in Fig. 4, predators behave as they did in the case of

n patches; they use the same range of thermal patches as prey use equally, but predators spend more time in the warmer patches.

Another interesting consequence of this model is that inter-generational, temporal variability in predator lethality may select for thermal specialists. When predator lethality is low, thermal specialists should be favoured by natural selection. But when lethality is high, thermal specialists and generalists should achieve equal fitness, such that selection cannot restore prey performance breadth; in fact, the only way that increased breadth could evolve in this case is through genetic drift. Thus, intermittent periods of high predation risk could ratchet the performance breadth to the point where extreme specialists evolve. Of course, this predation ratchet might be counteracted by other selective forces we have not considered in our model. For example, a high cost of travel between preferred patches favours generalists in some foraging models (Rosenzweig 1991, Mitchell 2000). If travel costs were added to our model, lethal predators might do more than simply eliminate the cost of generalization; they might increase selection for generalists.

Discussion

Game theory has contributed significantly to several areas of modern biology (Nowak & Sigmund 2004), but this theory has been largely ignored by physiological ecologists. Even with respect to behavioural ecology, most models of evolutionary games either explicitly or implicitly focus on foraging for food rather than abiotic resources (e.g., see Hugie & Dill 1994; Sih 1998). Only recently has a simple game between competing individuals been adapted to consider the interaction between food and temperature (Hughes & Grand 2000). Since then, Lampert and colleagues used game theory to predict the distribution of *Daphnia* spp. along vertical clines of water

temperature (Lampert, McCauley & Manly 2003; Lampert 2005). These extensions of game theory led to novel insights about the thermoregulatory behaviour of ectotherms. In this paper, we developed more complex models of frequency-dependent selection in a heterogeneous thermal environment.

Our model of a thermal game between predators and prey leads to a unique perspective on the evolution of thermoregulatory behaviour. Other researchers have addressed the effect of predation risk on thermoregulation (e.g. Downes & Shine 1998; Polo *et al.* 2005; Herczeg *et al.* 2008), but they implicitly treated predators as inert features of the environment. A thermal game, on the other hand, requires one to account for the flexible responses of predators. If predators cannot respond to prey, the prey can simply discount the value of a patch by the fixed risk of predation. In this case, when the risk of predation in a warm patch becomes too high, prey can simply shift most of their time to another patch. But if predators can respond, prey that spend the majority of their time in a single patch, either warm or cool, invite the full attention of predators. Thus prey should divide their time among multiple patches to reduce the risk of predation. But this strategy of prey can only be evolutionarily stable if predators hunt more frequently in warmer patches. Modelling the environment as a continuum of thermal patches did not significantly change this prediction. In general, greater predation risk expands the range of thermal patches that prey should use. Although prey should occupy some patches with equal frequencies, this behaviour reflects an active strategy of thermoregulation because patches characterized by extreme operative temperatures would be avoided.

Our model assumes that individuals can divide their time among a set of microhabitats that differ in operative temperature. As such, our model is an example of a 'rapid' model (Abrams *et al.* 2007) in which the movement of individuals among patches occurs at a rate that is rapid relative to the time-scale of demographic processes of birth and death. In fast models, an individual's fitness depends on the proportions of time spent in different patches. Alternatively, we could imagine a 'slow' model (Abrams *et al.* 2007), in which the rate of movement among patches is slow relative to demographic processes. In slow models, an individual may spend the majority of its life in a single patch, and its fitness would depend on the conditions of that patch alone. If we were to model a thermal predator-prey game assuming such slow movement dynamics, we would undoubtedly arrive at some predictions that differ from those presented here. For example, in the rapid model we analyse, prey subject to very lethal predators may allocate some proportion of their time to patches in which they receive no energetic gain, because doing so reduces their rate of encounter with predators. But it seems unlikely that a prey in a slow model which moved but once in its life would choose to migrate to and settle in such a patch.

In this paper, we analysed how predator lethality could influence the evolution of thermal sensitivity, but we neither analyse its role in the evolution of the thermal optimum, nor consider the possibility that predators may promote

the coexistence of two (or more) prey performance curves. Finally, we did not analyse the case in which predators as well as prey exhibit thermal sensitivity in their performance. All of these topics would be worth pursuing in future studies. One intriguing possibility is that predators may promote the coexistence of two different prey species with different thermal performance curves. Indeed, previous theoretical results (Doebeli & Dieckmann 2000; Mitchell 2000; Doebeli & Dieckmann 2003) suggest that frequency-dependent interactions may actually promote ecological or sympatric speciation, which could generate a diversity of coexisting performance curves.

We assumed that thermoregulation imposes no energetic cost, but such a cost would further increase the range of thermal patches used by prey (see Huey & Slatkin 1976). Thus, energetic costs can work in concert with predation risk to reduce the accuracy of thermoregulation. If prey must spend considerable time searching for preferred patches, thermoregulation might entail substantial energetic costs. Of course, the actual energetic cost depends not only on the frequency distribution of thermal patches but also on their spatial distribution (Sears & Angilletta 2007). Consequently, we need to model a spatially explicit thermal game to integrate the costs of energetic expenditure and predation risk.

The variation in body temperature caused by predation risk has implications for the evolution of thermal physiology. Although we used a symmetric performance curve, empirical measurements suggest that most performance curves possess some degree of asymmetry. When body temperature varies, individuals with an asymmetric performance curve should maintain a mean body temperature below the thermal optimum for performance (Martin & Huey 2008). This strategy provides a safety margin that reduces the loss of performance when body temperatures exceed the mean. We simplified the presentation of our models for the cases of two patch types and n discrete patches by ignoring temperatures above the thermal optimum, but our qualitative predictions hold for environments composed of hot and cold patches. To consider patches that are hotter than the thermal optimum, we would merely rank these patches and the colder patches according to their impact on performance when determining the Nash equilibrium (see eqns 19–23). The outcome of this exercise would be qualitatively identical to the result described above: a risk of predation should cause prey to use colder and hotter patches than they do in the absence of predation. Thus, we can conclude that predation risk should generally increase the variance of body temperature, which would indirectly favour a mismatch between the preferred temperature and the thermal optimum.

Similarly, our game model of co-adaptation makes a unique prediction about the evolution of thermal physiology. In the absence of frequency-dependent selection, the environment that we modelled would favour the evolution of thermal specialists (see Gilchrist 1995). Yet, frequency-dependent selection dramatically relaxes selection for specialization. In fact, generalists and specialists achieve equal fitness given an extreme risk of predation (see Fig. 5). This potentially

unexpected result stems from our interpretation of the Nash equilibrium behaviour of prey; the energetic advantage of specialization disappears if a prey attempts to avoid its predators by dividing its time among different thermal patches (see Fig. 4). This phenomenon enables generalists to evolve by genetic drift during periods of extreme predation risk. Moreover, natural selection would favour generalists over specialists when thermoregulation enhances survivorship as well as fecundity (see Lynch & Gabriel 1987). Because we linked thermoregulatory benefits directly to fecundity, we potentially underestimated the selective pressure on the breadth of performance that results from predation. This consideration bolsters the conclusion that predation can lead to the evolution of thermal generalists.

The thermal game modelled here represents one of many that are worthy of consideration. In particular, we ignored travel costs (Mitchell 2000), intraspecific competition (Sih 1998; Day 2000; Ackermann & Doebeli 2004), and behavioural cascades (Rosenheim 2004). All of these complexities have been modelled for games that focus on food or an unspecified resource, and all have been interesting departures from models of frequency-independent selection. Similar extensions of game theory could explore the impact of these factors on adaptation to thermal heterogeneity. Despite the simplicity of our model, we generated novel predictions about thermoregulatory behaviour and thermal physiology. We believe such models of frequency-dependent selection can become a critical extension of the current theory of thermal adaptation.

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Supporting Information

Additional Supporting Information can be found in the online version of this article:

Appendix S1. Asymptotic stability of the behavioural equilibrium

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