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# Modelling thermal preference and fitness consequences in scenarios of decreasing temperature predictability

Master's thesis in Master of Science in Biology

Supervisor: Irja Ida Ratikainen

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## Samandrag

Klimaendringane er venta å auke snittemperaturen, men også variasjon og føreseielegheit i temperatur. Nøyaktige predikasjonar av framtidig førekomst og foredling av artar må difor ta omsyn også til desse faktorane. Fordi ektoterme dyr har kroppstemperatur i likevekt med omgivnadane, treng dei strategiar for å takle variasjon og føreseielegheit i erfarte temperaturar. Varmeregulering gjennom åtferd gjer det mogleg å halde ei tett fordeling av kroppstemperatur rundt ein føretrekt temperatur. Føretrukne temperaturar er ofte predikert ut frå den termisk yteevna til ein eigenskap, og ofte er dette skildra gjennom asymmetriske kurver (thermal performance curves). Grunna Jensen si ulikheit vil variasjon i kroppstemperatur resultere i føretrekt temperatur ulik optimal temperatur,  $T_{opt}$ , som gir maksimum yting.

I dette prosjektet undersøker eg åtferdsstrategiar i eit tilstandsbundne rammeverk ved ulike nivå av føreseielegheit i temperatur, og effektar av auka temperaturvarians på fitness. Eg visar at føretrekt temperatur å søke etter føde i, minkar med føreseielegheita, men at dei òg avheng av kroppskondisjon. Vidare ser eg at det ikkje alltid er mogleg å predikere føretrekt temperatur ut i frå den samansette eigenskap forventa netto vinst. I tillegg blir fitness redusert, gjennom auka daudelegheit og lågare kroppskondisjon for alle scenario av føreseielegheit i temperatur. Det er nokre fordelar eit bytte til optimale åtferdsstrategiar i høgare variasjon, som er realisert gjennom lågare daudelegheit og høgare kroppskondisjon.

Føretrekke temperatur er i samsvar med Jensen si ulikheit og teori som omhandlar risiko sensitivt fødesøk, og er ulik den optimale temperaturen som gir høgast yteevne. Negative effektar på fitness har to moglege forklaringar. Hovudårsaka er at varmereguleringa er mindre nøyaktig med låg føreseielegheit i temperatur. Dette gir større variasjon i opplevd temperatur, og fitness minkar då yteevna er lågare for alle ikkje-optimale temperaturar. Den lågare føretrekke temperaturen i desse scenarioa reduserer på same måte fitness snittet, samanlikna med dei optimale strategiane i høg føreseielegheit.

## Abstract

Climate change is predicted to not only increase mean temperatures, but also to change patterns of variation and predictability of temperatures. This necessitates incorporating variation and unpredictability into modelling approaches to predict future species persistence and distributions. Ectotherm animals with body temperatures in equilibrium with their surroundings, need strategies to deal with variation and predictability in experienced temperatures. One such strategy is behavioural thermoregulation, which enables animals to stay closer to their preferred temperatures. Preferred temperatures are often predicted from thermal performance curves (TPC), which describes temperature dependence of trait performance. Following Jensen's inequality, it is generally predicted that variation in body temperatures leads to shifts in the preferred body temperatures away from optimal temperatures yielding maximum performance.

In this project I investigate optimal behavioural strategies in a state-dependent framework at different levels of temperature predictability, and effects of increased temperature variability on fitness. Here I show that preferred temperatures of foraging decrease in temperature scenarios with lower predictability, but that preferred temperatures also depend on body condition. Predictions based on the compound trait expected net benefit is not always suitable to explain behavioural strategies. All decreases in temperature predictability increased mortality and decreased body condition of animals. Some advantage of allowing for behavioural optimization to lower temperature predictability is evident through lower mortality and higher body condition than for non-optimal behaviours.

Preferred temperatures follow predictions from risk-sensitive foraging theory, with shifts away from the optimal temperature depending on both temperature predictability and body condition. Detrimental effects on fitness with decreased temperature predictability has two possible explanations in my model. The main explanation for the decrease in fitness with lower temperature predictability is reduced thermoregulatory accuracy. This results in higher variation in experienced temperatures, and thus lower mean fitness because of performance loss in most non-preferred temperatures. The lower preferred temperature in low predictability scenarios also has reduced mean fitness, compared to optimization in high predictability scenarios.

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## Tables

*Table 1. Parameter choices for the specialist and the generalist using dynamic state variable modelling to find an optimal behavioural strategy of foraging temperatures in the trade-off between increased foraging efficiency and metabolism with temperature. The only difference in the two models is the shift in inflection point ( $\tau$ ) for feeding efficiency from temperature 5 in the generalist to temperature 6 in the specialist. Temperature variation scenario A0.55 is only used in forward simulation. \_\_\_\_\_9*

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Living organisms display a variety of strategies to deal with variation and unpredictability in environment. With the predicted increase in variation and unpredictability following climate change, major questions relate to consequences of a more variable and less predictable future, and to the opportunities of rescue from population decline and extinction by for example behavioural adjustment, acclimatization, phenotypic plasticity, range expansion and evolution (Vasseur *et al.*, 2014; Urban *et al.*, 2016). Ectotherms are organisms in thermal equilibrium with its surroundings, and as environmental temperature influence body temperature and in turn performance, virtually every aspect of an ectotherms life and fitness is influenced by environmental temperature and its variation (Angilletta Jr., 2009). Because of this tight link between performance, body temperature and environmental temperature in ectotherms, changing patterns of thermal variation and temperature predictability represents an interesting and important area of study in ectotherms. Performance and fitness consequences during rapid change of thermal regimes and predictability, with accompanying opportunities for rescue through behavioural or physiological adjustment, are important aspects of short-time persistence of ectotherms.

Temperature dependent performance of ectotherms is often represented through thermal performance curves, TPCs (Huey and Stevenson, 1979; Angilletta, Niewiarowski and Navas, 2002; Sinclair *et al.*, 2016). The performance traits are fitness or fitness proxies when these are possible to measure (Huey and Berrigan, 2001; Corkrey *et al.*, 2012), or lower level animal traits thought to be important for survival and reproduction, for example is digestion rates (Angilletta, 2001) or lizard sprint speed commonly measured (Hertz, Huey and Stevenson, 1993). TPCs for ectotherms are usually modelled through an asymmetric and unimodal curve (Figure 1) (Huey and Berrigan, 2001; Angilletta Jr., 2009; Dell, Pawar and Savage, 2011). Tolerance range describes the temperatures of animal function, between  $CT_{min}$  and  $CT_{max}$ , while performance breadth or range refers to the temperature range of a certain function, often 50% or 20 % performance loss compared to the optimal temperature (Angilletta, Niewiarowski and Navas, 2002; Sinclair *et al.*, 2016). Differences in performance breadth are often used to describe species that display different patterns of response to temperature. Specialists have TPC with narrow performance breadth but high maximal performance at optimal temperatures. Generalists are characterised by wider performance breadths, usually at the expense of lower maximal performance (Huey and Slatkin, 1976; Gilchrist, 1995).

In the case of no variation in experienced body temperatures, fitness is maximized when body temperature is equal to the optimal temperature,  $T_{opt}$ . However, this scenario is rarely observed in nature. As a result of the mathematical relationship known as Jensen's inequality, fitness is maximized for preferred temperatures lower than the optimal temperature at maximum performance (Martin and Huey, 2008; Vercken *et al.*, 2012). Intuitively, this can be explained through observing that loss of fitness is higher at temperatures above the  $T_{opt}$  than below it (Figure 1) (Vercken *et al.*, 2012), and the mean fitness across the temperature distribution is not the same as the fitness at the mean temperatures.

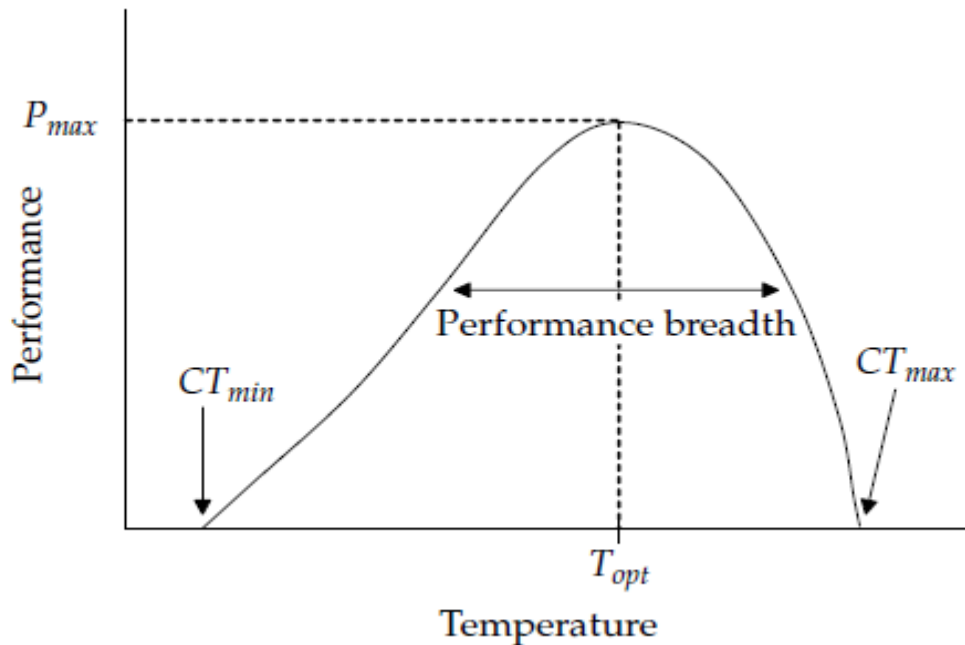


Figure 1. Thermal performance curve with performance dependent on body temperature. Performance increases slowly from a critical minimum ( $CT_{min}$ ) to an optimum, before it falls quickly towards a critical maximum ( $CT_{max}$ ). Preferred temperatures generally fall to the left of the optimal temperature,  $T_{opt}$ , due to Jensen's inequality.

Preference for sub-optimal temperature is an insurance strategy, where a non-optimal mean temperature is chosen to alleviate effects of environmental variation (Haaland *et al.*, 2019). In contrast, considerations of risk-sensitive foraging strategies are done with scenarios where all options have the same mean change in animal state, but with different levels of variation in the pay-off (Stephens, 1981; Real and Caraco, 1986; McNamara, Merad and Houston, 1991). Concave fitness functions promote risk-aversion and choice of low variance options, while convex fitness relationships support risk-prone strategies of high variance options. This framework is relevant when survival is dependent on an energy state of the animal, (Stephens, 1981; Real and Caraco, 1986; Higginson *et al.*, 2012), but can also be extended to reproduction (McNamara, Merad and Houston, 1991; Bednekoff, 1996). Optimal change between risk-averse and prone strategies is thus determined by fitness, which is dependent on the energetic state of the animal and remaining time to forage, or time to reproduction. The asset protection principle was proposed to predict risk sensitive strategies in state dependent frameworks (Clark, 1994). When animals have high asset values (i.e. body condition or similar), they employ risk averse behaviours to minimize losses and protect current assets, implying a convex fitness function. On the other hand, animals with insufficient assets are predicted to display risk prone behaviour to gain the higher possible rewards, implying concave fitness functions.

Faced with variation in environmental temperatures, being either predictable, for example seasonal changes, or unpredictable and unanticipated variations, many ectotherms can behaviourally thermoregulate to obtain a preferred body temperature. Exploiting different microhabitats where temperature vary depending on factors such as radiation, convection

and humidity, in both time and space, allows animals to keep body temperatures within a narrow preference range (Spotila, O'Connor and Bakken, 1992; Angilletta Jr., 2009).

If and when ectotherms should thermoregulate can be modelled as a trade-off between the cost and benefits of maintaining a tight distribution of body temperatures (Huey and Slatkin, 1976). Costs are either energetic, for example metabolism (Huey *et al.*, 1989), movement between suitable habitats (Sears *et al.*, 2016), or associated with morphological changes, as shifting between different colour morphs (Nielsen, 2017), or loss of opportunities for other activities, such as foraging, predator avoidance and reproduction (Clark and Levy, 1988; Downes and Shine, 1998; Levy *et al.*, 2017). Benefits are usually linked to a TPC, where more accurate thermoregulators have body temperatures nearer the preferred temperature and higher performance. Inherent in calculations of the costs and benefits of thermoregulation, is the range of temperatures animals experience. Lower accuracy of thermoregulation can result in higher variation in experienced body temperatures which in turn reduces net benefit.

The ability to adjust behavioural strategies may halt deleterious effects of novel temperature scenarios, for example by shifts in the time of activity to previously unavailable timeslots or habitats (Fey *et al.*, 2019, Sears, Raskin and Angilletta, 2011; Levy *et al.*, 2017). But loss of opportunity connected to increased time spent in hiding can lead to fitness loss and extinction (Sinervo *et al.*, 2010), and ultimately, behavioural rescue might lead to limited adaptation to novel environments and abrupt decreases in fitness with further increases in mean temperature (Huey *et al.*, 2012; Buckley, Ehrenberger and Angilletta, 2015). Decreased environmental predictability and higher variation might be conquered in a similar manner, with adjustment of preferred temperatures following Jensen's inequality to maximize performance in the new, more variable, environment. However, the scope for behaviour to rescue populations threatened by changes in variation and predictability is even less explored.

A combination of TPCs and thermoregulatory behaviour can be used to investigate organismal vulnerability to changing patterns of temperature variation during climate change. Inclusion of variance in experienced temperature is needed to accurately predict effects of temperatures on animal fitness. For example, comparing performance from yearly, monthly and daily mean temperatures, give different patterns and magnitude of fitness change (Vasseur *et al.*, 2014) (Clusella-Trullas, Blackburn and Chown, 2011; Sheldon and Dillon, 2016). Time-series of experienced temperatures are important, as not only the total number of warmer days impact fitness but also their sequence, think for example of heat waves (Sinervo *et al.*, 2010; Dillon and Woods, 2016; Williams *et al.*, 2016). Lower predictability in temperatures might reduce thermoregulatory effectiveness. The ability of organisms to anticipate future temperatures and find suitable microhabitats might decline, or temperatures within the performance range become less available.

Changes in temperature variation are expected to affect generalist and specialist organisms differently because they have likely evolved under different levels of variation resulting in unequal performance breadth (Gilchrist, 1995; Amarasekare and Johnson, 2017). Considerable attention has been given to their prospects in future climates, with tropical versus temperate species often being used as examples. When TPCs are being used to infer fitness, specialist species are believed to suffer the greatest loss of fitness. Generalists are expected to incur smaller losses of fitness because they have broader thermal performance ranges. In addition, particularly temperate generalists are believed to live below their temperature optima, such that predictive models including a rising mean

temperature initially show increased fitness (Deutsch *et al.*, 2008; Tewksbury, Huey and Deutsch, 2008; Huey *et al.*, 2012; Sheldon and Dillon, 2016; Johansson, 2019).

My project aims to investigate optimal behavioural strategies when animals encounter different levels of temperature predictability, and how they affect fitness both in the environment that they are adapted to and in novel environments. The approach is twofold. Firstly, optimal behavioural strategies of the expected temperatures animals encounter are determined for different temperature variation scenarios and performance breaths of a TPC. The preferred temperatures from the optimal behavioural strategies are predicted to follow Jensen's inequality, where lower temperatures result from decreased predictability and increased variation of environmental temperatures. Secondly, I explore fitness outcomes of following the optimal behavioural strategies. By forward simulations I gain insight into fitness at both the temperature variation scenarios they are optimized for, and in novel scenarios of lower predictability. I expect decreases in fitness to follow greater variation in experienced temperature. Optimized models should do better in their environments than models optimized for a different temperature variation scenario, indicating possibilities of behavioural rescue from shifts in preferred temperatures according to Jensen's inequality.

## Methods

This project aims to incorporate temperature unpredictability to optimal foraging behaviour dependent on energetic condition. The result is thermoregulatory strategies of preferred temperatures during foraging. To find the optimal thermal preference in different thermal scenarios I built a state-dependent model where an animal can choose from a range of expected temperatures. These expected temperatures can be interpreted as, for example, the mean temperatures in different patches of habitat, and will therefore be referred to as expected patch temperatures. Experienced temperatures depend on the predictability of the environment, where a less predictable environment is associated with higher variation in temperatures.

A key assumption of my model is that there should be a trade-off between temperature dependent foraging efficiency and metabolic costs. The metabolic cost,  $M$ , increases exponentially with temperature (Gillooly *et al.*, 2001; Dell, Pawar and Savage, 2011; Huey and Kingsolver, 2011),

$$M = e^{-\alpha * \text{Temperature}} \quad (1)$$

where  $\alpha$  is a scaling parameter for the increase in metabolic cost with temperature. Foraging efficiency,  $E$ , is a compound of traits that are temperature dependent, for example mobility, speed, prey capture rates and accuracy, (Dreisig, 1981; Avery, Bedford and Newcombe, 1982; Damme, Bauwens and Verheyen, 1991; Greenwald, 2017), modelled through a logistic function

$$E = \frac{1}{1 + e^{-\beta(\text{Temperature} - \tau)}} \quad (2)$$

Where  $\beta$  is the scaling parameter for the increase in efficiency with temperature and  $\tau$  is the temperature at the inflection point. Higher temperature gives higher probability of gaining a benefit, and  $E$  is a probabilistic variable in the range [0,1].

For simplicity I assume maximum energy intake is limited by ingestion, and not food abundance, and therefore keep maximum benefit available constant across all temperatures. Metabolic cost, feeding efficiency and benefit combines to a thermal performance curve with net expected benefit as the performance trait (see Results under Preferred temperatures, Figures 2 and 3) (Huey and Stevenson, 1979; Sinclair *et al.*, 2016). When there is little to no uncertainty in the experienced temperatures, the preferred temperature is expected to match the optimal temperature that yields maximal expected net benefit. When there is variation in the experienced temperatures, the preferred temperatures are expected to be lower than the optimal temperature,  $T_{\text{opt}}$  (Martin and Huey, 2008).

## Optimal behavioural strategies

Optimal behavioural strategies are determined through a method called dynamic state variable modelling (Houston and McNamara, 1999; Clark and Mangel, 2000), or stochastic dynamic modelling. This framework embeds the context of the individual animal, represented through intrinsic and extrinsic states, and time, into calculations of optimal behaviour. Expected future fitness for a pre-set range of possible choices is calculated for each combination of states and time. The optimal behavioural choice is the one maximizing expected fitness, and the resulting behavioural strategy consists of the combination of these optimal choices.

The model presented in this project considers two state variables. Temperature information, which describes the abiotic environment, and animal body condition, both are explained in further detail below. Time represents a season where the animals can feed in the attempt to increase body condition towards a reproductive event at the terminal time step, i.e. the end of the season (for discussion on subject Bonnet, Bradshaw and Shine, 1998). The resulting behavioural strategy of which expected patch temperature to forage in consists of optimal behavioural choices for each combination of time, body condition and temperature information.

The state variable describing temperature information,  $D_{t-1}$ , is the deviation from the expected patch temperature as experienced in the previous time step. This variable is introduced to model uncertainty in the temperature the animal experiences. The experienced temperature in the current time step is not known to the animal. Decisions of which expected patch temperature to forage at are made based on knowledge of the expected patch temperature  $j$ , the temperature deviation from the mean in the previous time-step,  $D_{t-1}$ , and the correlation of temperature deviations in the environment. The probability of temperature  $k = j + D$  at time  $t$ , is given by a pre-set matrix with entries

$$P(\text{temperature } k = j + D \mid D_{t-1}) = P(D \mid D_{t-1}) \quad (3)$$

$$\text{with } \sum_{D=D_{\min}}^{D=D_{\max}} P(D \mid D_{t-1}) = 1$$

where  $j$  is the expected patch temperature and  $D$  the deviation from expectation, with temperature deviation  $D_{t-1}$  at time  $t-1$ . No uncertainty in expected temperature is experienced when the condition that, for all  $D_{t-1}$  there is a  $D$  in  $[D_{\min}, D_{\max}]$  with  $P(D \mid D_{t-1}) = 1$  is fulfilled. Predictability of temperatures can be divided into two components. The first is the probability of experiencing a  $D_t$  different from  $D_{t-1}$ , or the autocorrelation in the environment. The second is the predictability in the new levels of  $D_t$  different from  $D_{t-1}$  (Tables A1-A4). For ease of understanding, different temperature variation scenarios are labelled with their overall autocorrelation in  $D$  (Table 1), calculated as rank autocorrelation of first order (Basawa, 1972).

While temperature variation scenario A0.54 has higher autocorrelation than scenario A0.37 (Equation 3), the latter is more predictable for some temperature deviation conditions,  $D$ . This is because, even though the overall autocorrelation is low in A0.37, there is high probability of the transitions  $D=\pm 2$  to  $D=\pm 1$  giving high predictability of which temperature deviation is encountered. Outside these two transition probabilities and autocorrelations for  $D$  equal to 1,0,-1, A0.37 has great spread of probabilities to other deviations. In contrast, A0.54 has a flat distribution, with  $P=0.3$  for the three deviations  $D_t = D_{t-1}$  and  $D_t = D_{t-1} \pm 1$ . This gives low predictability in which of these three temperature deviations will be experienced in the next time step, but high probability ( $P=0.9$ ) that it will be one of these three.

Optimal behavioural choice might also depend on the intrinsic state variable representing energetic state, the body condition,  $C$ . Higher body condition is presumed to be associated with greater fitness, e.g. through higher survival probability and reproductive output (Jakob, Marshall and Uetz, 1996; Pangle *et al.*, 2004; Baron *et al.*, 2013; Jaumann and Snell-Rood, 2019). Body condition state dynamics are determined by the costs and benefits at the experienced temperatures. The metabolic cost,  $M$ , is a non-linear increase with temperature given (Equation 1). Influences of size on metabolism is not included as body condition is easily reversible and will thus not include growth and increased size. The probability of obtaining food is determined by the feeding efficiency,  $E$  (Equation 2). Two



possible changes in body conditions  $C$ , at time  $t$  with experienced temperature  $k$  is possible depending on whether the individual finds food or not:

$$C_{food} = C_t + B - M(k) \quad (4)$$

with probability  $P(\Delta C = B - M(k)) = E(k)$

$$C_{no\ food} = C_t - M(k) \quad (5)$$

with probability  $P(\Delta C = M(k)) = 1 - E(k)$

with limits of  $C_{t+1}$  at  $C_{min}$  and  $C_{max}$ . If  $C < C_{min}$  the animal is dead and has zero expected future fitness. The change in body condition is thus dependent on temperature in two ways, firstly through an increasing absolute cost and secondly through an increase in the probability of finding food. The spread of net benefits possible at each temperature, making up the expected net benefit, is thus very variable with temperature, as is the degree to which the expected net benefit is determined by metabolic cost or foraging efficiency.

A backwards iteration from the terminal time step,  $T_{terminal}$ , is used to find the optimal behavioural strategy. Only the terminal fitness,  $F(C, T_{terminal})$  needs to be predefined, as the backwards calculations of fitness from the terminal step gives the next state dependent fitness,  $F(C, t)$ . Terminal fitness  $F(C, T)$  is modelled as a linear function of body condition,

$$F(C, T_{terminal}) = \frac{2}{C_{max}}(C - C_{min}). \quad (6)$$

Expected future fitness in time step  $t$  is calculated for expected temperature  $j$ , previous deviation  $D_{t-1}$ , body condition  $C$  and the expected future fitness  $F(C, D_{t-1}, t+1)$

$$F(C_t, j, D_{t-1}, t) = \sum_{k=j+D} P(k | D_{t-1}) * \left( E(k) * F(C_{food}, t+1) + (1 - E(k)) * F(C_{no\ food}, t+1) \right) \quad (7)$$

where  $k = j + D$  refers to all temperatures  $k$  possible from the expected patch temperature  $j$ ,  $P(k)$  is found by bl combination of body condition  $C$  and previous deviation  $D_{t-1}$ , is the expected patch temperature  $j$  that maximizes expected fitness in equation 7.

Two parameter sets for equations 1 and 2 are used, giving two distinct thermal performance curves (Table 1 and Figures 2 and 5), and can generously be interpreted as a generalist and a specialist. Caution should be applied to comparisons, a generalist-specialist trade-off is not employed between these two parameters sets, and net expected benefits and expected future fitness is higher in the generalist. For both the generalist and specialist TPC, behavioural strategies and expected fitness are found with three temperature variation scenarios, A0, A0.37 and A0.86. A total of six different behavioural strategies are thereby computed (Table 2 for overview of combinations for optimization). These are optimal behavioural strategies of a TPC and a temperature variation scenario. Preferred temperatures within a behavioural strategy will depend on both the state variables, temperature information  $D_{t-1}$  and body condition  $C$ , and time. For comparisons with expectations relating to the preferred temperature predicted by Jensen's inequality, I use the preferred temperatures that have the highest probability for each  $D_{t-1}$  (Equation 3), occurring for the highest number of combinations of  $C$  and time.

Table 1. Parameter choices for the specialist and the generalist using dynamic state variable modelling to find an optimal behavioural strategy of foraging temperatures in the trade-off between increased foraging efficiency and metabolism with temperature. The only difference in the two models is the shift in inflection point ( $\tau$ ) for feeding efficiency from temperature 5 in the generalist to temperature 6 in the specialist. Temperature variation scenario A0.55 is only used in forward simulation.

Parameter	Functions	Range
Expected patch temperatures, j	Integer steps	[2,11]
Temperature deviation, D	Integer steps	[-2,-1,0,1,2]
Possible temperatures, k	$k = j + D$	[0,13]
Time	Integer steps	[1,30]
Benefit, B	Integers, all expected temperatures	8
Body condition, C	Integer steps Dynamics determined by equations 4 and 5	[1,20]
Terminal fitness	Linear increase with state C, equation 6	[0,1.9]
Metabolic cost, M	Equation 1, zero decimal places $\alpha = 0.22$	[1,17]
Feeding efficiency, E	Equation 2, three decimal places $\beta = 0.75$ Specialist: $\tau = 6$ Generalist: $\tau = 5$	[0,1]
Temperature variation scenarios	6 matrices with entries DxD of probabilities, equation 3. Full matrices in Tables A1-A4	Autocorrelations 0.86, 0.37, 0.55, 0

## Forward simulation by Monte Carlo method

Insight into distributions of experienced temperatures, body conditions, and fitness, is gained through forward simulations of animals following a behavioural strategy through a season. The Monte Carlo method is suitable because of the probabilistic effects of unpredictable temperatures and feeding efficiency.

At each time step through the season the expected temperature choice is determined by the behavioural strategy for a given body condition, experienced deviations in temperature and time. The experienced temperature  $k$  for the given behavioural choice, is then determined by the probability distributions of the temperature deviations (Equation 3) for all deviations  $D_{t-1}$ . The change in body condition is found by equations 4 and 5. The new body condition will determine the next behavioural decision together with the deviation in temperature  $k$ .

Forward simulations are done according to Table 2. This explores both performance in historic environment the animals are adapted to and performance in novel environments.

For each TPC, distributions of body conditions, including mortality at  $C_0$ , are evaluated with chi-square test of significance level 0.05. There is no comparison between the two different TPCs. Three effects are investigated. 1) The difference between the three optimal behavioural strategies simulated in their respective temperature variation scenarios, A0.86, A0.37 and A0, in other words performance of behavioural strategies in the temperature variation scenarios they are optimized for. 2) The difference between temperature variation scenarios simulated with the optimal behavioural strategy from temperature variation scenario A0.86, giving performance of the behavioural strategy of scenario A0.86 in novel temperature variation scenarios of lower predictability. 3) The difference in performance of strategies within a temperature variation scenario, which highlights the fitness consequence of optimizing behaviour, i.e. performance within scenarios A0.37 and A0 of their respective optimal strategies and the strategy from A0.86. Body condition levels 1 to 10 were always combined due to low occurrence of individuals in these conditions.

Starting values of body condition are drawn from a uniform probability distribution and experienced temperature deviation from the probability distribution [0.1, 0.25, 0.3, 0.25, 0.1]. I use 1000 replicates of simulations with 1000 individuals. Animals reaching body conditions  $C < C_{\min}$  have terminated seasons with assigned  $C=0$  and  $F=0$ , and the total number of individuals in this category is used as an estimate of mortality.

Table 2. Overview of optimal behavioural strategies and forward simulations. Six behavioural strategies are made, optimized for each combination of a TPC and temperature variation scenarios outlined below. Forward simulations with Monte Carlo method for each behavioural strategy is done in temperature variation scenarios according to the last column. Full transition matrices for each temperature variation scenario is given in Tables A1-A5.

<b>Optimal behavioural strategies</b>		<b>Temperature variation scenarios used in forward simulations</b>
<b>TPC</b>	<b>Temperature variation scenarios</b>	
SPECIALIST TPC, Figure 2	A0.86	A0.86
		A0.59
		A0.55
		A0.37
		A0
	A0.37	A0.37
	A0	A0
GENERALIST TPC, Figure 3	A0.86	A0.86
		A0.59
		A0.55
		A0.37
		A0
	A0.37	A0.37
	A0	A0

## Results

The resulting behavioural strategies depend on the temperature deviations  $D_{t-1}$ , body condition  $C$  and time, to a lesser or greater degree under different environmental conditions (Figures A1-A6). The optimal behavioural strategy ensures that the most probable experienced temperature  $k$  is kept at the same preferred temperature for all deviations  $D_{t-1}$ . To achieve this, lower expected patch temperatures are the optimal choice for positive temperature deviations, and vice versa. For the two extreme  $D_s$ ,  $D_{t-1}=\pm 2$ , the most probable next deviation is  $D_t=\pm 1$ . The behavioural strategies at these deviations thus resemble those for  $D_{t-1}=\pm 1$ . Temperature variation scenario A0 is the exception, as there is no predictability in temperature deviations, and they all have the same strategy.

A risk-averse strategy for high values of body condition is also universal (Figure A1-A6). Low expected temperatures are preferred, with small costs but also near to no benefit. Seemingly risk-prone behaviour in low body conditions is common, where higher expected temperatures are preferred. There is no easily recognizable general pattern of time-dependence of behavioural strategy, but the generalist TPC does seem to prefer a lower temperature near the terminal time step (Figures A1-A6).

Optimal behavioural strategies with A0.86 has overall high expected future fitness. Scenarios A0.37 and A0 produce subsequently lower expected future fitness. Both have a temporal pattern. Expected future fitness increasing towards the terminal time step, and differences between expected future fitness for different body conditions increase as well.

Differences between the optimal behavioural strategies made with the specialist and the generalist TPCs indicates that behavioural dependence on body condition decreases and disappears when the expected net benefits are low (Figures A1-A6). The specialist TPC has less possible temperatures with expected net benefit above zero, and thus generally fewer suitable choices.

### Preferred temperatures and performance of behavioural strategies in temperature variation scenarios of optimization

#### The specialist thermal performance curve

Preferred temperatures from the behavioural strategies at the three temperature variation scenarios for the specialist, is shown in Figure 2. At high predictability (scenario A0.86), the preferred temperature coincides with the optimal temperature that yields maximum expected net benefit,  $T_{prefA}$ . At an intermediate level of predictability (scenario A0.37) the behavioural strategy is divided to avoid temperatures with expected net benefit below zero. Temperature deviations  $D_{t-1} > 0$  result in preferred temperature at  $T_{prefA}$ , as the highest temperature possible then becomes  $T_{prefA} + 1$ , while  $D_{t-1} < 0$  result in preferred temperature at  $T_{prefB}$ , and minimum possible temperature is  $T_{prefB} - 1$ . When there is no predictability in temperature deviations, scenario A0,  $T_{prefB}$  is the preferred temperature.

Forward simulations of behavioural strategies in their respective temperature variation scenarios show that distributions of body conditions, including mortality at  $C=0$ , is related to predictability of the temperature variation scenario ( $\chi^2=197.81$ ,  $df=22$ ,  $p < 2.2 \cdot 10^{-16}$ )

(Figures 3 and 4). Higher predictability has both less mortality and a higher proportion of individuals in the maximum obtainable body condition.

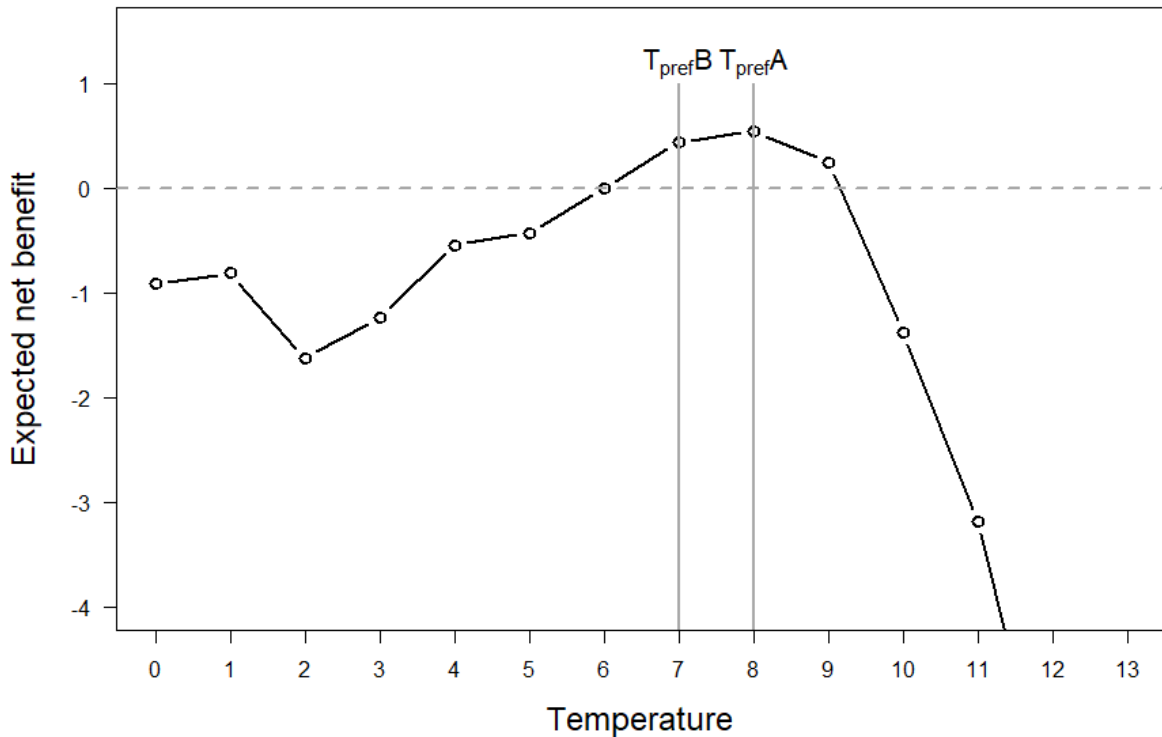


Figure 2. Specialist TPC, expected net benefits dependent on body temperature. Computed from the feeding efficiency  $E$ , metabolic costs  $M$  and constant benefit  $B$ .  $T_{prefA}$  is the preferred temperature for temperature variation scenario A0.86 and the high, positive deviations  $D_{t-1}$  in scenario A0.37.  $T_{prefB}$  is the preferred temperature for temperature variation scenario A0 and the low, negative deviations  $D_{t-1}$ . Note,  $T_{prefA}$  coincides with the optimal temperature choice,  $T_{opt}$ .

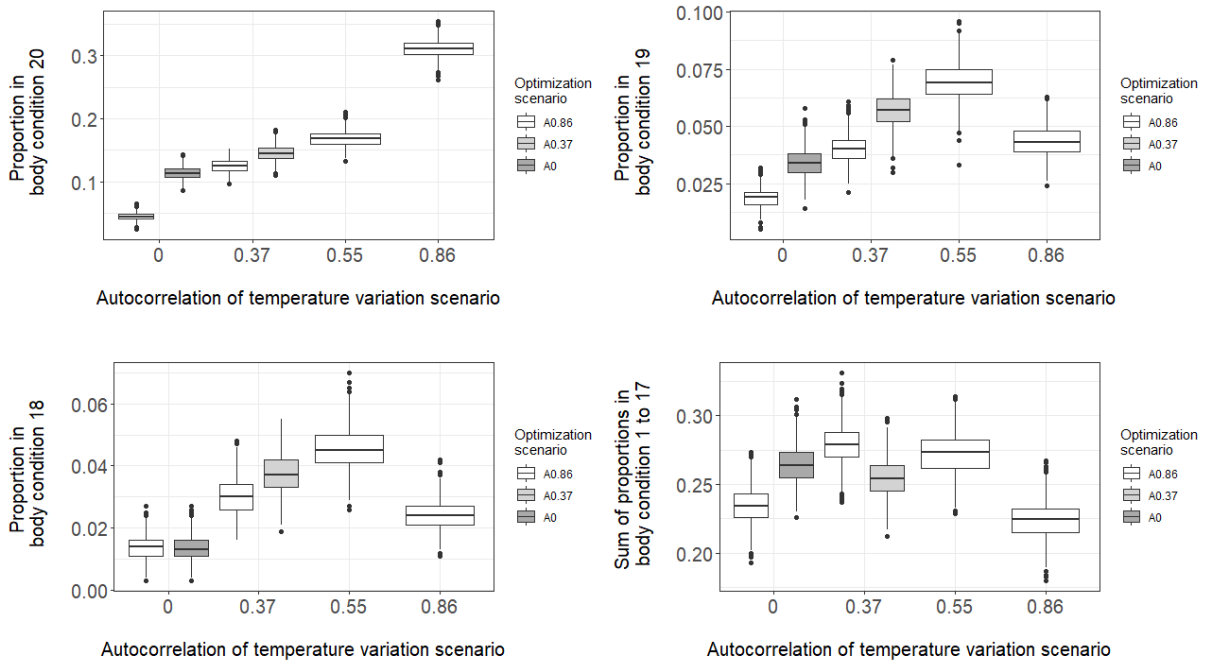


Figure 3. Proportion of individuals at body conditions  $C=20$ , 19, 18 and summed 1-17, of forward simulations with the specialist TPC, and temperature variation scenario indicated by autocorrelation on axis. Optimization temperature variation scenarios are given by colours, legend at the right.

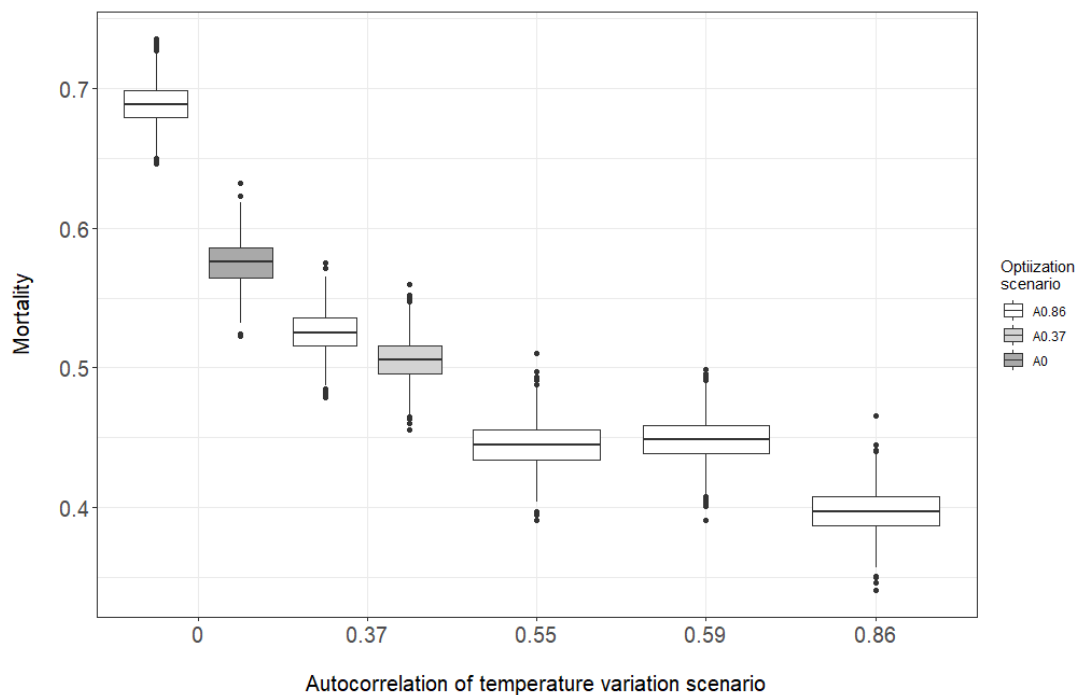


Figure 4. Mortality, the proportion of individuals at body condition  $C=0$ , of forward simulations with the specialist TPC, and temperature variation scenario indicated by autocorrelation on axis. Optimization temperature variation scenarios are given by colours, legend at the right.

## The generalist thermal performance curve

Preferred temperatures from behavioural strategies in the three temperature variation scenarios for the generalist is shown in Figure 5. In scenario A0.86, the preferred temperature,  $T_{\text{pref}C}$ , falls to the right of the optimal temperature with maximum expected net benefit. Scenarios of lower predictability have preferred temperatures at  $T_{\text{pref}D}$  and  $T_{\text{pref}E}$ . Scenario A0.37 has the same shift in preferred temperature with the experienced temperature deviations  $D_{t-1}$  as in the specialist.  $T_{\text{pref}D}$  is common for negative temperature deviations  $D_{t-1}$  and  $T_{\text{pref}E}$  for positive temperature deviations  $D_{t-1}$ . When there is no predictability in experienced temperatures, scenario A0,  $T_{\text{pref}D}$  is common for low body conditions and  $T_{\text{pref}E}$  for high body conditions.

Like the specialist, forward simulation shows that distributions of generalist body conditions, including mortality at  $C=0$ , is related to temperature predictability ( $\chi^2=168.65$ ,  $df=22$ ,  $p < 2.2 \cdot 10^{-16}$ ) (Figures 6 and 7). Higher predictability is associated with less mortality and a higher proportion of animals in the maximum obtainable body condition.

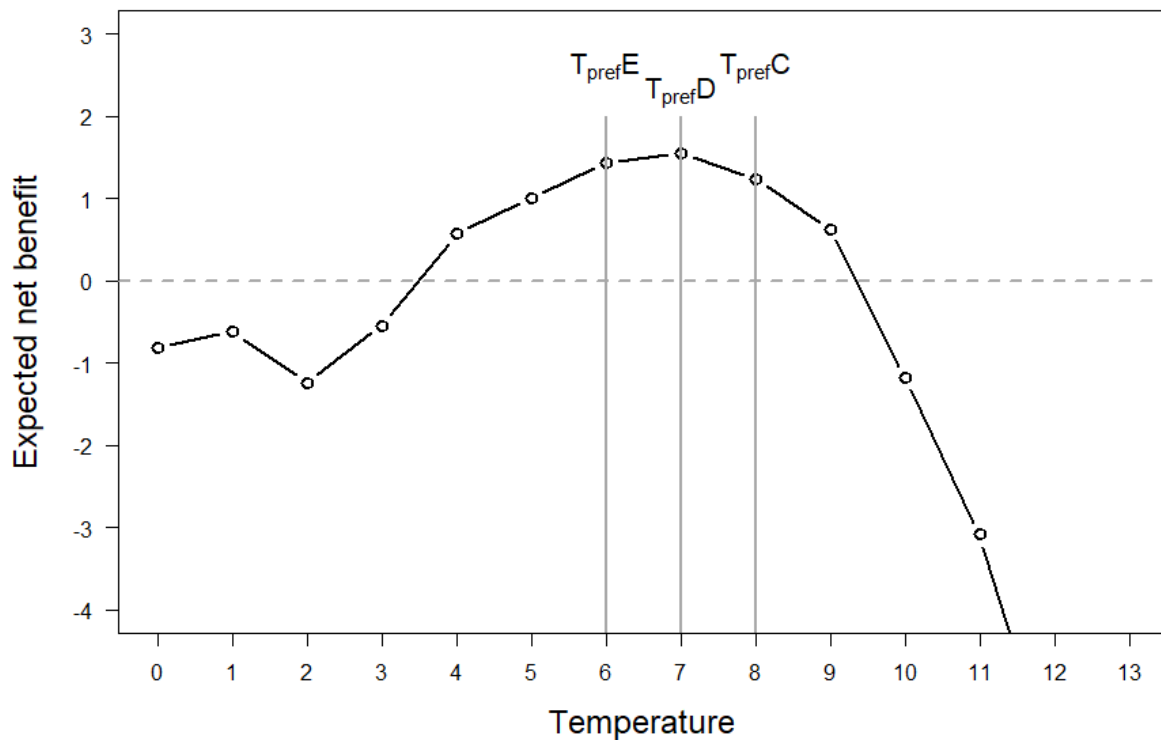


Figure 5. Generalist TPC, expected net benefits dependent on body temperature. Computed from the feeding efficiency  $E$ , metabolic costs  $M$  and constant benefit  $B$ .  $T_{\text{pref}C}$  is the preferred temperature for temperature variation scenario A0.86, while A0.37 and A0 has a division between  $T_{\text{pref}D}$  and  $T_{\text{pref}E}$  by previous temperature deviation  $D_{t-1}$  or body condition  $C$ , respectively. Note,  $T_{\text{pref}D}$  coincides with the optimal temperature choice.



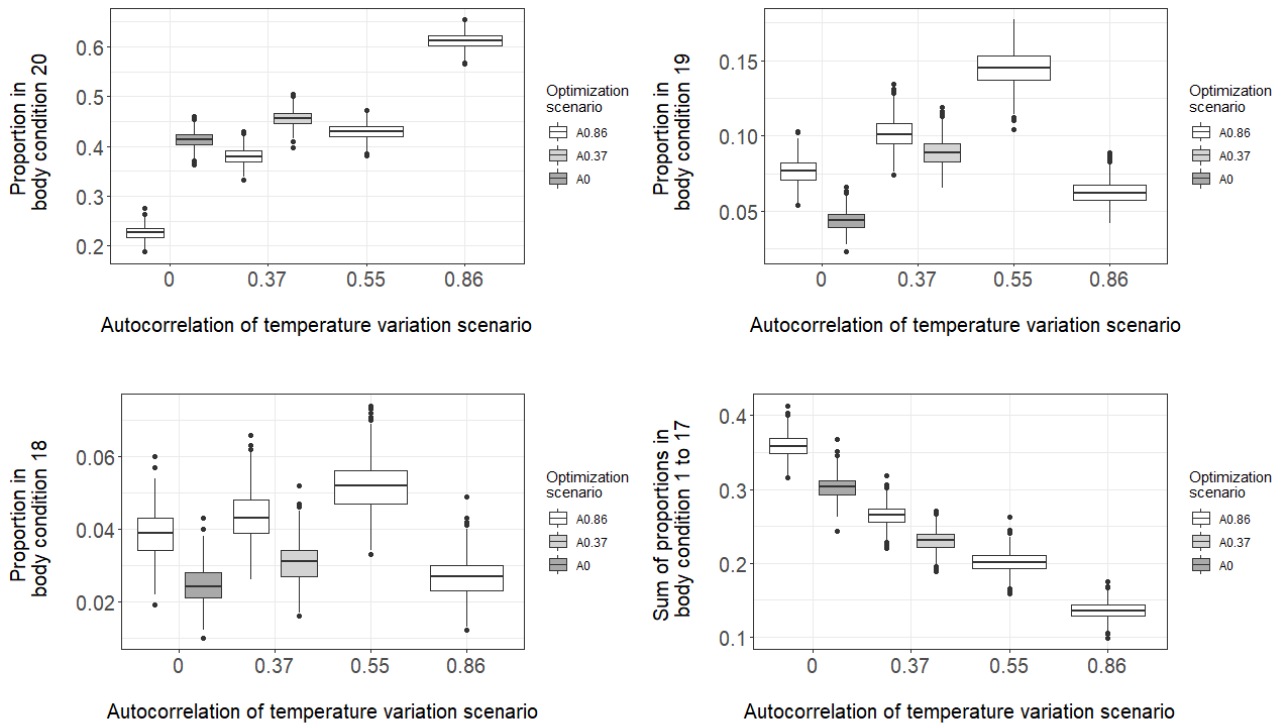


Figure 6. Proportion of individuals at body conditions  $C=20$ , 19, 18 and summed 1-17, of forward simulations with the generalist TPC, and temperature variation scenario indicated by autocorrelation on axis. Optimization temperature variation scenarios are given by colours, legend at the right.

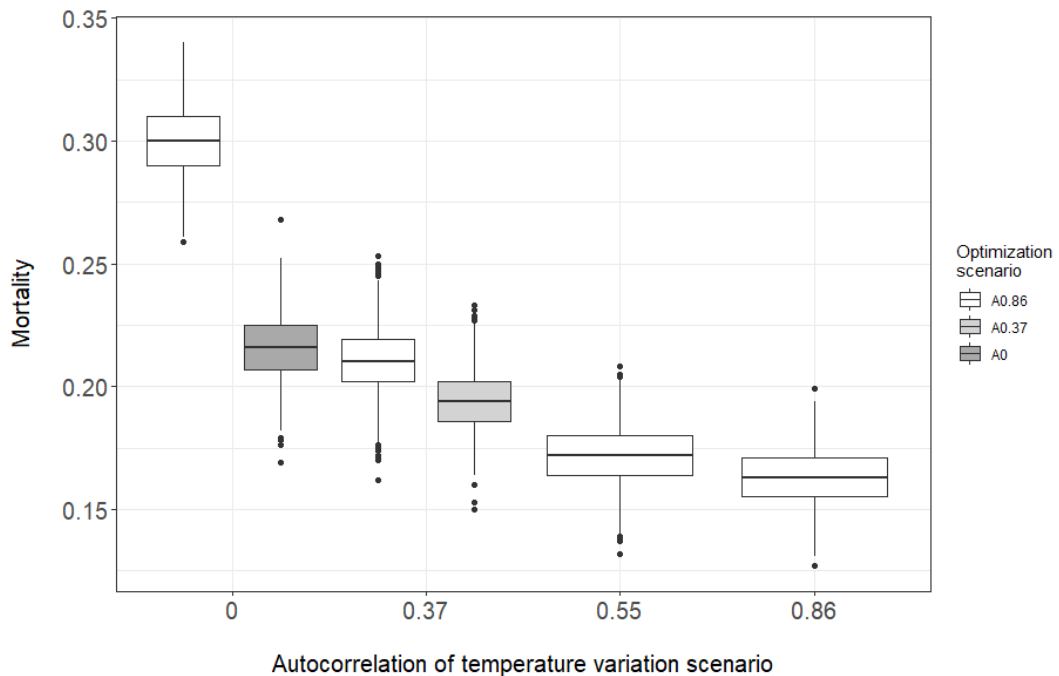


Figure 7. Mortality, the proportion of individuals at body condition  $C=0$ , of forward simulations with the generalist TPC, and temperature variation scenario indicated by autocorrelation on axis. Optimization temperature variation scenarios are given by colours, legend at the right

## Performance of behavioural strategies from A0.86 in novel temperature variation scenarios

### The specialist thermal performance curve

Thermoregulatory accuracy decreases, as distributions of experienced temperatures in forward simulations have higher variation in lower predictability scenarios (Figure 8). This leads to fitness declines, evident in the lower body condition and higher mortality of these scenarios (Figures 3 and 4). Distributions of body conditions from scenario's A0, A0.36 and A0.55 differ from the expected proportions calculated from scenario A0.86, A0 ( $\chi^2 = 503$ ,  $df = 11$ ,  $p < 2.2 \cdot 10^{-16}$ ), A0.54 ( $\chi^2 = 134.35$ ,  $df = 11$ ,  $p < 2.2 \cdot 10^{-16}$ ), and A 0.37 ( $\chi^2 = 204.19$ ,  $df = 11$ ,  $p < 2.2 \cdot 10^{-16}$ ).

Two main effects contribute to the difference. There is a decrease in the number of individuals in the highest obtainable body conditions (Figure 3). Shifts towards the lower ten to fifteen states is not evident. In addition, mortality ( $C=0$ ) increases when temperature predictability decreases (Figure 4)

The behavioural strategy optimized in A0.86 have poorer performance in scenario A0 than the behavioural strategy optimized for A0 ( $\chi^2 = 171.16$ ,  $df = 11$ ,  $p < 2.2 \cdot 10^{-16}$ ) (Figure 3 and 4). In scenario 0.37 there is no difference in strategy optimized for A=0.86 and A0.37 ( $\chi^2 = 17.14$ ,  $df = 11$ ,  $p=0.10$ ).

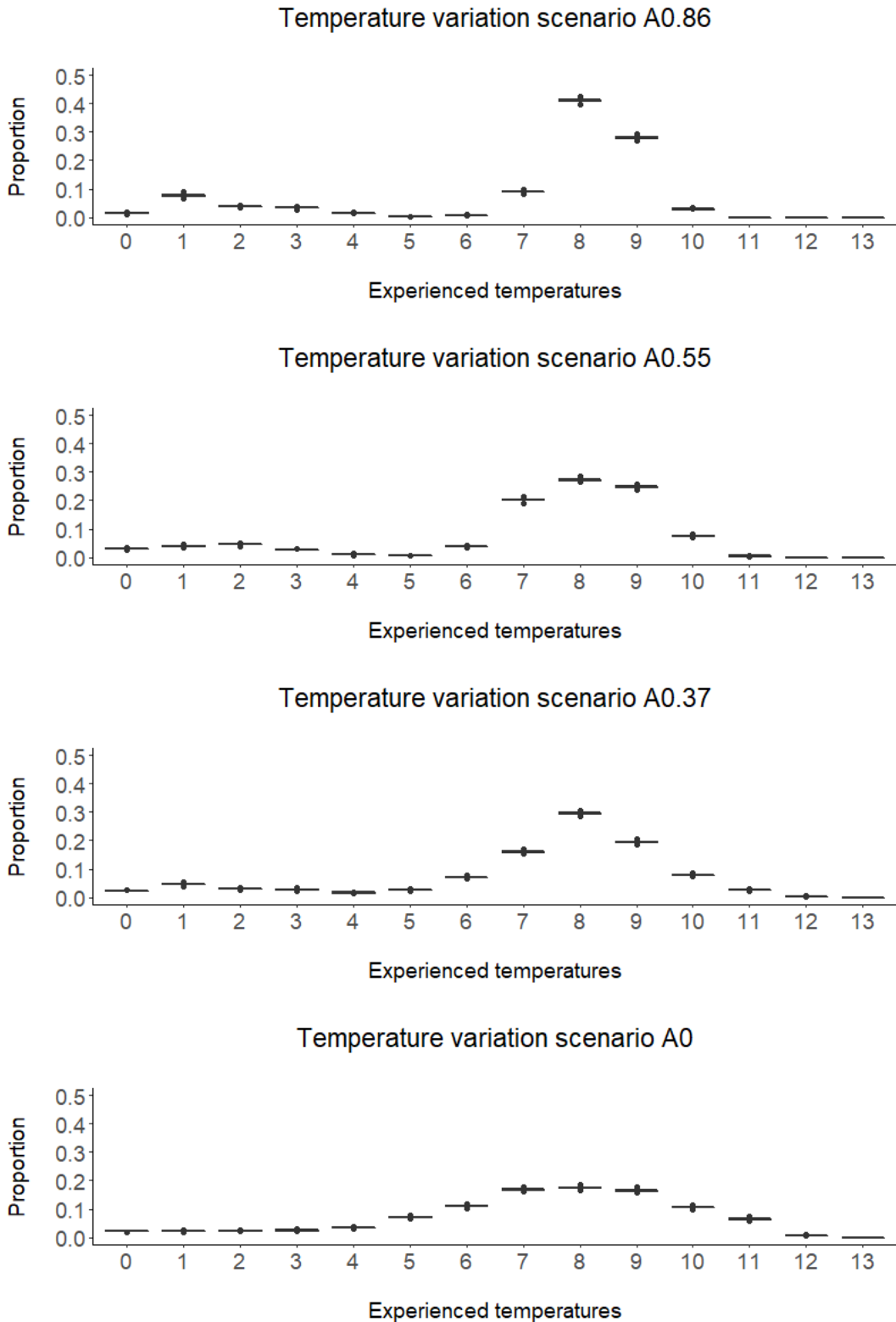


Figure 8. Distributions of experienced temperatures in forward simulations of specialist behavioural strategy optimized in A0.86. Distributions have sample sizes,  $N_{A0.86} = 21029847$ ,  $N_{A0.55} = 19079952$ ,  $N_{A0.37} = 20525619$ ,  $N_{A0} = 16102137$ , where animals that die no longer contribute to experienced temperatures.

## The generalist thermal performance curve

Temperature distributions from forward simulations of behavioural strategy optimized in A0.86 have higher variation in low predictability scenarios (Figure 9). This lower accuracy of the thermoregulatory strategy leads to fitness declines, evident in higher mortality and lower body conditions. The distributions of body conditions with strategy optimized in A0.86, in scenario's A0, A0.37 and A0.55 differ from the expected proportions calculated from scenario A0.86, A0 ( $\chi^2 = 960.03$ ,  $df = 11$ ,  $p < 2.2 \cdot 10^{-16}$ ), A0.55 ( $\chi^2 = 257.35$ ,  $df = 11$ ,  $p < 2.2 \cdot 10^{-16}$ ) and A0.37 ( $\chi^2 = 390.81$ ,  $df = 11$ ,  $p < 2.2 \cdot 10^{-16}$ ).

Forward simulations concur with the high expected fitness in this model, and for scenario A0.86 there is very high occurrence of the highest body condition. The most important factor influencing the differences in distribution of body condition is a downward shift of high values of body conditions in more variable temperature scenarios (Figure 6). Mortality also increases in less predictable temperature variation scenarios (Figure 7).

The behavioural strategy optimized for A0.86 has poorer performance in both scenario A0.37 and A0 than their respective optimal behavioural strategies, A0.37 ( $\chi^2 = 45.29$ ,  $df = 11$ ,  $p < 4.32 \cdot 10^{-6}$ ) and A0 ( $\chi^2 = 241.84$ ,  $df = 11$ ,  $p < 2.2 \cdot 10^{-16}$ ). Behavioural optimization reduces mortality and results in better body conditions (Figures 6 and 7).

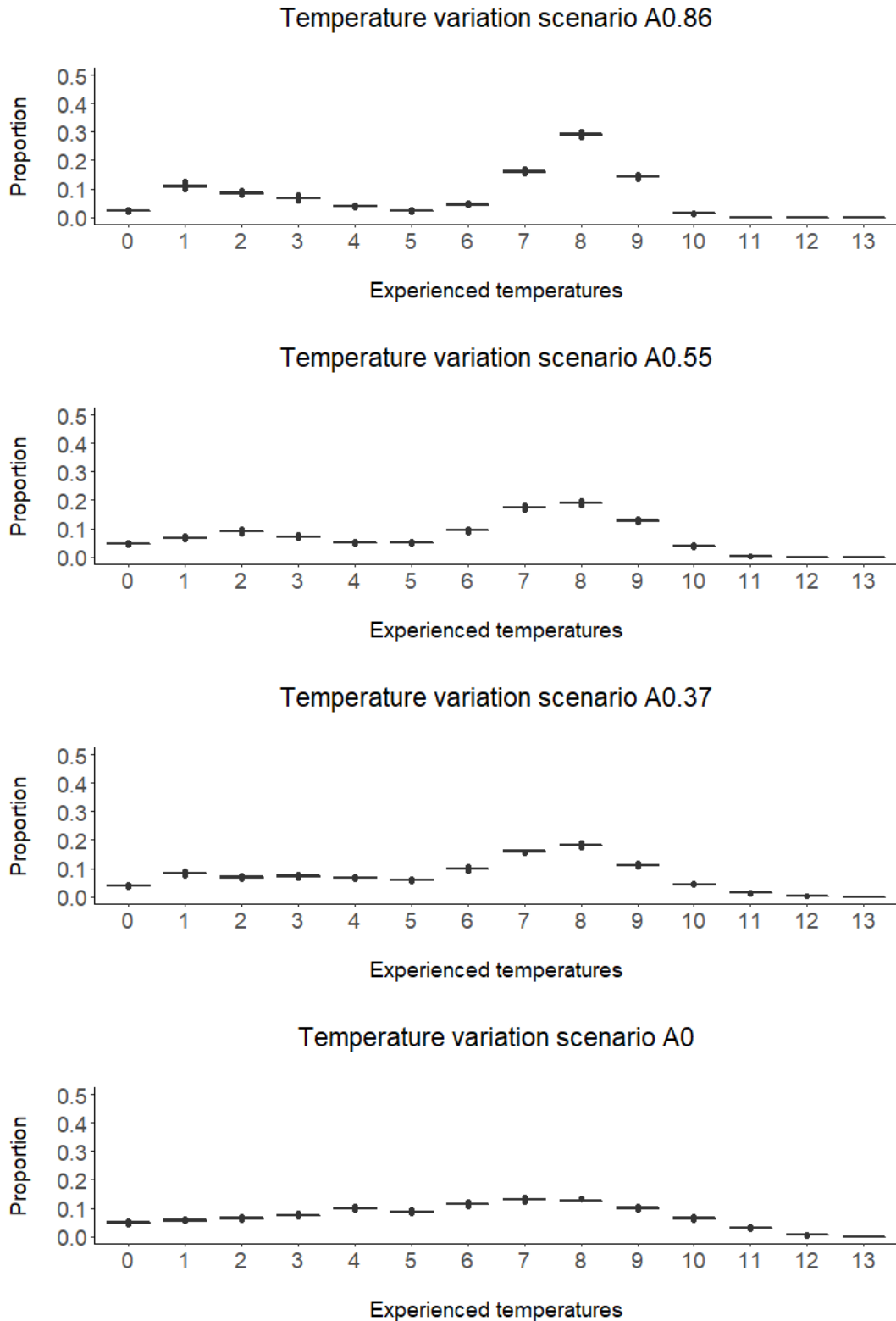


Figure 9. Distributions of experienced temperatures in forward simulations of generalist behavioural strategy optimized in A0.86. Distributions have sample sizes  $N_{A0.86} = 25327197$ ,  $N_{A0.55} = 24563637$ ,  $N_{A0.37} = 25326468$ ,  $N_{A0} = 22953826$ , where animals that die no longer contribute to experienced temperatures.

## Discussion

Optimal behavioural strategies show some agreement with predictions from Jensen's inequality, with lower preferred temperatures in high temperature variation scenarios. Based on the optimal behavioural strategies, expected net benefit alone is not the appropriate performance trait to base expectations off. Specialist performance breadth is too narrow to allow a great shift in preferred temperature, and the generalist is particularly affected by the probabilistic properties of feeding efficiency.

Thermoregulatory accuracy determines the experienced body temperatures of an ectotherm. Spatial configuration and variation in temperature might both decrease and increase accuracy, the latter resulting in opportunities of behavioural rescue (Huey and Slatkin, 1976; Sears, Raskin and Angilletta, 2011; Sears and Angilletta, 2015). When animals use information about expected temperature and previous temperature deviations to inform behavioural strategies, an argument can be made that temporal unpredictability, decreases the accuracy of the thermoregulatory strategy. Experienced temperature distributions have higher variation in less predictable environments (Figures 8 and 9). Decreased performance and thus fitness are evident (Figures 3, 4, 6 and 7). However, substantial changes to predictability are needed before severe fitness loss sets in. For A0.55, there is only a minor increase in mortality. Decrease in body conditions are confined to the upper three values. Still, this does translate into reduced reproduction.

Optimization to low predictability scenarios have decreased fitness compared to optimization to high predictability scenarios. These effects are likely a combination of the lower mean expected net benefit of lower preferred temperatures and higher variation in experienced temperatures.

### Preferred temperatures and risk management

Preferred temperatures are often predicted to be lower than optimal temperatures at high to moderate variation in temperature distributions due to effects of Jensen's inequality on asymmetrical thermal performance curves (Martin and Huey, 2008; Vercken *et al.*, 2012). Both the specialist and the generalist follow this pattern in my model, but in addition, the preferred temperature also depends on the previous temperature deviation  $D_{t-1}$ .  $D_{t-1}$  determines the upper and lower limits of possible new temperatures. Shifts in preferred temperatures thus avoid temperatures with expected net benefits below zero. There is no evidence for a shift that is greater for the specialist than the generalist (Figure 2 and 5) as is often predicted (Martin and Huey, 2008).

Part of the explanation for the small shifts in preferred temperature, is that stochastic dynamic modelling requires integers, while nature is continuous (Clark and Mangel, 2000). This necessitated incorporation of high costs and benefits, as I wanted a wide range of temperatures. Still, only a few temperatures are beneficial for each TPC, resulting in only a few, minor shifts in preferred temperatures. Particularly the specialist is limited in its temperatures with expected net benefit above zero. High fluctuations in body conditions and the low occurrence of lower body states is likely also a result of this, as animals either recover to higher body conditions or die. A partial resolution is including more state levels and potential temperatures.

The preferred temperature of the specialist in high predictability, fall at the optimal temperature of maximum expected net benefit. In contrast, at high predictability, the generalist has a higher preferred temperature than the optimal temperature (Figure 5). Foraging efficiency, rather than expected net benefit may explain this aberration.

Calculation of expected net benefit attempt to combine two possible outcomes at each time-step, finding food and not finding food, based on their probabilities. But expected temperature choices seem to be determined by the balance of the probability of obtaining a benefit, net benefits and the costs associated with not feeding. Because optimal risk sensitive behaviours depend on body condition and patterns of expected future fitness, this balance of influencing factors on behavioural choice is body condition and time dependent (Stephens, 1981; Clark, 1994; Bednekoff, 1996). For each expected temperature there is a wide range of possible net benefits. They arise from the combined effect of the probabilistic effect of temperature deviations, giving a range of experienced temperatures, and of feeding efficiency at each temperature. In the generalist, high preferred temperature is a low risk foraging strategy (Stephens, 1981; McNamara, Merad and Houston, 1991; Bednekoff, 1996). The probability of success is very high for these temperatures and have little variation as the upper part of the logistic curve is reached but comes with higher metabolic costs.

## Fitness consequences of novel temperature variation scenarios

Behavioural strategies optimized for the most predictable scenario, A0.86, have increased mortality and loss of body condition when confronted with a novel environment of lower temperature predictability (Figures 3, 4, 6 and 7). Thermoregulatory accuracy is decreased, and variance of experience temperatures are increased (Figures 8 and 9).

For both the specialist and the generalist, experiencing scenario A0.37 is more detrimental to body condition than A0.55. Explanations lie in the two components of unpredictability, and the specific matrices used to make the different temperature variation scenarios (Tables A1, A2 and A3). A0.55 has a higher autocorrelation than A0.37 because of high probability of staying in the two most extreme deviations when they are experienced. In comparison, A0.86 and A0.37 have high predictability in which new state D is experienced but low probability of staying in the two extreme Ds. In addition, A0.55 has a tighter probability distribution around the  $D_{t-1}$  than A0.37. Experienced temperatures in A0.37 are very rarely outside the expected temperatures of A0.86, which the strategy is optimized for.

Optimization of the behavioural framework with A0.86 give animals higher vulnerability to temperatures that fall outside those previously possible from  $D_{t-1}$ , than to variation within the temperatures it could previously expect to experience. This does not mean temperatures outside its range of previously experienced temperatures, just which were previously predicted from each  $D_{t-1}$ . This highlights the need to know what effects of higher temperature variance is important in order to create accurate predictive models of ectotherm persistence (Buckley, 2008; Buckley, Cannistra and John, 2018). Optimal behaviours and population persistence through heat waves would be an interesting addition to the model, where temperatures are in the upper thermal limits for prolonged times (Williams *et al.*, 2016).

## Comparison of specialist and generalist vulnerability to temperature predictability

Combined, it seems that ectotherms are vulnerable to substantial changes to predictability in temperature when it affects their ability to thermoregulate accurately (Sinervo *et al.*, 2010; Huey *et al.*, 2012; Vasseur *et al.*, 2014; Buckley, Ehrenberger and Angilletta, 2015; Sheldon and Dillon, 2016). An initial increase in generalist fitness from an increase in mean

temperature is hypothesised in literature (Deutsch *et al.*, 2008; Sheldon and Dillon, 2016). My model does not incorporate an increase in mean temperature, and together with the generalist optimal behavioural strategy with a preferred temperature to the right of their optimal temperature, no increases of fitness are witnessed.

Despite the caution applied to comparing the specialist and the generalist, the generalist tend to cope better with moderately high changes in temperature predictability (Deutsch *et al.*, 2008; Huey *et al.*, 2012). The main difference is the very steep increase in mortality in the specialist, but less of a reduction in proportion in high body conditions in the generalist also contributes. The high specialist mortality in scenario A0.86 implies that the specialist is more vulnerable to decreases in survival.

Vulnerability to reduced predictability in the environment will also be determined by plasticity and acclimatization. These abilities are a result of evolution and likely to depend on the previous level of variability encountered by the organism (Siepielski, Dibattista and Carlson, 2009; Markle and Kozak, 2018). Thus, previous levels of variability might determine animal robustness to future changes. Higher temperature variability is usually assumed as prerequisite for the evolution of generalists, rendering these animals more robust in the face of climate change (Gilchrist, 1995).

## Opportunities for behavioural rescue

Behavioural rescue is adjustment of behaviour to avoid extreme temperatures and high fitness-losses. Within my project, performance of optimal behavioural strategies from A0.87 in scenarios A0.37 and A0 is compared to performance of optimized behavioural strategies from these scenarios, A0.37 and A0, respectively. Differences in mortality and body condition distributions indicates whether it is beneficial to adjust behavioural strategies after predictions of Jensen's inequality. Some decrease in performance is expected due to the lower mean performance of the lower preferred temperatures.

The larger downward shift in preferred temperature hypothesized for the specialist is not evident in my model, discussed earlier, and similar arguments can be made when assessing the effects of behavioural optimization, i.e. optimization to the new temperature variation scenario. Exploitation of this possibility is limited owing to the small ranges of temperatures that are beneficial, for example with expected net benefits above zero (Figures 2 and 5), or even temperatures with moderate probability of net benefit above zero. The specialist cannot employ insurance strategies to a substantially greater degree, and no matter the preferred temperature, detrimental high or low temperatures are always encountered. In contrast, the generalist has more opportunity of avoiding very detrimental temperatures. It could be argued that both the TPCs described in this article are specialist, and that a generalist needs a much wider performance breadth.

Even with opportunities for behavioural adjustment to lower preferred temperatures, mortality and proportions in higher body conditions is are far from levels in A0.86. Particularly the specialist is limited by the availability of favourable temperatures, with only minor, non-significant increases in fitness with behavioural optimization to A0.37. The effect is more pronounced in A0, where mortality decreases by more than 10 percent (Figures 3 and 4). The generalist benefits from behavioural optimization in both A0.37 and A0 (Figures 6 and 7), with almost a 10% decrease in mortality in A0, despite the much lower overall mortality in the generalist.



## Risk sensitivity in body condition- and time-dependent behavioural choices

In addition to effects of temperature predictabilities, all behavioural strategies depend to some degree on animal body condition and time (Figures A1-A6). These results are best explained by risk sensitive foraging and the asset protection principle (Stephens, 1981; Clark, 1994; Bednekoff, 1996) and are commonly found in optimal foraging theory (Stephens, 1981; Clark and Levy, 1988; McNamara and Houston, 1990).

Individuals in high body conditions should have risk-averse choices, while low body condition results in risk-prone strategies. In the current model risk averse strategies can be realised as a preference for low expected temperatures, which minimizes loss of body condition. This is evident for animals in high body conditions, where only loss of body condition and reductions in expected fitness are possible. The situation is opposite at low body conditions, where loss of condition mostly leads to death. These animals attempt to increase their probability of finding food by employing risk-prone strategies. These animals prefer high expected temperatures, with high efficiencies but also lower net benefits (Figures A1-A6).

These same arguments can be extended to body conditions equal to the cost associated with the optimal behavioural choice, and the lower body conditions. In the first case, animals are risk-averse, and potential costs dominate. In the latter case, increased efficiency dominates, and animals employ a risk-prone strategy of high expected patch temperatures (Figures A1-A6).

The asset protection principle can explain both these body-condition dependent risk sensitive strategies, but also the shift in strategy at later time stages (Clark, 1994; Bednekoff, 1996). The specialist is relatively unchanged, with some more pronounced risk-averse or prone strategies following body condition as described above. This is also present in the generalist, but in addition there is a preference of a lower temperature at mid-body conditions (Figure A4-A6). The preferred temperature at early to mid-times is higher than  $T_{opt}$ , and the decrease brings preferred temperatures in scenario A0.86 to  $T_{predD}$  and in scenario A0.37 to coincide with  $T_{predD}$  and  $T_{predE}$ , for respectively negative and null, and positive deviations  $D_{t-1}$ . The probable explanation is a risk-prone strategy to obtain the highest possible body conditions. At early to mid-times, there is ample opportunity for body condition to fluctuate, and the optimal is a risk-averse strategy favouring high feeding efficiency. At the later time stages, the opportunity for increase in body condition to the highest values are smaller, and high feeding efficiency is sacrificed for the higher net benefits available at  $T_{pre} = T_{opt}$ , which is a risk-prone strategy. There are indications in reptiles that gravid females thermoregulate more accurately and at slightly different temperatures than non-gravid individuals, and if you expect this effect to arise from energy optimization, it might be comparable to the strategy shifts seen at later time stages in these models (Blouin-Demers and Weatherhead, 2001; Herczeg *et al.*, 2006).

## Further work and conclusion

Implementing TPCs to understand effects of temperature on animal performance is a popular tool in several modelling frameworks (Buckley, 2008; Vasseur *et al.*, 2014; Sheldon and Dillon, 2016; Fey *et al.*, 2019). But, as ever with simplified tools, TPCs should be used with a measure of caution (Huey *et al.*, 2012; Sinclair *et al.*, 2016; Buckley, Cannistra and John, 2018). A major problem is which traits are used and establishing links to measures of fitness. If these are in place, a second drawback is that TPCS are rarely

constant, and can vary with individuals and populations, through time and temporal experience and with life-stages (Asbury and Angilletta Jr., 2010; Huey *et al.*, 2012; Sinclair *et al.*, 2016; Williams *et al.*, 2016). Interesting physiological or behavioural adjustment could be modelled by incorporating changing TPCs as a way of modelling plasticity and acclimatization. A cost of acclimatization of the TPC coupled with an increase in temperature could be used to assess the possibilities of shifting the optimal temperature within a season or lifetime (Gvoždík, 2012). Selection on and evolution of TPCs are possibilities, but not relevant at the short timescale proposed here. It should also be mentioned that dynamic state variable models are single individual models, and do not incorporate any interactions with other living organisms beyond those specified in state variables. Competition may play an important role in population responses to climate change, for example through availability of suitable temperatures and thus accuracy of thermoregulation. It might therefore be necessary to include the current results in a density dependent framework to understand the full response.

Evolution of thermal performance curves are not only concerned with the optimal temperatures, but also performance breadths and critical thermal maxima. Selection does not only depend on experienced variation in temperature, but could also be influenced by mean temperatures, high temperatures or heat waves or rainfall and similar abiotic factors (Izem and Kingsolver, 2005; Clusella-Trullas, Blackburn and Chown, 2011; Huey *et al.*, 2012; Johansson and Laurila, 2017). Performance responses to extreme temperatures might even not be determined by the TPC alone, but be modelled by previous experience and the time-series of temperatures (Kingsolver and Woods, 2016; Sinclair *et al.*, 2016). Generally, critical thermal maximum of a species is assumed to be similar for all traits, as they are adapted to the same thermal environment. However, this is not true for animals experiencing great temperature variation. Decoupling of behavioural and physiological trait TPCS are documented, where temperature ranges of behavioural traits are constrained to a small area of the physiological tolerance range (Monaco, McQuaid and Marshall, 2017). Here also lies potential explanations of observed preferred temperatures below optimal temperatures of performance, where measurements are done in laboratory settings with only weak links to fitness established, and possible decoupling of measured traits. This raises the possibility that the measured temperature variance is not the correct for the trait being studied, and prediction from Jensen's inequality combining these will be incorrect. Because of this, traits and accompanying distributions of body temperatures must be carefully considered before implementation into any modelling approach.

Most research into behavioural thermoregulation and rescue have been done on reptiles, mainly small lizards. The generality of thermoregulatory strategies and behavioural rescue is therefore not well established. For a wide range of, particularly reptilian, taxa, there is a balance between thermoregulatory behaviours, like basking and retreat site selection, and foraging, predation-avoidance or reproduction (Avery, Bedford and Newcombe, 1982; Hertz, Huey and Stevenson, 1993; Downes and Shine, 1998; Sinervo *et al.*, 2010; Nordberg and Schwarzkopf, 2019). In a similar vein, behavioural thermoregulation is usually thought to impose extra costs in addition to the increase in metabolism with temperature (Huey and Slatkin, 1976; Herczeg *et al.*, 2006), for example cost of movement between habitats (Sears, Raskin and Angilletta, 2011; Sears and Angilletta, 2015; Sears *et al.*, 2016), or a loss of opportunity. To tackle further questions about behavioural rescue and loss of opportunity, dynamic state variable models could be made with these different behaviours and costs in mind. Being able to reduce costs of incorrect thermoregulation or even reduce the variation in experienced temperatures, might increase the efficiency of adjusting behaviour to novel environments.

Feeding efficiency could be exchanged with a related trait that measures proportional exploitation of a resource. Digestion may have a similar temperature response and is suitable for consideration of behavioural choice of preferred temperatures (Huey *et al.*, 1989; Levy *et al.*, 2017). Some effort has been made to understand the interplay of water and temperature on ectotherm fitness and the evolution of performance curves (Kearney, Shine and Porter, 2009; Clusella-Trullas, Blackburn and Chown, 2011; Buckley, Cannistra and John, 2018). An exchange of energetic state with hydration status in a similar behavioural model could give some insight into water balance in ectotherms.

Ectotherm animals unable adjust behaviour to mitigate effects of increased variation and unpredictability in their environment, will suffer fitness loss and elevated mortality. Implications of this project is that animals are more vulnerable to temperatures outside those they are behaviourally adapted to, than a general decrease in predictability and increased variation.

## References

- Amarasekare, P. and Johnson, C. (2017) 'Evolution of Thermal Reaction Norms in Seasonally Varying Environments', *The American Naturalist*, 189(3), pp. E31–E45. doi: 10.1086/690293.
- Angilletta Jr., M. J. (2009) *Thermal Adaptation*. Oxford University Press. doi: 10.1093/acprof:oso/9780198570875.001.1.
- Angilletta, M. J. (2001) 'Thermal and physiological constraints on energy assimilation in a widespread lizard (*Sceloporus Undulatus*)', *Ecology*. Wiley Online Library, 82(11), pp. 3044–3056. doi: 10.1890/0012-9658(2001)082[3044:TAPCOE]2.0.CO;2.
- Angilletta, M. J., Niewiarowski, P. H. and Navas, C. A. (2002) 'The evolution of thermal physiology in ectotherms', *Journal of Thermal Biology*, pp. 249–268. doi: 10.1016/S0306-4565(01)00094-8.
- Asbury, D. A. and Angilletta Jr., M. J. (2010) 'Thermodynamic Effects on the Evolution of Performance Curves', *The American Naturalist*, 176(2), pp. E40–E49. doi: 10.1086/653659.
- Avery, R. A., Bedford, J. D. and Newcombe, C. P. (1982) 'The role of thermoregulation in lizard biology: Predatory efficiency in a temperate diurnal basker', *Behavioral Ecology and Sociobiology*, 11(4), pp. 261–267. doi: 10.1007/BF00299303.
- Baron, J.-P. et al. (2013) 'Intermittent breeding and the dynamics of resource allocation to reproduction, growth and survival', *Functional Ecology*. John Wiley & Sons, Ltd (10.1111), 27(1), pp. 173–183. doi: 10.1111/1365-2435.12023.
- Basawa, I. V. (1972) 'Estimation of the Autocorrelation Coefficient in Simple Markov Chains', *Biometrika*, 59(1), pp. 85–89.
- Bednekoff, P. A. (1996) 'Risk-Sensitive Foraging, Fitness, and Life Histories: Where Does Reproduction Fit into the Big Picture?', *American Zoologist*, 36(4), pp. 471–483.
- Blouin-Demers, G. and Weatherhead, P. J. (2001) 'Thermal Ecology of Black Rat Snakes (*Elaphe obsoleta*) in a Thermally Challenging Environment', *Ecology*. Ecological Society of America, 82(11), pp. 3025–3043. doi: 10.2307/2679832.
- Bonnet, X., Bradshaw, D. and Shine, R. (1998) 'Capital versus Income Breeding: An Ectothermic Perspective', *Oikos*. [Nordic Society Oikos, Wiley], 83(2), pp. 333–342. doi: 10.2307/3546846.
- Buckley, L. B. (2008) 'Linking Traits to Energetics and Population Dynamics to Predict Lizard Ranges in Changing Environments', *The American Naturalist*, 171(1), pp. E1–E19. doi: 10.1086/523949.
- Buckley, L. B., Cannistra, A. F. and John, A. (2018) 'Leveraging organismal biology to forecast the effects of climate change', *Integrative and Comparative Biology*, 58(1), pp. 38–51. doi: 10.1093/icb/icy018.
- Buckley, L. B., Ehrenberger, J. C. and Angilletta, M. J. (2015) 'Thermoregulatory behaviour limits local adaptation of thermal niches and confers sensitivity to climate change', *Functional Ecology*, 29(8), pp. 1038–1047. doi: 10.1111/1365-2435.12406.
- Clark, C. W. (1994) 'Antipredator behavior and the asset-protection principle', *Behavioral Ecology*, 5(2), pp. 159–170. doi: 10.1093/beheco/5.2.159.
- Clark, C. W. and Levy, D. A. (1988) 'Diel Vertical Migrations by Juvenile Sockeye Salmon and the Antipredation Window', *American Naturalist*, 131(2), pp. 271–290.
- Clark, C. W. and Mangel, M. (2000) *Dynamic State Variable Models in Ecology, Oxford Series in Ecology and Evolution*.
- Clusella-Trullas, S., Blackburn, T. M. and Chown, S. L. (2011) 'Climatic Predictors of Temperature Performance Curve Parameters in Ectotherms Imply Complex Responses to

- Climate Change', *The American Naturalist*, 177(6), pp. 738–751. doi: 10.1086/660021.
- Corkrey, R. *et al.* (2012) 'Universality of Thermodynamic Constants Governing Biological Growth Rates', *PLoS ONE*. Edited by V. N. Uversky, 7(2), p. e32003. doi: 10.1371/journal.pone.0032003.
- Damme, R. Van, Bauwens, D. and Verheyen, R. F. (1991) 'The Thermal Dependence of Feeding Behaviour, Food Consumption and Gut-Passage Time in the Lizard *Lacerta vivipara* Jacquin', *Functional Ecology*, 5(4), p. 507. doi: 10.2307/2389633.
- Dell, A. I., Pawar, S. and Savage, V. M. (2011) 'Systematic variation in the temperature dependence of physiological and ecological traits', *Proceedings of the National Academy of Sciences*, 108(26), pp. 10591–10596. doi: 10.1073/pnas.1015178108.
- Deutsch, C. A. *et al.* (2008) 'Impacts of climate warming on terrestrial ectotherms across latitude', *Proceedings of the National Academy of Sciences of the United States of America*, 105(18), pp. 6668–6672. doi: 10.1073/pnas.0709472105.
- Dillon, M. E. and Woods, H. A. (2016) 'Introduction to the symposium: Beyond the mean: Biological impacts of changing patterns of temperature variation', *Integrative and Comparative Biology*, 56(1), pp. 11–13. doi: 10.1093/icb/icw020.
- Downes, S. and Shine, R. (1998) 'Heat, safety or solitude? Using habitat selection experiments to identify a lizard's priorities', *Animal Behaviour*. Academic Press, 55(5), pp. 1387–1396. doi: 10.1006/ANBE.1997.0705.
- Dreisig, H. (1981) 'The Rate of Predation and Its Temperature Dependence in a Tiger Beetle, *Cicindela Hybridus*', *Oikos*. [Nordic Society Oikos, Wiley], 36(2), p. 196. doi: 10.2307/3544446.
- Fey, S. B. *et al.* (2019) 'Opportunities for behavioral rescue under rapid environmental change', *Global Change Biology*, 25(9), pp. 3110–3120. doi: 10.1111/gcb.14712.
- Gilchrist, G. W. (1995) 'Specialists and Generalists in Changing Environments. I. Fitness Landscapes of Thermal Sensitivity', *The American Naturalist*, 146(2), pp. 252–270.
- Gillooly, J. F. *et al.* (2001) 'Effects of Size and Temperature on Metabolic Rate', *Science*, 293(5538), pp. 2248–2251.
- Greenwald, A. O. E. (2017) 'Thermal Dependence of Striking and Prey Capture by Gopher Snakes', *American Society of Ichthyologists and Herpetologists*, 1974(1), pp. 141–148.
- Gvoždík, L. (2012) 'Plasticity of preferred body temperatures as means of coping with climate change?', *Biology Letters*, 8(2), pp. 262–265. doi: 10.1098/rsbl.2011.0960.
- Haaland, T. R. *et al.* (2019) 'Short-term insurance versus long-term bet-hedging strategies as adaptations to variable environments', *Evolution*. Wiley Subscription Services, Inc., 73(2), pp. 145–157. doi: <http://dx.doi.org/10.1111/evo.13659>.
- Herczeg, G. *et al.* (2006) 'Experimental support for the cost–benefit model of lizard thermoregulation', *Behavioral Ecology and Sociobiology*, 60(3), pp. 405–414. doi: 10.1007/s00265-006-0180-6.
- Hertz, P. E., Huey, R. B. and Stevenson, R. D. (1993) 'Evaluating Temperature Regulation by Field-Active Ectotherms: The Fallacy of the Inappropriate Question', *The American Naturalist*, 142(5), pp. 796–818. doi: 10.1086/285573.
- Higginson, A. D. *et al.* (2012) 'Generalized Optimal Risk Allocation: Foraging and Antipredator Behavior in a Fluctuating Environment', *The American Naturalist*, 180(5), pp. 589–603. doi: 10.1086/667885.
- Houston, A. and McNamara, J. M. (1999) *Models of adaptive behaviour*. Edited by J. McNamara. Cambridge: Cambridge University Press.
- Huey, R. B. *et al.* (1989) 'Hot Rocks and Not-So-Hot Rocks: Retreat-Site Selection by Garter Snakes and Its Thermal Consequences', *Ecology*, 70(4), pp. 931–944. doi:

10.2307/1941360.

Huey, R. B. *et al.* (2012) 'Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1596), pp. 1665–1679. doi: 10.1098/rstb.2012.0005.

Huey, R. B. and Berrigan, D. (2001) 'Temperature, demography, and ectotherm fitness', *The American Naturalist*, 158(2), pp. 204–210.

Huey, R. B. and Kingsolver, J. G. (2011) 'Variation in universal temperature dependence of biological rates', *Proceedings of the National Academy of Sciences of the United States of America*, 108(26), pp. 10377–10378. doi: 10.1073/pnas.

Huey, R. B. and Slatkin, M. (1976) 'Cost and benefits of lizard thermoregulation', *The Quarterly Review of Biology*, 51(1), pp. 3–47.

Huey, R. B. and Stevenson, R. D. (1979) 'Integrating Thermal Physiology and Ecology of Ectotherms: A Discussion of Approaches', *American Zoologist*, 19, pp. 357–366.

Izem, R. and Kingsolver, J. G. (2005) 'Variation in Continuous Reaction Norms: Quantifying Directions of Biological Interest', *The American Naturalist*, 166(2), pp. 277–289. doi: 10.1086/431314.

Jakob, E. M., Marshall, S. D. and Uetz, G. W. (1996) 'Estimating Fitness: A Comparison of Body Condition Indices', *Oikos*, 77(1), p. 61. doi: 10.2307/3545585.

Jaumann, S. and Snell-Rood, E. C. (2019) 'Adult nutritional stress decreases oviposition choosiness and fecundity in female butterflies', *Behavioral Ecology*, 30(3), pp. 852–863. doi: 10.1093/beheco/arz022.

Johansson, F. (2019) 'Impact of global warming on insects: are tropical species more vulnerable than temperate species?', pp. 1–21.

Johansson, M. P. and Laurila, A. (2017) 'Maximum thermal tolerance trades off with chronic tolerance of high temperature in contrasting thermal populations of *Radix balthica*', *Ecology and Evolution*, 7(9), pp. 3149–3156. doi: 10.1002/ece3.2923.

Kearney, M., Shine, R. and Porter, W. P. (2009) 'The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming', *Proceedings of the National Academy of Sciences of the United States of America*, 106(10), pp. 3835–3840. doi: 10.1073/pnas.0808913106.

Kingsolver, J. G. and Woods, H. A. (2016) 'Beyond Thermal Performance Curves: Modeling Time-Dependent Effects of Thermal Stress on Ectotherm Growth Rates', *The American Naturalist*, 187(3), pp. 283–294. doi: 10.1086/684786.

Levy, O. *et al.* (2017) 'Diminishing returns limit energetic costs of climate change', *Ecology*, 98(5), pp. 1217–1228. doi: 10.1002/ecy.1803.

Markle, T. M. and Kozak, K. H. (2018) 'Low acclimation capacity of narrow-ranging thermal specialists exposes susceptibility to global climate change', *Ecology and Evolution*, 8(9), pp. 4644–4656. doi: 10.1002/ece3.4006.

Martin, T. L. and Huey, R. B. (2008) 'Why "Suboptimal" Is Optimal: Jensen's Inequality and Ectotherm Thermal Preferences', *The American Naturalist*, 171(3), pp. E102–E118. doi: 10.1086/527502.

McNamara, J. M. and Houston, A. I. (1990) 'The value of fat reserves and the tradeoff between starvation and predation', *Acta Biotheoretica*, 38(1), pp. 37–61. doi: 10.1007/BF00047272.

McNamara, J. M., Merad, S. and Houston, A. I. (1991) 'A model of risk-sensitive foraging for a reproducing animal', *Animal Behaviour*, 41(5), pp. 787–792. doi: 10.1016/S0003-3472(05)80345-8.

Monaco, C. J., McQuaid, C. D. and Marshall, D. J. (2017) 'Decoupling of behavioural and

physiological thermal performance curves in ectothermic animals: a critical adaptive trait', *Oecologia*. Springer Berlin Heidelberg, 185(4), pp. 583–593. doi: 10.1007/s00442-017-3974-5.

Nielsen, M. E. (2017) 'No geographic variation in thermoregulatory colour plasticity and limited variation in heat-avoidance behaviour in *Battus philenor* caterpillars', *Journal of Evolutionary Biology*, 30(10), pp. 1919–1928. doi: 10.1111/jeb.13168.

Nordberg, E. J. and Schwarzkopf, L. (2019) 'Heat seekers: A tropical nocturnal lizard uses behavioral thermoregulation to exploit rare microclimates at night', *Journal of Thermal Biology*, 82, pp. 107–114. doi: 10.1016/j.jtherbio.2019.03.018.

Pangle, K. L. *et al.* (2004) 'Overwinter Survival of Juvenile Lake Herring in Relation to Body Size, Physiological Condition, Energy Stores, and Food Ration', *Transactions of the American Fisheries Society*, 133(5), pp. 1235–1246. doi: 10.1577/T03-127.1.

Real, L. and Caraco, T. (1986) 'Risk and foraging in stochastic environments', *Annual Review of Ecology and Systematics*, 17, pp. 371–390.

Sears, M. W. *et al.* (2016) 'Configuration of the thermal landscape determines thermoregulatory performance of ectotherms', *Proceedings of the National Academy of Sciences*, 113(38), pp. 10595–10600. doi: 10.1073/pnas.1604824113.

Sears, M. W. and Angilletta, M. J. (2015) 'Costs and Benefits of Thermoregulation Revisited: Both the Heterogeneity and Spatial Structure of Temperature Drive Energetic Costs', *The American Naturalist*, 185(4), pp. E94–E102. doi: 10.1086/680008.

Sears, M. W., Raskin, E. and Angilletta, M. J. (2011) 'The World Is not Flat: Defining Relevant Thermal Landscapes in the Context of Climate Change', *Integrative and Comparative Biology*, 51(5), pp. 666–675. doi: 10.1093/icb/icr111.

Sheldon, K. S. and Dillon, M. E. (2016) 'Beyond the mean: Biological impacts of cryptic temperature change', in *Integrative and Comparative Biology*, pp. 110–119. doi: 10.1093/icb/icw005.

Siepielski, A. M., Dibattista, J. D. and Carlson, S. M. (2009) 'It's about time: The temporal dynamics of phenotypic selection in the wild', *Ecology Letters*, 12(11), pp. 1261–1276. doi: 10.1111/j.1461-0248.2009.01381.x.

Sinclair, B. J. *et al.* (2016) 'Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures?', *Ecology Letters*, 19(11), pp. 1372–1385. doi: 10.1111/ele.12686.

Sinervo, B. *et al.* (2010) 'Erosion of Lizard Diversity by Climate Change and Altered Thermal Niches', *Science*, 328(5980), pp. 894–899. doi: 10.1126/science.1184695.

Spotila, O'Connor and Bakken (1992) 'Biophysics of heat and mass transfer', in Feder and Burggren (eds) *Environmental Physiology of the Amphibians*. University of Chicago Press.

Stephens, D. W. (1981) 'The logic of risk-sensitive foraging preferences', *Animal Behaviour*, 29(2), pp. 628–629. doi: 10.1016/S0003-3472(81)80128-5.

Tewksbury, J. J., Huey, R. B. and Deutsch, C. A. (2008) 'Ecology: Putting the heat on tropical animals', *Science*, 320(5881), pp. 1296–1297. doi: 10.1126/science.1159328.

Urban, M. C. *et al.* (2016) 'Improving the forecast for biodiversity under climate change', *Science*, 353(6304), p. aad8466 1-9. doi: 10.1126/science.aad8466.

Vasseur, D. A. *et al.* (2014) 'Increased temperature variation poses a greater risk to species than climate warming', *Proceedings of the Royal Society: Biological Sciences*, 281(1779), pp. 1–8. doi: 10.1098/rspb.2013.2612.

Vercken, E. *et al.* (2012) 'Don't Fall Off the Adaptation Cliff: When Asymmetrical Fitness Selects for Suboptimal Traits', *PLoS ONE*. Edited by M. Heil, 7(4), p. e34889. doi: 10.1371/journal.pone.0034889.

Williams, C. M. *et al.* (2016) 'Biological Impacts of Thermal Extremes: Mechanisms and Costs of Functional Responses Matter', *Integrative and Comparative Biology*, 56(1), pp. 73–84. doi: 10.1093/icb/icw013.



## Appendix

### Appendix 1.

Temperature deviation transition matrices (Tables A1-A4).

Optimal behavioural strategies for generalist and specialist TPCs in temperature variation scenarios A0.86, A0.37 and A0. (Figures A1-A5)

# Appendix 1

## Temperature variation scenarios

All temperature variation scenarios are shown in table A2 1 to 5 with experienced temperature deviations,  $D_{t-1}$ , in rows (column 1) and probability of transition to state D in columns. Different temperature variation scenarios are labelled with their autocorrelation calculated as rank autocorrelation of first order (Basawa, 1972)

A1. Temperature variation scenario matrix of A0.86, with autocorrelation 0.85929.

D	-2	-1	0	1	2
-2	0.4	0.4	0.1	0	0
-1	0.1	0.8	0.1	0	0
0	0	0.1	0.8	0.1	0
1	0	0	0.1	0.8	0.1
2	0	0	0.1	0.4	0.4

Table 23. Temperature variation scenario matrix A0.37 with autocorrelation 0.36667.

D	-2	-1	0	1	2
-2	0.2	0.4	0.2	0.2	0
-1	0.2	0.4	0.2	0.1	0.1
0	0.1	0.2	0.4	0.2	0.1
1	0.1	0.1	0.2	0.4	0.2
2	0	0.2	0.2	0.4	0.2

Table A3. Temperature variation scenario matrix A0.54, with autocorrelation 0.54377.

D	-2	-1	0	1	2
-2	0.3	0.3	0.3	0.1	0
-1	0.3	0.3	0.3	0.1	0
0	0	0.3	0.4	0.3	0
1	0	0.1	0.3	0.3	0.3
2	0	0.1	0.3	0.3	0.3

Table A4. Temperature variation scenario matrix A0, with autocorrelation 0.

D	-2	-1	0	1	2
-2	0.2	0.2	0.2	0.2	0.2
-1	0.2	0.2	0.2	0.2	0.2
0	0.2	0.2	0.2	0.2	0.2
1	0.2	0.2	0.2	0.2	0.2
2	0.2	0.2	0.2	0.2	0.2

## Optimal behavioural strategies

Optimal behavioural strategies obtained from stochastic dynamic programming shows optimal expected patch temperatures to forage at depending on previous experienced temperature deviation,  $D_{t-1}$ , body condition  $C$  and time for each temperature variation scenario A0.86, A0.37 and A0. For A0 choice of temperature is not dependent on previous experienced deviation, as all deviations are equally probable in the new time-step. The expected patch temperatures  $j$  are before modulation by the temperature deviations.

Optimal foraging strategies for parameter choices 1, the specialist.

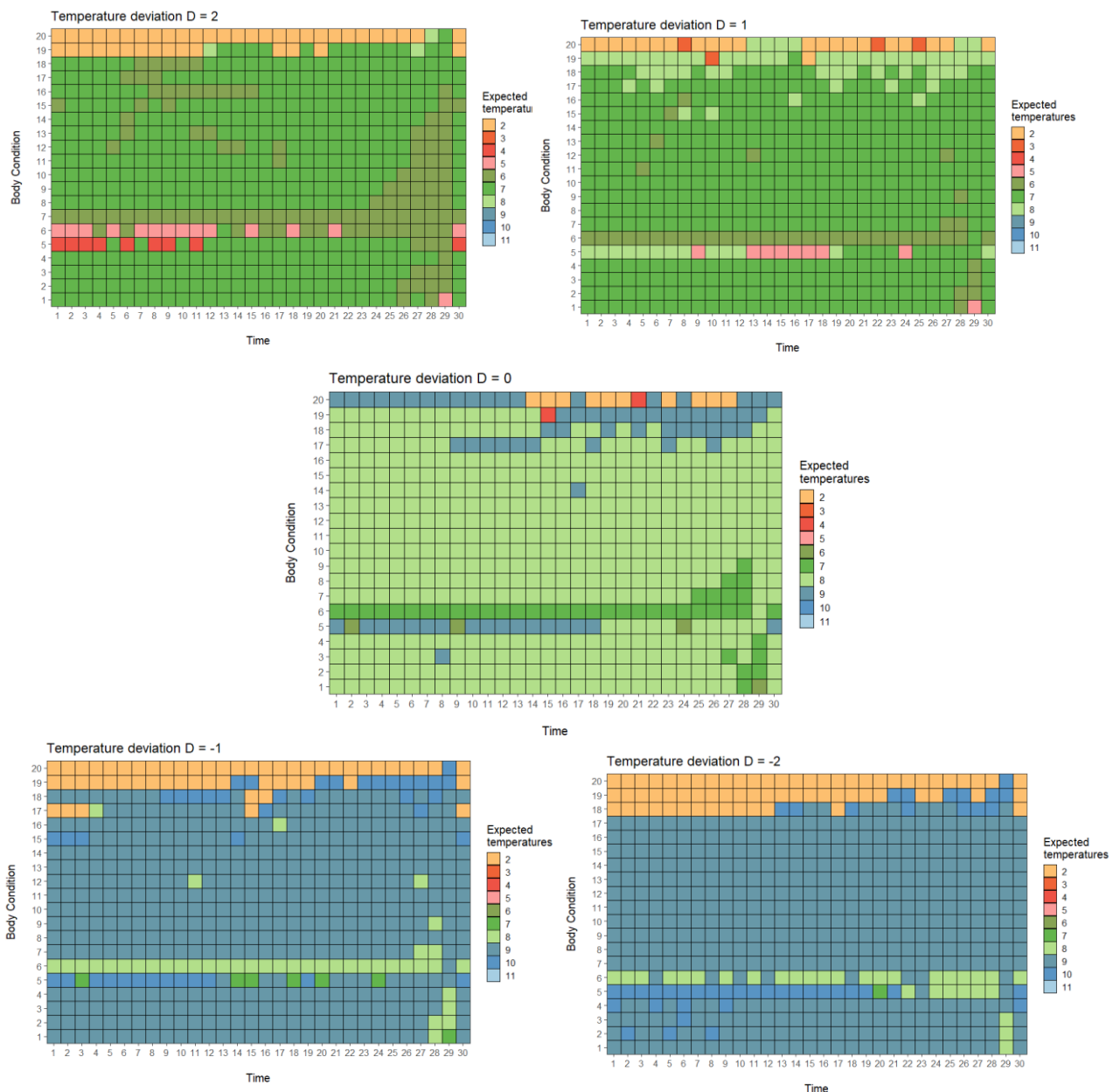


Figure A1: Optimal behavioural strategy of specialist TPC in A0.86 giving expected patch foraging temperatures.

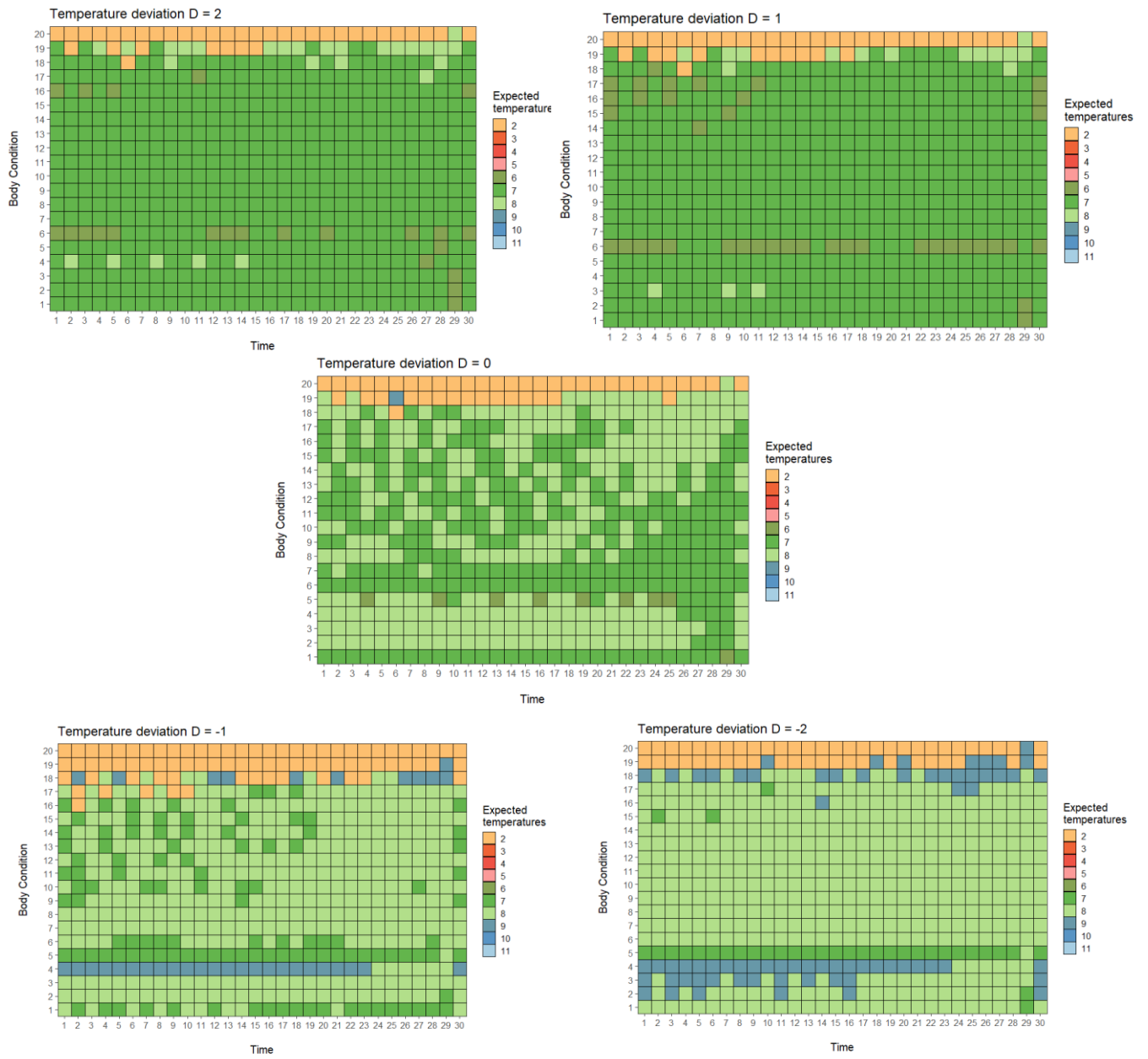


Figure A2: Optimal behavioural strategy of the specialist TPC at A0.37 giving expected patch temperatures to forage at.

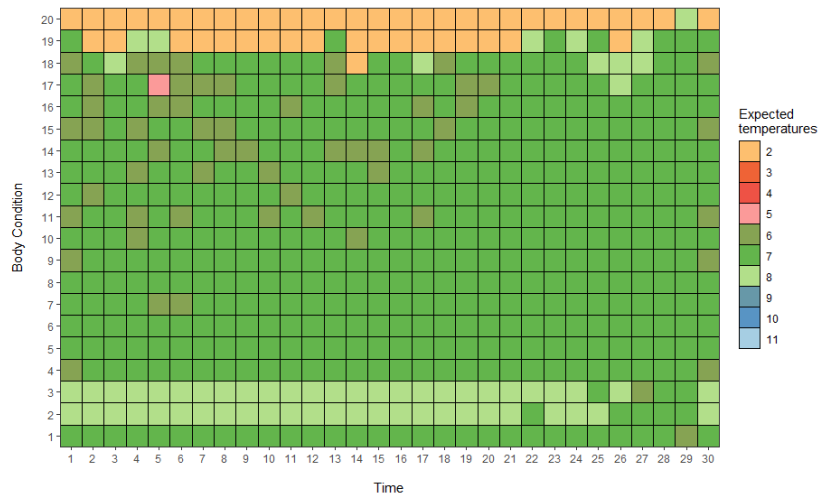


Figure A3: Optimal behavioural strategy for the specialist TPC at A0 giving expected patch temperature to forage at.

# Optimal foraging strategies for parameter choices 2, the generalist.

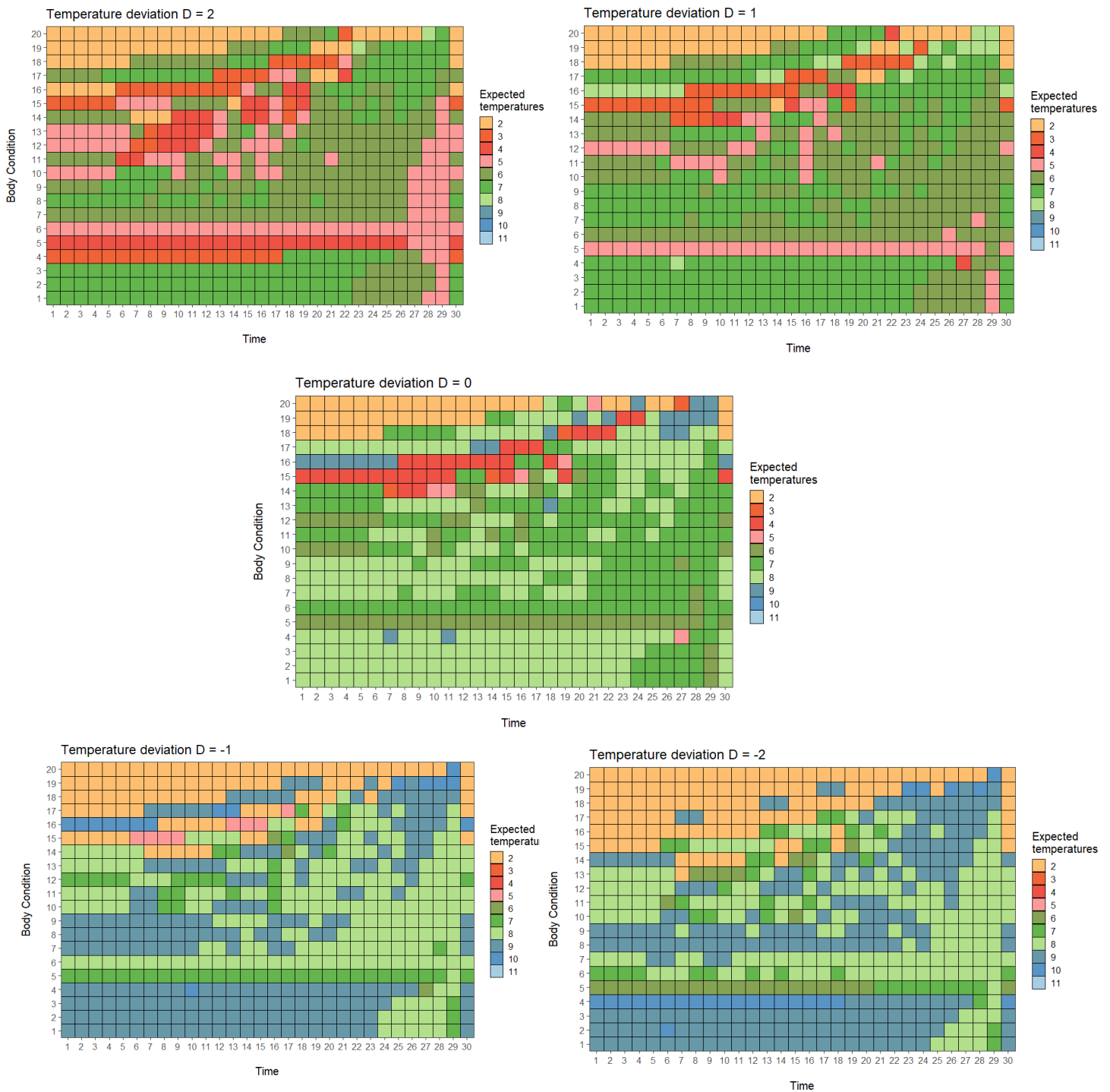


Figure A4: Optimal behavioural strategy for the generalist TPC at A0.86 giving expected patch temperature to forage at.

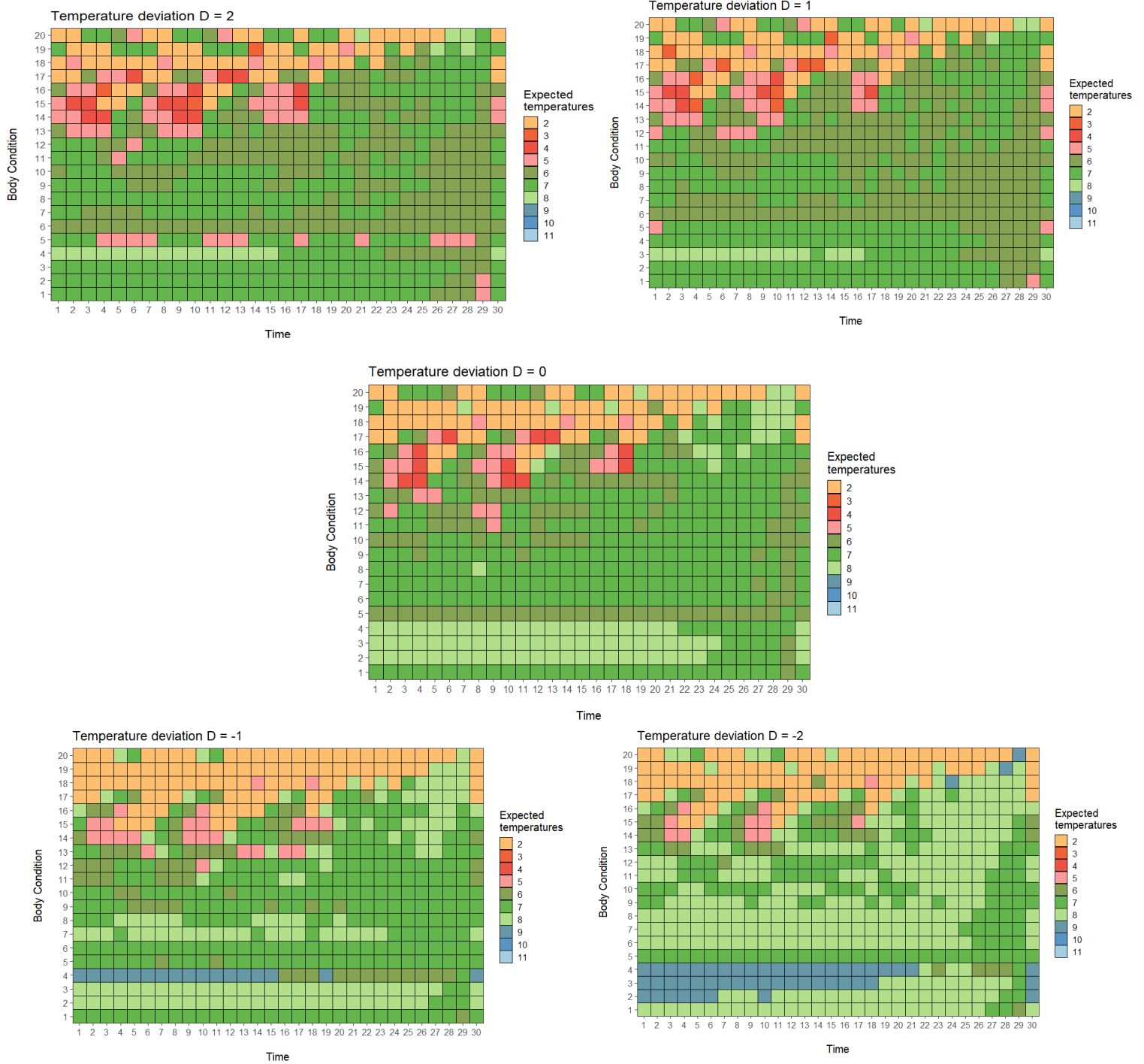


Figure A5: Optimal behavioural strategy for the generalist at A0.37 giving expected patch temperature to forage at.



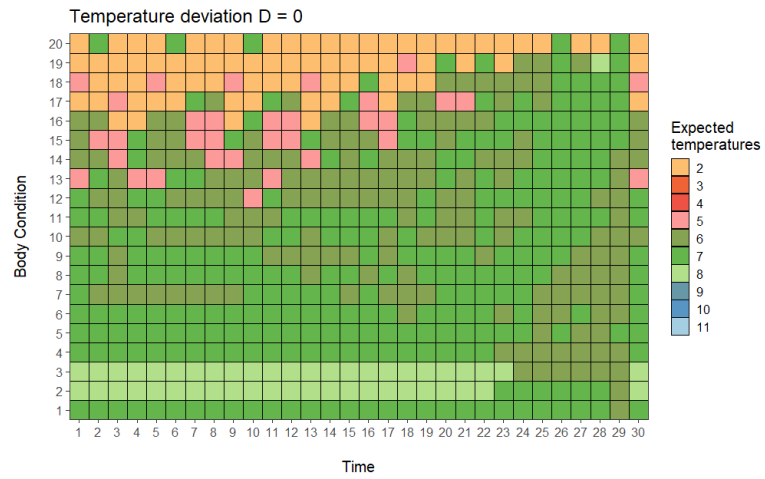


Figure A6: Optimal behavioural strategy for the generalist in A0 giving expected temperature to forage at.

