

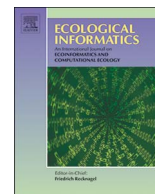


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Plasticity in foraging behaviour as a possible response to climate change

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A B S T R A C T

Climate change is regarded as one of the major concerns of the 21st Century, with mean temperatures expected to increase by about 3 °C over the next 100 years. Species responses to climate change are not consistent, with some species apparently able to respond more quickly than others, thus producing changes in community structure. One increasingly common observation is that species at lower trophic levels respond more quickly to change in climate than species at higher levels. This can result in, for example, the timing of a predator's peak food requirements being separated in time from the point at which their prey is most available. It has been suggested that this creates an additional risk for the persistence of species at high trophic levels as the climate alters; there is an alternative possibility — that predators may change their diets in response to changing prey availability. Models of diet choice make several predictions, for example they suggest that whether a predator includes a secondary prey into its diet depends on the availability of the primary prey and not on characteristics of the secondary prey. By switching between one prey type and another, a predator population may be able to persist in a particular location longer than they would otherwise. Using a simple demonstration model we show that this idea is theoretically plausible.

1. Introduction

There are two commonly proposed biological responses to climate change: changes in distributions, and changes in the timing of biological events (phenology). In a warming world it is easy to conceptualise species ranges moving latitudinally towards the poles and upwards in altitude. There has been substantial attention paid to the possibility of range shifts, typically through the use of climate envelope modelling (Huntley et al., 2008; Millennium Ecosystem Assessment, 2005). Secondly, at least at temperate latitudes, climate warming is advancing the timing of reproductive seasons. Despite the fact that seasonal reproduction in endotherms is rarely directly controlled by temperature (Dawson et al., 2001; Follett, 1984), species do vary their phenology from year-to-year depending on the 'lateness' of the spring (Charmantier et al., 2008; Evans and Goldsmith, 2000). This may not always be straight-forward, for example fish in raised temperatures terminate spring spawning early and delay in autumn spawning (Pankhurst and Munday, 2011).

The ability of species to respond to climate and shift their ranges will be affected by dispersal ability. Thus, while alpine butterflies seem capable of keeping up with the movement of isotherms (Parmesan et al., 1999), the plants on which they feed appear to be lagging behind by up to a metre a year (Grabherr et al., 1994). It is also increasingly common to find that species at lower trophic levels advance their

phenology faster than species at higher trophic levels (Dell et al., 2013; Thackeray et al., 2016; Thackeray et al., 2010; Visser and Both, 2005; Winder and Schindler, 2004). Both the physical movement of species and changing phenology of species can lead to community structure altering if species move spatially and/or temporally at different rates, with the most extreme case being the extinction of species that lag behind their food supplies.

While it is widely accepted that organisms might change their phenology of reproduction and migration in response to changing conditions, there have been fewer considerations of plasticity in other behavioural traits (Bitterlin and Van Buskirk, 2014; Crick et al., 1997; Visser et al., 2003). Most organisms are capable of changing their diets to switch from one prey species to another (Murdoch, 1969). Prey switching has been well studied as a general phenomenon, but has received relatively little attention in the context of climate change. It has recently been suggested that polar bears (*Ursus maritimus*) have adapted to energy deficits due to their foraging period being shortened (Gormezano and Rockwell, 2013a, b) by switching to different prey (Gormezano and Rockwell, 2013a, b; Prop et al., 2015). Similarly Cassin's auklet (*Ptychoramphus aleuticus*) and pigeon guillemots (*Cephus columba*) show climate-related prey switching between preferred and less-preferred prey species (Abraham and Sydeman, 2006; Litzow et al., 2002), and juvenile sockeye salmon (*Oncorhynchus nerka*) are spending about twice as long feeding on less-preferred prey species than

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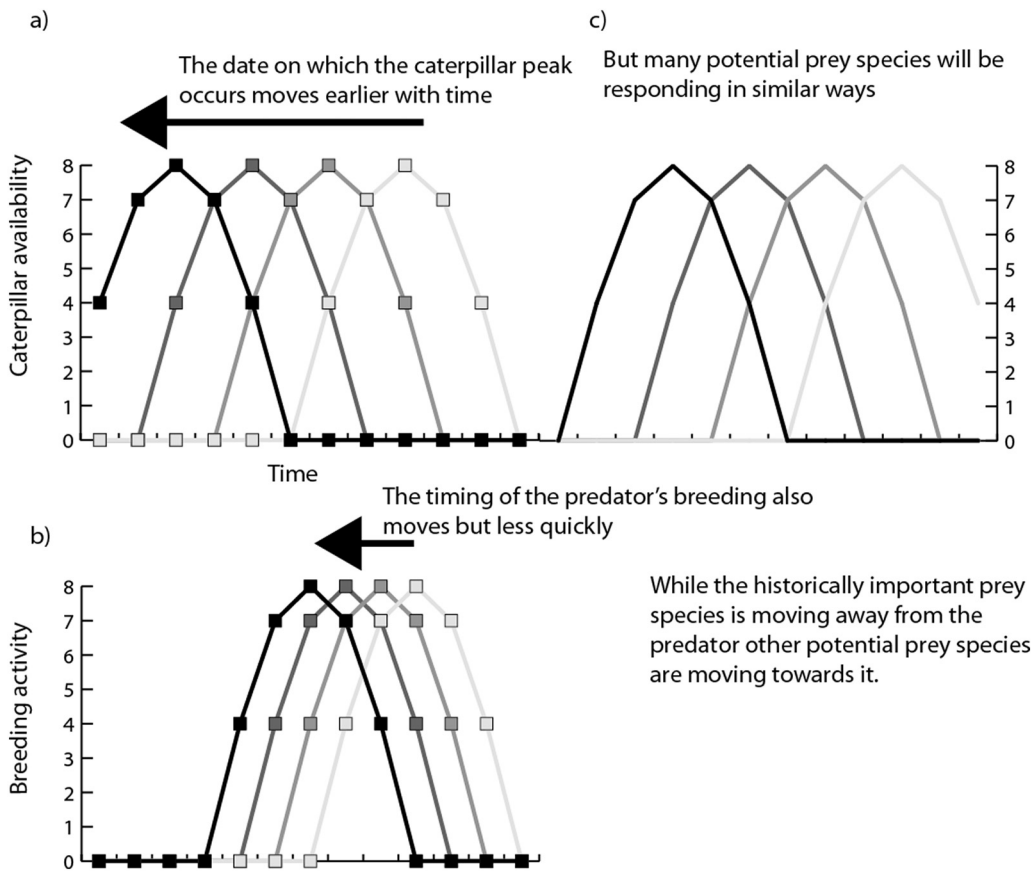


Fig. 1. Schematic representation of results such as those found by Both et al. (2009), Visser et al. (2004) and Visser et al. (2006) and shows: a) the availability of the original prey changes relatively quickly over time (curves represent availability in different years), b) but the timing of the food demand from predator species changes relatively slowly over time, and c) in theory there could be potential prey species reproducing later in the season the availability of which gradually moves closer to the predator species' food demand.

they did previously (Hampton et al., 2006).

In an ecosystem affected by climate change in which the phenology of species is changing, prey species become available earlier in the season (Fig. 1). Originally the availability of prey and the peak food demand coincide, if the prey species changes phenology faster than the predator species then the availability of the prey species moves away from the demand from the predator (Both et al., 2009; Visser et al., 2006). However, in many ecosystems there are other potential food supplies in the environment, the phenology of which is also likely to be changing in response to climate changes. If a second prey species, which once developed late in the season, also changes its phenology more quickly than that of the predator then its availability will gradually move closer to the predator's demand for prey (Fig. 1). Eventually, the potential new prey species will start appearing during the period when the predator is reproducing. At this point individual predators might be faced with the two prey types.

Finding the solution to the problem faced by a predator confronted with a choice between two types of prey is a classic and extensively studied problem in optimal foraging (Krebs et al., 1977; Stephens and Krebs, 1986). This tells us that if there are two prey types, with energetic values E_1 and E_2 , handling times of h_1 and h_2 and encounter rates of λ_1 and λ_2 , then a predator should; either focus exclusively on the most profitable prey (the one in which E/h is greatest), or include both prey types in its diet in the proportions in which they are encountered. This decision depends crucially on its encounter rate with the most preferred prey. It does not depend on the encounter rate with the less-preferred prey. The point at which predators start taking prey type 2 as well as prey type 1 will occur at:

$$E_2/h_2 = E_1/(h_1 + 1/\lambda_1) \quad (1)$$

Because $1/\lambda$ can also be considered as the search time (S_1) for a prey item, Eq. (1) can be written as:

$$E_2/h_2 = E_1/(h_1 + S_1)$$

This means that if we know how common the prey types are in the environment, the energetic values of the prey, and times required to catch and eat a prey item, we should be able to predict whether an individual predator will feed on just the preferred prey type or both types at the frequency in which they are found in the environment.

We have developed and analysed a demonstration model (Evans et al., 2013) to determine whether, in a highly simplified system, a population of predators could be rescued from extinction by a second prey species if the phenology (and hence availability) of its favoured prey alters such that it no longer coincides with the period when the predators require food. We stress that this model is not based on any particular species but on general relationships observed in nature and described in theoretical models. The results are not directly applicable, but will give information about the possibilities for species changing their diets in response to climate change induced phenological changes in their prey.

2. The model

The model used is a simple, spatially explicit, individual-based model, implemented in NetLogo 5.1 (Wilensky, 1999). This model describes the characteristics of a predator population, and the populations of two prey species. The purpose of the model is to determine how the predator population changes in response to changes in the timing of prey availability in relation to the timing of the predator's need for prey.

2.1. Predator and prey characteristics

The predator species has high food demands during a relatively short reproductive season. The predator can only move, catch prey and reproduce during time steps 9–11 throughout the simulation. In reality

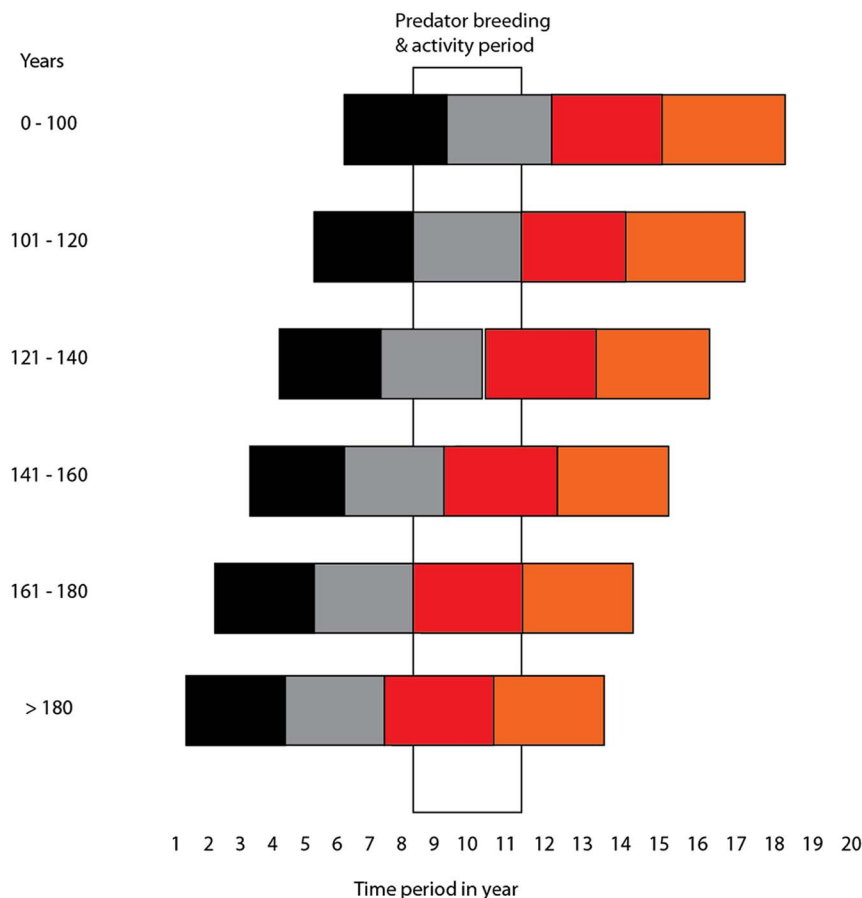


Fig. 2. The period over which prey are available to the predator changes over simulated time. For the first 100 years prey species 1 coincides with the predator's period of demand for prey, while prey species 2 appears when the predator no longer requires prey. Between years 101 and 180 the phenology of both prey species changes such that it moves one time step earlier per 20 years. This gradually takes prey species 1 out of the predator's period of prey demand and prey species 2 into this period. After 181 years the model simulates a stable new state in which prey species 2 coincides with the predator's demand for prey and prey species 1 appears in the environment too early to be eaten by the predator. Black and grey represent the period during which prey species 1 is present, red and orange when prey species 2 is present. Black and red show the periods during which the two prey species breed and so become increasingly common. During the grey and orange periods the prey does not breed and so gradually becomes rarer. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

a predator would eat during the non-reproductive season but we are only interested in the relationship between the predator and two seasonally abundant prey species, therefore we assume that the predator maintains itself on some other prey outside this time.

Both prey species are simulated such that they behave like seasonal annual species; they appear in the environment, exist for a period of time, become abundant through reproduction and then disappear (Fig. 2). The two species differ only in their phenology and in their profitability to the predator. Individual prey gain energy units by consuming resources found in each cell, these resources regenerate 30 time steps after consumption (Wilensky, 1997). They move one cell in a random direction per time step, and lose energy units per time step (Wilensky, 1997) (Table 1). A fixed number of both prey species appear in the environment (in randomly selected cells) during a certain time period in each year, the favoured prey species appearing six time periods earlier than the less favoured prey species, they move and breed during their season.

Table 1
Summary of values of variables used to instantiate the model.

	Prey 1	Prey 2	Predator
Energy gained by consuming patch resources	15	15	NA
Energy lost per time step	2	2	25
Number appearing per year	1000	1000	0
Probability of reproducing per time step	0.33	0.33	0.20
Life span (time steps)	6	6	100
Energy gained from consuming prey species 1 (E_1)	NA	NA	240
Energy gained from consuming prey species 2 (E_2)	NA	NA	80
Handling time of prey species 1 (h_1)	NA	NA	1
Handling time of prey species 2 (h_2)	NA	NA	3

2.2. Prey choice behaviour

If the predator moves into a cell in which there is a prey individual the predator can kill it and gain energy (Wilensky, 1997). A predator will kill any individual of prey species 1 that it encounters, but will only kill an individual of prey species 2 if:

$$S_1 > (E_1 \times (h_2/E_2)) - h_1. \quad (2)$$

Therefore the decision of the predator to take the less-preferred prey depends on a combination of the energy it will obtain from the two types of prey, the time it will take to process the two types of prey and its experience of the time it takes to locate the preferred prey. In our model we have considered that predator takes S_1 to be the time since it last encountered the preferred prey.

To disentangle the covariance between the decreasing availability of the preferred species and increasing availability of the less-preferred species we created a second scenario. In this scenario the preferred prey species changes its phenology as in the first scenario, but the availability of the less-preferred prey species remains constant throughout. To achieve this, prey species 2 was introduced at the same time as prey species 1 at the start of the simulation and its timing of arrival and reproduction were kept constant throughout. This scenario aims to represent a situation where a less-preferred prey was present throughout and could be chosen by the predator at any time, irrespective of the presence or absence of the preferred prey species 1.

Further details of the model are provided in the supplementary materials and in Table 1.

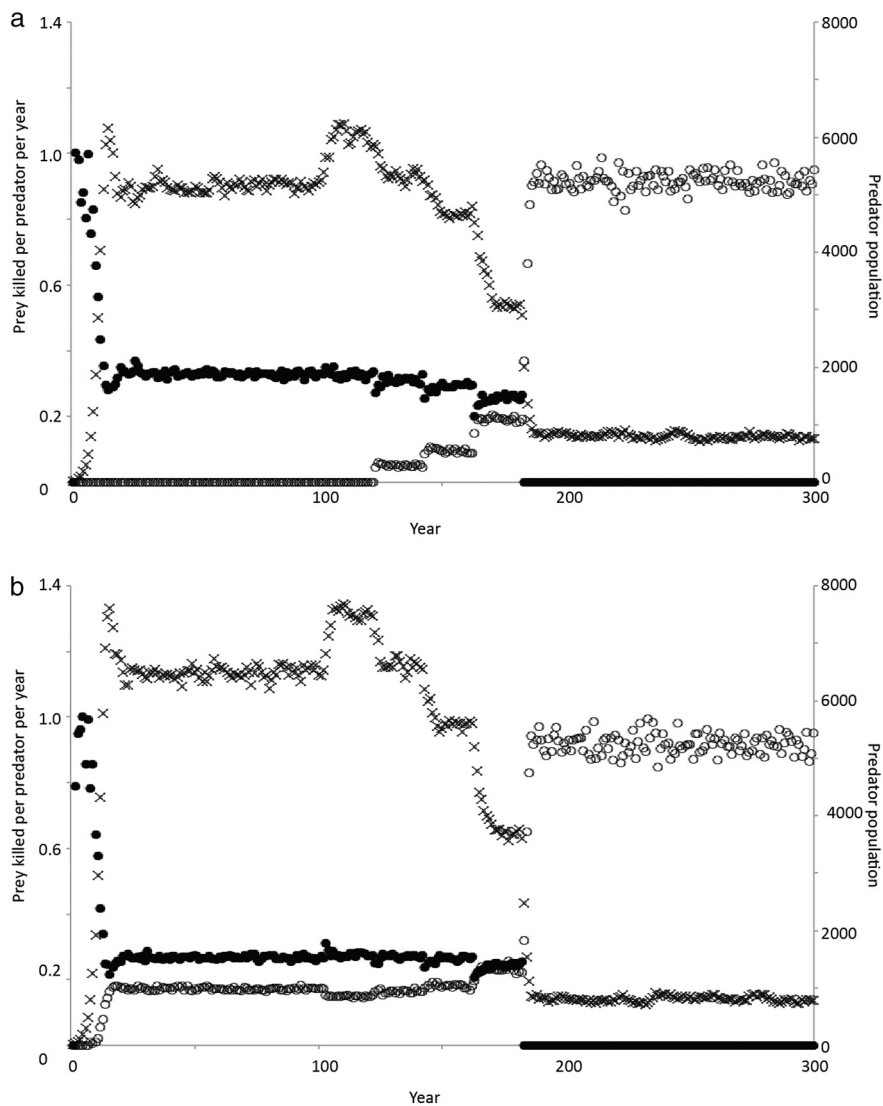


Fig. 3. Changes in predator population size over the simulated 300 years of a model run (predator population size at the end of the year is given by the crosses and the right axis). The mean number of prey items killed per year per predator are given on the left axis, with the preferred prey 1 being the filled circles and the less-preferred prey the open circles). The periods during which the two prey species are available to the predator are shown in Fig. 2.

a) Results from scenario one, when both prey species change their phenology with respect to the predator.

b) Results from scenario two, when the preferred species changes phenology but the phenology of prey species two remains constant.

3. Results

3.1. Both prey species change phenology

After an initial period of transient dynamics as the predator population builds up, the predator population reaches a stable equilibrium that is maintained until prey phenology starts to change. Immediately after phenology starts to alter prey species 1 is slightly more abundant during the predator's active period this results in the predator population rising (Fig. 3a). However, as its phenology changes further prey species 1 becomes less abundant during the predator's active period while prey species 2 becomes more abundant. The predator starts consuming prey species 2, initially at a low rate but increasingly frequently as prey species 1 becomes less abundant and prey species 2 more abundant. Pearson's correlation during the period that both prey are available between the mean number of prey 1 available and the number of the prey 2 consumed was high ($R = -0.92$, $P < 0.0001$, d.f. = 60). Over the same period there was also positive correlation between mean number of prey 2 and the number of prey 2 consumed ($R = 0.93$, $P < 0.0001$, d.f. = 60). Given that there is a high negative correlation between the numbers of preferred and less-preferred prey ($R = -0.90$, $P < 0.0001$, d.f. = 60), this is perhaps unsurprising. After 180 years of simulated time, prey species 1 disappears from the predator's active period (Fig. 2) and the predator can only consume

prey species 2, which it does at a high rate and in proportion to their availability ($R = 0.47$, $P < 0.0001$, d.f. = 120). After this point the predator population drops to a low, but stable equilibrium level at around 15% of its pre-climate change levels (Fig. 3a).

3.2. Only prey species 1 changes phenology

In general terms the results of this scenario are very similar to that of the first scenario. The predator population reaches a similarly high initial equilibrium, during which it consumes the preferred prey at just over 1.5 times the rate of the less-preferred prey (Fig. 3b). As the preferred prey becomes less available the predator starts to consume greater numbers of the less-preferred prey ($R = -0.93$, $P < 0.0001$, d.f. = 180). Note that this change occurs even though the less-preferred prey is equally present throughout. After the preferred prey species has become completely unavailable the predator consumes the less-preferred prey in proportion to its own abundance ($R = 0.56$, $P < 0.0001$, d.f. = 120), and the predator population reaches a low, stable equilibrium similar to that reached in scenario one (Fig. 3b).

An analysis of the model's sensitivity to different prey energy contents and handling times is provided in the supplementary materials.

4. Discussion

Flexibility in diet choice could be a biological response to climate change (Peers et al., 2014), analogous to flexibility in timing of reproduction (Crick et al., 1997; Parmesan, 2007; Phillimore et al., 2016; Thackeray et al., 2016; Visser et al., 2003; Visser et al., 2004; Walther et al., 2001) or migration behaviour (Bitterlin and Van Buskirk, 2014; Usui et al., 2016). This could result in species being capable of maintaining populations in regions that might otherwise seem unsuitable because traditional prey species have disappeared. This would obviously avoid the situation where the predator became extinct (Visser et al., 1998), but may also mitigate against selection on range shifting (Huntley et al., 1995; Huntley et al., 2008; Parmesan et al., 1999).

Our simple, individual-based, model demonstrates that, at least in theory, plasticity in diet choice can result in persistence of predator populations. The models show that a predator population, if it obeyed well-understood optimal diet choice rules (Krebs et al., 1977), could switch to a new prey species as its traditional prey species became unavailable. We emphasise that this model simply demonstrates the fact that our proposed mechanism could work in a world such as that described by our model, which is obviously a rarefied version of reality (Evans et al., 2013). In our model the two prey species differed substantially in their profitability to the predator. Prey species 1 was nine times more profitable to the predator than prey species 2. Nevertheless, a predator population can be sustained on the less profitable prey, and as predicted the predator chose to consume prey species two once its preferred prey was sufficiently rare. It would be expected that predators facing a choice between prey species that were closer to one other in profitability would switch earlier to start taking the less profitable prey type.

An example of prey switching in nature that has been proposed to be due to climatic change may be found in polar bears (*Ursus maritimus*). Recent studies have reported that polar bears have adapted to energy deficits due to shortened foraging period caused by melting ice habitats (Gormezano and Rockwell, 2013a, b; Prop et al., 2015). Polar bears are employing novel foraging strategies, switching to different prey, such as snow geese and their eggs (Gormezano and Rockwell, 2013a, b). We can use data from polar bear hunting to parameterise Eq. (1), an immediately post-weaned ringed seal (*Phoca hispida*) contains 119,000 kcal (Stirling and McEwan, 1975) and polar bear females spend an average of 57.5 min per hunt (Stirling, 1974) with 1.7–4% of hunts ending in a kill (Gjertz and Lydersen, 1986; Stirling, 1974). Polar bears take about 30 min to consume a seal (Stirling, 1974), resulting in a total handling time per seal eaten of 1468 min. If the alternative prey to ringed seals are snow geese (*Chen caerulescens*), which contain just 625 kcal but can be caught and consumed in just over 16 min (Iles et al., 2013) then polar bears should start hunting geese in addition to seals when the encounter rate with seals drops below λ_1 , which can be calculated from eq. (1):

$$E_2/h_2 = E_1/(h_1 + 1/\lambda_1)$$

$$625/16.25 = 119,000/(1468 + 1/\lambda_1)$$

and so $\lambda_1 = 0.000597 \text{ min}^{-1}$ or 0.86 day^{-1} (assuming a 24 hour day).

It is therefore not surprising that polar bears adopting foraging phenotypic plasticity make the switch into eating geese as seals become less available due to reductions in the extent and duration of sea ice.

It is unsurprising that some animals are capable of modifying their diet in the face of changing prey communities as many species clearly feed on different prey in different parts of their range. It is at least conceivable that behavioural plasticity of foraging behaviour could present animals with greater flexibility in their response to changing conditions and could allow for longer persistence times of species at locations from which they might have been assumed to be lost. This is not to advocate any reduction in the seriousness with which climate change may impact on the natural world but it may suggest that a more

holistic approach, that accounts for the total behavioural repertoire of species may yield a more rounded view.

While this article has been presented in the context of responses to climate change switching between prey types is a more general phenomenon. The approach taken here could be usefully applied in a number of other contexts. For example where environmental conditions vary and result in changes in the availability of prey both temporally and spatially. This creates the opportunity for synergistic effects between the physical environment (which may affect an organism directly) and the biological environment (which may affect an organism indirectly via food availability). Such interactions could act to mediate the effect of environmental change (as here) or potentially to exacerbate it. Using this type of information would allow trends in future populations sizes to be honed by the inclusion of ecological information.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.ecoinf.2017.08.001>.

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