Behavioral flexibility as a mechanism for coping with climate change

Erik A Beever[1,2]*, L Embere Hall[3], Johanna Varner[4], Anne E Loosen[5], Jason B Dunham[6], Megan K Gahl[7], Felisa A Smith[8], and Joshua J Lawler[9]

Of the primary responses to contemporary climate change – "move, adapt, acclimate, or die" – that are available to organisms, "acclimate" may be effectively achieved through behavioral modification. Behavioral flexibility allows animals to rapidly cope with changing environmental conditions, and behavior represents an important component of a species' adaptive capacity in the face of climate change. However, there is currently a lack of knowledge about the limits or constraints on behavioral responses to changing conditions. Here, we characterize the contexts in which organisms respond to climate variability through behavior. First, we quantify patterns in behavioral responses across taxa with respect to timescales, climatic stimuli, life-history traits, and ecology. Next, we identify existing knowledge gaps, research biases, and other challenges. Finally, we discuss how conservation practitioners and resource managers can incorporate an improved understanding of behavioral flexibility into natural resource management and policy decisions.

Front Ecol Environ 2017; doi:10.1002/fee.1502

Anthropogenic climate change is having measurable impacts on animal populations. Observed responses include alterations in species' abundance, distribution, physiology, morphology, and phenology (eg Staudinger *et al.* 2013). However, the role of animal behavior as a mechanism for coping with changing climate has yet to be fully explored (see also Berger-Tal *et al.* 2015).

Behavioral flexibility – the capacity of individuals or populations to alter behaviors in response to environmental conditions (as defined by Hadfield and Strathmann [1996]) – can provide species with an immediate pathway to mitigate some of the negative effects associated with a rapidly changing climate (Van Buskirk 2012). Because behaviors tend to be reversible and quickly exhibited, they allow organisms to secure the benefits of a phenotype that better matches current conditions without committing to maintaining that phenotype in an uncertain future (Chevin *et al.* 2010). Although behavioral shifts are subject to numerous constraints (eg access to resources, or the cognitive capacity to enact a behavior), behavioral reaction times are potentially much shorter than other ecological responses such as changes in demography or occupancy. Behaviors are also more immediately observable, as compared to processes that take place over much longer timescales. Consequently, they may provide an early signal of the effect of climate stressors, prior to detectable range shifts or population declines (Berger-Tal *et al.* 2011).

Several recent studies have identified behaviors that help individual species cope with climate change (eg Sih *et al.* 2010; Snell-Rood 2013), and the extent to which individuals or populations modulate behavior to buffer climate stressors (eg Kearney *et al.* 2009; Murray and Smith 2012). However, scientists lack a comprehensive understanding of the contexts in which animals change their behavior in response to climate variability. Furthermore, to our knowledge, no study has provided a synthesis of behavioral flexibility in animals that simultaneously addresses both multiple taxa and multiple climate stressors. Such a contribution is particularly timely because natural resource managers are often faced with conservation mandates for multiple species, and variation in behavior may provide some species with a first line of defense against novel conditions. In addition, future conservation strategies aimed at mitigating the effects of

In a nutshell:

- Behavioral changes may allow animals to cope with rapid climate change; however, the ecological contexts in which animals can exhibit behavioral flexibility remain poorly understood
- Research to date has focused on a fairly limited suite of taxa, behaviors, ecological contexts, and climatic stimuli
- Shifts in behavior may be observed before shifts in demography or distribution, allowing for climate-change impacts on species to be more quickly detected
- Understanding the fitness implications, demographic effects, and limitations of behavioral flexibility is essential if behavior is to be integrated into management decisions
- Quantifying connections between climate variability and animal behavior will improve conservation initiatives

---

[1] *US Geological Survey (USGS), Northern Rocky Mountain Science Center, Bozeman, MT* *(ebeever@usgs.gov); [2] *Montana State University, Department of Ecology, Bozeman, MT;* [3] *Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY;* [4] *Colorado Mesa University, Department of Biological Sciences, Grand Junction, CO;* [5] *University of Alberta, Department of Biological Sciences, Edmonton, Canada;* [6] *USGS, Forest and Rangeland Ecosystem Science Center, Corvallis, OR; continued on last page*

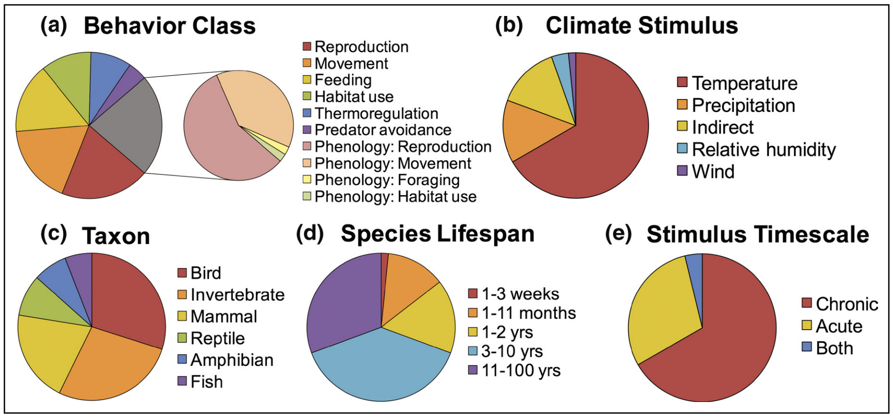


Figure 1. *Patterns of behavioral responses represented in the literature. Studies in the literature search that documented behavioral response to climate variability (n = 186) were classified with respect to: (a) the class of behavior modified in response to climate, (b) the climatic stimulus apparently eliciting a response, (c) the taxonomic classification of organisms exhibiting behavioral responses, (d) the average lifespan of species with responses, and (e) the timescale over which the climatic stimulus caused the animal to change its behavior. In (a), the gray wedge comprises all studies in which the behavior was an aspect of phenology; these behaviors are more-finely parsed and classified in the smaller pie chart.*

climate change could benefit from considering a species' capacity for behaving flexibly.

Here, we examine patterns of behavioral flexibility across the animal kingdom and highlight illustrative examples. We also identify knowledge gaps and research biases in the literature, and describe the contexts in which animals have responded behaviorally to variation in climate. Finally, we discuss potential implications of these results for policy and provide behavior-based considerations for resource managers and other conservation practitioners.

Published patterns of behavioral responses to climate

We systematically reviewed the scholarly literature to assess both current understanding and the research effort to date focused on behavior as a response to changing environmental conditions. Our review represented a qualitative survey of the literature and provided information on the breadth of documented behavioral flexibility in response to climate stimuli across the animal kingdom. It was not, however, designed to comprehensively evaluate the relative importance of behavioral flexibility in species' persistence, nor was it intended to be a quantitative meta-analysis.

Using the search terms "plastic* and behav* and climat*" in Web of Science, we identified 626 peer-reviewed articles. Because different disciplines and researchers use different terms to describe plasticity (Pigliucci 2001), we subsequently also searched for "flexibility and climat* and behav*". Finally, because some researchers rely on spatial gradients to assess behavioral response to climate, we searched for "climat* and behav* and space-for-time substitution". Across all search strings, we identified 186 articles (WebPanel 1) that documented behavioral responses to climate-derived variables across six animal taxa: invertebrates, amphibians, reptiles, birds, mammals, and fishes (including jawless, cartilaginous, and bony fishes). We classified each study according to several criteria described below. Full details of our methods are provided in WebPanel 2 and WebFigure 1.

Changes in phenology (ie the timing of life-cycle events like reproduction or migration) are widely reported as the most-common response to climate change (Cleland *et al.* 2007). In our classifications, phenological responses occurred in 22.6% of the studies considered (Figure 1a). However, when these studies were examined in more detail, we found that changes in reproductive behaviors were the most-common mode of response across all taxa – occurring in 32.2% of all studies (Figure 1a). Changes in dispersal or migration (collectively, "Movement") were the next-most-common response, reported in 23.7% of all studies (Figure 1a; WebPanel 3). Less-common responses included shifts in feeding or foraging, habitat or microhabitat use, thermoregulation, and predator avoidance (see WebPanel 2 for a detailed description of behavioral classifications).

Within the examined literature, a majority of studies (67.0%) identified temperature as the climate aspect responsible for, or correlated with, behavioral modification (Figure 1b). By contrast, connections to precipitation (including metrics of rain and snow), humidity, or wind were much less common (19.5% collectively; Figure 1b). The remainder (13.5%) attributed behavioral responses to indirect effects of climate, such as changes in food resources or microhabitat structure (Cahill *et al.* 2012).

There was substantial heterogeneity in the representation of taxa among our results (Figure 1c). Invertebrates (27.4% of the total) and birds (29.6%) were most frequently studied; mammals represented 20.4% of reports. Together, reptiles and amphibians represented only 16.7%, even though these two taxa are widely studied and predicted to face a greater risk of extinction than other taxonomic groups (eg Stuart *et al.* 2004; Böhm *et al.* 2013). Similarly, although responses by fishes constituted only 5.9% of the studies, behavioral responses of fish to environmental variables have been well documented (eg Pitcher 2012). These results likely reflect limitations imposed by our selection of search terms or how behavioral responses are described in the literature associated with these taxa (Pigliucci 2001), rather than an actual inability of fishes, reptiles, or amphibians to behaviorally respond to climate or a lack of studies focusing on the taxon in question – although the latter certainly remains possible.

Behavioral responses were most commonly observed in species that lived at least 3 years (Figure 1d). Moreover, behavioral shifts in response to chronic stimuli (eg increase in average summer temperature; WebPanel 2) were more common than shifts in response to acute stressors (eg anomalous high-precipitation events; Figure 1e), and behavioral shifts were most likely to be enacted over long timescales, such as seasons (WebFigure 2a). Although there may be a research bias toward species with longer lifespans, taken together, these results could also suggest that species with longer life spans have greater exposure to climate variability and have therefore evolved an increased capacity for altering behavior in response to chronic climate stimuli. Due to increased time available for trial-and-error and corresponding behavior modifications, comparatively long-lived animals might also have more opportunities to adjust to changing cue–response systems, especially if a mismatched climate cue does not directly affect individual survival (Sol and Maspons 2015). Nest placement, for example, is a common strategy for dealing with both microclimatic and predation constraints. Some bird species, such as Brewer's sparrows (*Spizella breweri*), use a "win-stay, lose-switch" strategy in which nests built after a nest-predation event are placed in areas with different nest-patch characteristics, as compared to those of the failed attempt (Chalfoun and Martin 2010). Longer-lived animals may be capable of similar experience-based adjustments in response to growing climatic stress (With 2015).

Our goal was to synthesize patterns of behavioral flexibility in response to a climate stressor across the animal kingdom. Consequently, we included only studies that positively documented climate-related behavioral flexibility. Studies that tested for flexibility but found that such a behavior was canalized (ie not responsive to environmental influences) were infrequent ($n = 10$; WebTable 1) and were not included in our literature review results. Suggested reasons for the apparent lack of behavioral flexibility in these cases included primacy of other factors, such as habitat quality or competitive interactions with invasive species (Corrigan *et al.* 2011), or insufficient variation in climate parameters to elicit behavioral shifts.

Some of our findings likely represent research gaps, study-effort effects, or under-reporting of negative results, rather than true limitations in the flexibility of animal behavior. For instance, most research documenting behavioral responses to climatic stimuli was conducted in temperate biomes (53.0%), rather than tropical, boreal, desert, or arctic/alpine biomes (4.3–17.8% each; WebFigure 2b). Similarly, over 75% of the studies were conducted in terrestrial or aerial environments, whereas fewer than 25% occurred in aquatic or amphibious environments (WebFigure 2c). Both of these results are consistent with research biases observed in other reviews of responses to climate change (ie toward terrestrial ecosystems in temperate zones; Parmesan 2006), although the lack of aquatic studies could be an artifact of the scarcity of fish studies included in our search results.

In addition, the majority of studies in our sample were observational; only 31.7% of studies experimentally manipulated climate variables (WebFigure 2d). This result could be a reflection of the difficulty of conducting controlled behavioral studies; however, different classes of behaviors may be easier than others to study in the lab. For example, among the studies that documented behavioral flexibility in thermoregulation and predator avoidance, 53% and 50%, respectively, documented the flexibility via laboratory-based investigation. In contrast, phenological flexibility was almost entirely recorded through observational studies conducted in situ (92.9% of 42 studies). When such flexibility was recorded in relation to climate variables, it was largely in response to temperature (76.2% of studies; WebFigure 2e).

Behavioral responses to climatic stimuli may be constrained by trade-offs with other activities essential for survival and reproduction (Van Buskirk 2012; WebFigure 3). Both terrestrial and aquatic animals often select microhabitats, such as rock interstices, that can naturally moderate climatic extremes (Hall *et al.* 2016). Many amphibians and reptiles will bask on warm logs or rocks (WebFigure 3). However, sheltering in microrefuges could involve restricting foraging or reproductive activities. Desert woodrats (*Neotoma lepida*) in Death Valley do not leave their den until ambient nighttime temperature falls below the lethal physiological threshold (Murray and Smith 2012; WebFigure 3). Consequently, woodrats spend substantially less time outside their dens overall as evening temperatures rise seasonally, which constrains the time available for the essential activities of mating, foraging, and finding water. However, regardless of temperature, they must eventually leave to forage and find water. Thus, woodrats are limited in their ability to behaviorally avoid unfavorable temperature regimes. Such regimes could become increasingly relevant, as climate changes result in temperatures more frequently exceeding the woodrats' lethal threshold (eg Murray and Smith 2012). Similarly, activity restriction to avoid temperature extremes during the reproductive season has been implicated in lizard population declines across the western hemisphere (Sinervo *et al.* 2010, but see Kearney 2013). Together, these results suggest that although some aspects of species' ecology and life history might be modified to avoid climatic stress, there are also trade-offs (eg reduced foraging time or restricted reproductive

Figure 2. *Microhabitat selection by American pikas. Although pikas are typically found in rockslides and boulder fields, we have recently detected them in unusual habitats such as (a) below the high-water line in a reservoir near the Columbia River Gorge or (b) in non-talus habitats. The existence of haypiles (food caches, small arrows) in these locations suggests extensive use of these habitats, which may buffer pikas against extreme winter temperatures.*

output) that may represent a barrier to long-term population viability and persistence.

Case study: the American pika

The American pika (*Ochotona princeps*) illustrates many of these flexible behaviors, as well as the complexity of species–climate relationships. Pikas are typically limited to high-elevation moist, rocky habitats in the mountains of western North America, but they employ a suite of behavioral responses to climatic variability, including changes in foraging strategy, habitat use, and thermoregulation. Although pikas have experienced climate-related declines in some parts of their range (eg Beever *et al.* 2016), flexibility in foraging and thermoregulatory behaviors appear to allow other populations of pikas to make use of suitable microclimates in a seemingly unsuitable landscape (eg Varner and Dearing 2014a).

Habitat use

Pikas are considered to have an obligate relationship to broken-rock features (eg talus, lava flows, mine tailings). However, we have recently detected pikas on lakesides and reservoir riprap below high-water level (Figure 2a), as well as in unusual, non-talus habitats such as downed logs, snags, slash piles, and coniferous forests up to 100 m from the nearest talus patch (Figure 2b). The existence of haypiles (food caches) in these locations suggests extensive use of these habitats, and recent evidence indicates that these non-talus habitats may buffer pikas against extreme winter temperatures. For example, in northwest Wyoming, winter temperatures inside non-talus haypiles were up to 0.9°C warmer than ambient temperatures and up to 1.7°C warmer than temperatures measured in the nearest talus located 101 m away.

Although pikas are typically found at higher elevations, they also persist at elevations as low as 22 m in the Columbia River Gorge (CRG) that separates Oregon and Washington (Figure 3a). In the CRG, pikas use the dense, heavily shaded rainforest adjacent to talus patches far more extensively than they do in more typical alpine habitat on nearby Mt Hood (analysis of variance, $F_{(2,\,113)} = 21.97$, $P < 0.001$; Figure 3b). Use of forest habitat is highest during the warm midday hours and appears to be higher at talus sites with relatively low moss cover, perhaps because moss cover itself provides strong insulation from warm summer temperatures (Varner and Dearing 2014b). Pikas may be selecting favorable microclimates in the nearby (shaded) forest, allowing them to remain surface-active at midday, when above-talus temperatures in full sun can be much higher. Such flexibility in habitat selection has never been observed over 23 years of study in the Great Basin, where sharp distributional declines have been observed (Beever *et al.* 2016).

Foraging

Pikas are central-place foragers, concentrating their activity around a haypile that they territorially defend, but pika populations vary in their selection of haypile sites across their range. In the Great Basin, haypile rocks were roughly two to four times larger than rocks 5 m away in the surrounding environment (EAB, unpublished data). Haypiles under smaller rocks occurred only on slopes less steep than 27°, suggesting that situating a haypile under a large rock could confer resistance to avalanches and rockslides on steeper slopes. In addition, larger rocks have greater thermal inertia, which may moderate microclimates in the haypile. Finally, by protruding above the snow, large rocks absorb solar radiation and might facilitate earlier spring snowmelt around the animal's activity center (C Ray, pers comm).

Conversely, in the CRG, pikas exhibit very different foraging strategies. First, several populations of CRG pikas consume large amounts of moss (up to 63% of their diet; Figure 3c) (Varner and Dearing 2014b). Mosses are abundant in this habitat all year (Figure 3a), and consuming them may allow pikas to focus on other activities during summer, instead of caching food for the winter. When haypiles were present in the CRG, the rocks under which they were situated were not larger than the surrounding rocks (paired $t = 0.46$, degrees of freedom = 9, $P = 0.66$). In this environment, steep rock slopes rarely experience persistent snow cover and are stabilized by the moss "blanket", which also moderates microclimates (Varner and Dearing 2014b). Thus, situating haypiles under large rocks might be less advantageous in the CRG.

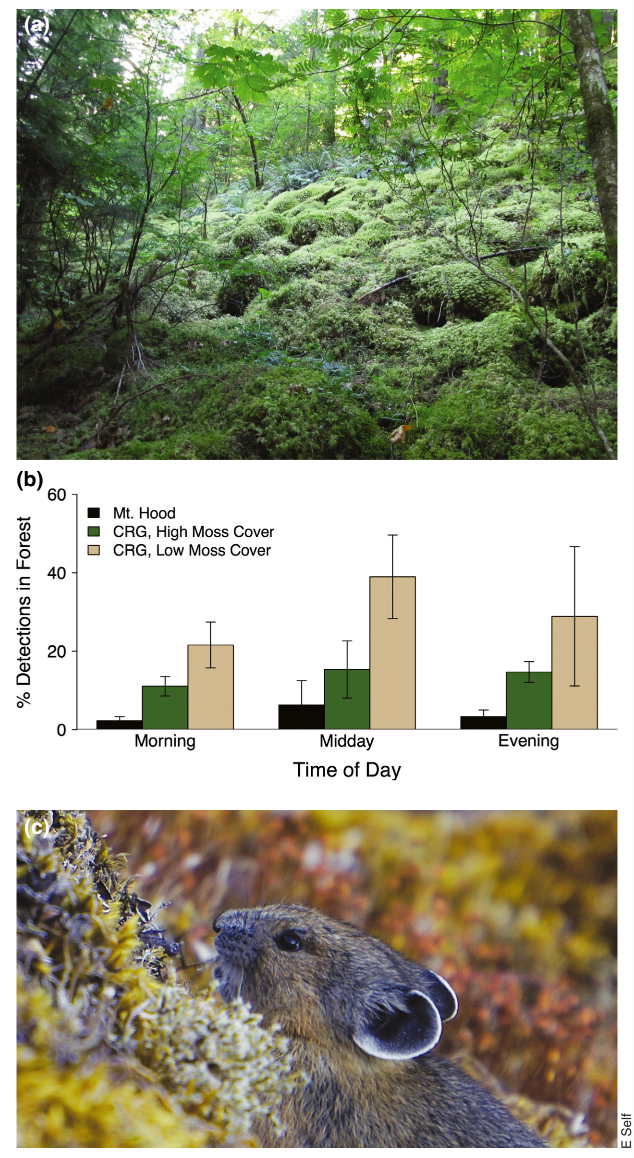
Finally, pikas do not typically drink free water; however, when water stress is highest (ie in late summer and early fall), they have been observed drinking from lakes or streams (EAB, JV, C Ray, pers comm). These observations were all made in drier portions of the species' range (eg the southern Sierras and interior Great Basin) or during drier times of the year, and corroborate evidence that pikas in warmer, low-elevation habitats are more selective for water content in their foraging (Smith and Erb 2013).

Thermoregulation

Pikas primarily thermoregulate by restricting their activity during the warmer portions of the day or by modifying their body shape (Smith 1974). At cooler latitudes and elevations (eg high-elevation habitats in Alberta, Canada), pikas can maintain higher activity levels during the middle of the day. By contrast, in warmer climates (eg low-elevation habitats in California and Nevada) pikas exhibit crepuscular activity patterns and are not surface-active during midday hours (EAB, JV, and LEH pers obs; Smith 1974). Similarly, by adopting a roughly spherical body shape (Figure 4a), pikas reduce their surface-area-to-volume ratio and minimize heat loss. In the northern portion of the species' range, where winter minimum temperatures are more extreme than summer maximum temperatures, pikas assume this spherical posture more frequently in the winter (73.7% of observations) than in the summer (12.0% of observations; $n_{\text{total}} = 194$ images, $\chi^2 = 44.10$; $P < 0.0001$; Figure 4b).

■ Addressing research gaps

Although we have shown that climate-linked flexibility in behavior has been documented in diverse animal taxa and across seven different behavior categories (Figure 1), many questions remain. Here, we highlight some outstanding knowledge gaps and propose ways to begin to address these questions.



E Self

Figure 3. *Pika ecology at low elevations in the Columbia River Gorge (CRG). (a) Low-elevation pika habitat in the CRG. Note high moss and forest-canopy cover. (b) Low-elevation pikas use forested habitat more frequently than do high-elevation pikas. Bars represent mean ± 1 standard error. (c) A pika consumes moss along the Columbia River.*

First, in addition to directional change, climate variability and the probability of extreme events are also likely to increase in coming decades, which might place a premium on the ability to respond to acute climatic triggers. Although our results suggest that nearly two-thirds of responses occurred in relation to chronic, rather than acute, triggers (Figure 1e), it remains unclear whether acute climate stress poses more of a challenge to animals' adaptive capacity (as defined by Beever *et al.* [2016], here and henceforth), or if these responses are simply less frequently studied. Similarly, only nine of 186 studies (< 5%) in our analysis documented responses to multiple aspects of climate. Statistically disentangling numerous climate triggers is a daunting challenge, but it will be

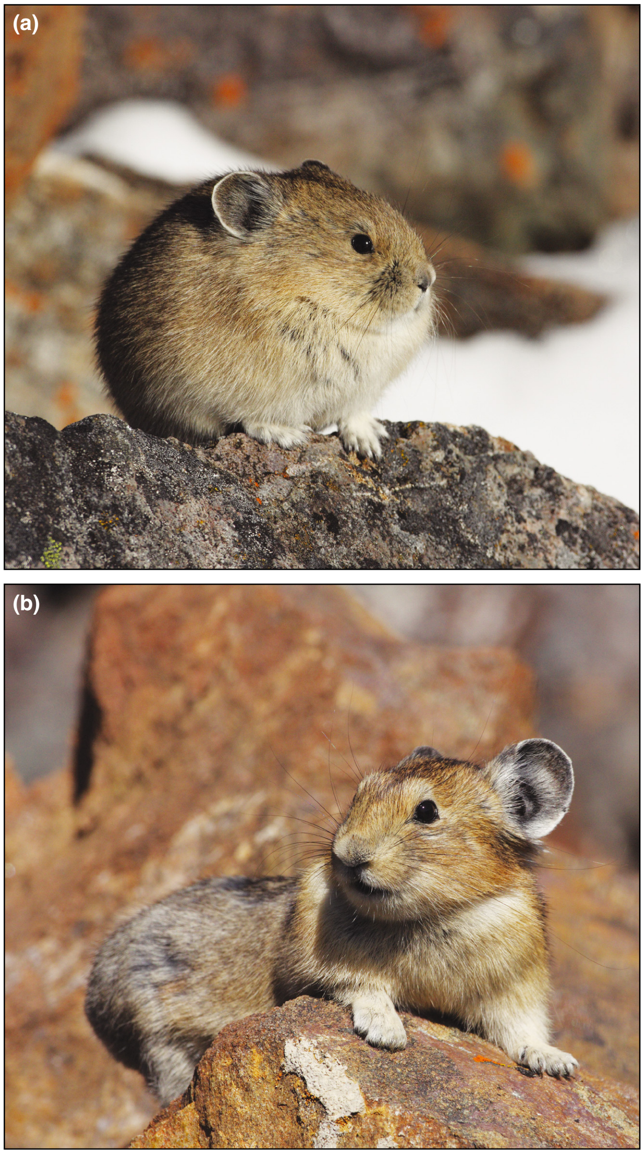


Figure 4. *Behavioral thermoregulation in pikas. Pikas are small mammals capable of marked behavioral plasticity, including the ability to thermoregulate (to some degree) by changing their body posture. In the northern portion of their range, pikas are more frequently observed with a roughly spherical body shape (a) in winter to conserve heat, whereas in summer, their body shape becomes more oblong (b).*

necessary to gain a more mechanistic understanding of behavior, which is often stimulated by multiple, simultaneous climatic cues. Investigating responses to metrics that integrate multiple aspects of climate, such as water-balance deficit, may provide an initial assessment of behavioral responses to multiple climatic factors.

Similarly, behavioral responses were most commonly documented over the course of a season in our literature review (40.3% of studies), although a total of 36.6% were observed on one of several shorter scales such as hours, days, or weeks (WebFigure 2a). Notably, responses occurring over multiple years represented only 7.0% of all studies (WebFigure 2a). This dearth may reflect the rarity of long-term behavioral shifts, or the difficulty of conducting year-round, multi-year studies, which could represent an important opportunity for future research.

Additional study will also be needed to better characterize the aspects of life history and ecology that can be most easily modified by behavior and to identify constraints limiting the capacity of organisms to accommodate to changes in climate. Species that are more generalist in their ecological niche (eg diet breadth, habitat associations, etc) may be better able to accommodate novel conditions than specialists (DeSantis and Haupt 2014). Similarly, dispersal ability could dictate the capacity to colonize formerly inhospitable environments or to move between patches of suitable habitat. Obligate use of microrefuges (eg thicker duff layer, or more structurally complex forests) within a largely inhospitable matrix may reduce effective connectivity for species with poor dispersal capabilities and further isolate populations. Understanding the limitations and context-dependencies of behavioral responses to climate change and variability are key areas for additional work.

Although experimental manipulations provide the strongest evidence of species' climatic thresholds, the majority of studies we uncovered were based on observational data collected in the field (WebFigure 2d). Logistical and ethical constraints often preclude experimental methods that might lead to stronger inference, such as empirically testing upper lethal limits of climatic tolerances. Despite these constraints, many studies have carefully manipulated climate-related parameters. Giroud *et al.* (2008), for example, found that captive gray mouse lemurs (*Microcebus murinus*) adjusted daily torpor and locomotion to compensate for prolonged reductions in food availability. Experimental food shortages were intended to mimic natural, unpredictable food shortages caused by droughts. Such creative, mechanism-based approaches can complement and strengthen observational studies. Future studies could also sample both climatic conditions and behavior across biophysical gradients within a species' distribution (Breshears *et al.* 2008), or document microclimates that animals select from a range of available conditions (Murray and Smith 2012). Detailed behavioral observations of populations that persist at range edges may also be informative of behaviors used to mitigate the effects of climatic extremes (Ruiz-Aravena *et al.* 2014).

Another pervasive challenge is that very few investigations simultaneously quantify behavior and the underlying genetic heritability. This limits the ability to determine whether observed behaviors represent plasticity or microevolutionary change (see review by Hoffmann and Merilä 1999). In the future, researchers could document the effects of local climatic conditions on both survival and reproduction within pedigreed populations, which would allow genetic heritability and selection to be (at least partially) disentangled from the

Table 1. Examples of behavioral responses to climate stimuli from our literature search and suggested behavior-based management considerations

Clade	*Climate stimulus*	*Response(s)*	*Constraints*	*Management considerations*	*References*
Invertebrates	Warmer winter temperatures	Pests alter phenology of reproduction or forego dormancy to increase reproduction	Availability of resources; controls on dormancy (temperature versus photoperiod)	To reduce pest populations, seek to remove resources necessary for pests to reproduce	Reisen *et al.* (1976); Thomas and McClintock (1996); Gambino (1991); da Silva *et al.* (2011)
Fishes	Warming water temperatures	Use of seasonal cold-water refugia	Knowledge of refuge availability; competition for access; predation pressure in refuge	Manage stream conditions to create larger, more-connected cold-water patches; improve access to refuges	Righton *et al.* (2010); Frost *et al.* (2013)
Amphibians	Reduced precipitation	Altering oviposition location to avoid offspring desiccation	Access to and knowledge of breeding sites with better conditions; food resources to sustain offspring post-hatch	Connect and conserve breeding sites; ensure adequate food resources post-hatch	Schulte and Lötters (2013); Touchon (2012)
Reptiles	Warming ambient temperature	Increased sheltering to maintain preferred body temperature	Availability of microclimates; trade-offs with foraging or other activities; spatial overlap between microclimates and resources needed for reproduction	Conserve available microrefugia; enhance habitat surrounding microrefugia to include both favorable temperatures and other resources required for reproduction	Rosen (1991); Seebacher *et al.* (2004); Valdecantos *et al.* (2013); Carter *et al.* (2012)
Birds	Warming spring temperatures	Earlier arrival at summer breeding grounds; adjusted egg-laying dates to better match resource availability	Reliability of cues that signal migration; ability to correctly assess changing cues; continued match between food and climate in breeding areas	Manage birds at multi-landscape scales, which are more likely to encompass a heterogeneous mosaic of resources and optimal niche conditions	Tottrup *et al.* (2010); Weidinger and Kral (2007); Mazerolle *et al.* (2011); Goodenough *et al.* (2011)
Mammals	Drought or reduced snowpack	Dietary shifts toward alternative food resources	Alternatives must be available, be recognized as food, and provide adequate nutrition	Maintain access to alternative food resources; possible transplanting of palatable food species adapted to future climate conditions	Sassi *et al.* (2011); Villegas-Amtmann and Costa (2010); Hansen *et al.* (2010); Varner and Dearing (2014b)

Notes: Behavior-based management considerations must account for constraints to behavioral responses within each taxon.

observed phenotypic plasticity. Finally, longer-term studies will be necessary to document whether flexible behavioral responses truly enhance fitness.

Implications of behavioral responses for management and conservation

A better understanding of relationships between climate and behavioral flexibility has the potential to improve animal conservation and management (Blumstein 2015). Recent calls for greater integration of behavior in conservation planning offer some initial guidance in this regard (Berger-Tal *et al.* 2015; Muñoz *et al.* 2015). However, explicit incorporation of behavioral considerations into climate-change ecology has been slow (Caro 2015). Understanding the degree to which fitness-related behaviors are flexible provides managers with an improved estimate of population vulnerability, as does quantification of the magnitude of behavioral effects (Blumstein 2015). Some populations of migratory birds, for instance, demonstrate sufficient flexibility to produce an optimal arrival date on breeding grounds despite rapidly changing spring conditions (Table 1; Both and Visser 2001; Charmantier *et al.* 2008). However, other populations with similar migration strategies are unable to keep pace through behavioral shifts alone (Van Buskirk *et al.* 2012). Incorporating behavioral flexibility into conservation assessments, such as species distribution models or climate change vulnerability assessments, will facilitate understanding a species' sensitivity to change (Glick *et al.* 2011; Muñoz *et al.* 2015).

Behavioral shifts can offer managers a tool to quickly detect species responses to warming climates. Behavioral flexibility provides organisms with a more rapid pathway to accommodate environmental variation, as compared to genetic adaptation or migration. Similar to approaches that systematically measure how behavior varies with risk (Brown and Kotler 2004), climate-induced variation in behavior can indicate how individuals perceive the environment and may be a useful indicator of potential adaptive capacity. In short, behavioral variability can be a helpful diagnostic for evaluating potential climate-related adaptive capacity in an organism.

Although behavioral flexibility can offer populations a pathway to persistence amid rapidly changing conditions, it can be an imperfect solution. Physiological limitations, trade-offs with other fitness-related activities, and the range of environmental conditions over which a behavior is flexible may limit the ability of animals to behaviorally accommodate to climate change. In addition, some behavioral shifts, such as those related to migration or habitat use, could be further constrained by urbanization and habitat fragmentation. In many cases, behavioral flexibility alone is insufficient to adjust to novel conditions without concomitant change in other traits (Van Buskirk *et al.* 2012). In fact, it may even produce detrimental responses (eg Van Buskirk 2012). These constraints may vary by taxonomic group and ecological context, but they will be critical to consider for developing effective, behavior-based conservation and management approaches (Table 1). As scientists and managers seek solutions to species conservation in novel environments, considering how flexibility produces beneficial responses (Van Buskirk 2012; Wong and Candolin 2015), as well as the limits of that flexibility, will be critical. The large number of species of conservation concern and the financial limitations of conservation practitioners demand that the best possible information be incorporated into species prioritization, including the extent and limits of behavioral flexibility.

Having a clear understanding of the potential for species to cope with climate change through behavior could affect not only the prioritization of species for conservation or management attention, but also the type of management actions that are selected. For example, in-stream cold-water refugia will be important for a species that is capable of shifting its habitat use to spend more time in these colder locations, and thus management to protect or create such refugia could be useful. Similarly, one might need to shift the timing of access limitations or even hunting seasons to address shifts in nesting phenology that track a change in climate. Furthermore, incorporating a more detailed understanding of behavioral flexibility might allow conservation practitioners to consider how behavior modifications will affect management outcomes, rather than assume that present behaviors are fixed (eg Muñoz *et al.* [2015]).

Conclusions

Behavioral flexibility offers species a way to mitigate some of the stressors associated with climate change and may facilitate persistence in otherwise unfavorable conditions. Many species have a clear capacity to modulate behavior in relation to variations in climate parameters. However, much remains to be learned about the trade-offs, fitness implications, and limitations of behavioral flexibility in the context of novel climate dynamics. Furthermore, populations of the same species may differ greatly in how much behavioral flexibility they exhibit to accommodate to climate change. Understanding linkages between climate parameters and local behaviors will facilitate conservation initiatives, but progress in this direction rests on additional engagement from both researchers and conservation practitioners. Effective, behavior-based conservation strategies in the face of climate change require clear information on the capacity of organisms to modify behavior and on the population-level implications of behavioral flexibility. Management approaches (see Table 1 for several examples) that allow for organisms to vary timing of migration, reproductive phenology, habitat use, and other behaviors promise to offer an effective step toward animal conservation in an uncertain future.

Acknowledgements

We thank P Billman and L Walker for assistance with literature searches; L Walker also helped draft text for WebPanel 3. B Sinervo provided valuable advice on material related to responses by reptiles and amphibians. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

References

Beever EA, Perrine JD, Rickman T, *et al.* 2016. Pika (*Ochotona princeps*) losses from two isolated regions reflect temperature and water balance, but reflect habitat area in a mainland region. *J Mammal* **97**: 1495–511.

Berger-Tal O, Blumstein DT, Carroll S, *et al.* 2015. A systematic survey of the integration of behavior into conservation. *Conserv Biol* **30**: 744–53.

Berger-Tal O, Polak T, Oron A, *et al.* 2011. Integrating animal behavior and conservation biology: a conceptual framework. *Behav Ecol* **22**: 236–39.

Blumstein DT. 2015. Prioritizing conservation behavior research: a comment on Wong and Candolin. *Behav Ecol* **26**: 674.

Böhm M, Collen B, Baillie JEM, *et al.* 2013. The conservation status of the world's reptiles. *Biol Conserv* **157**: 372–85.

Both C and Visser ME. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* **411**: 296–98.

Breshears DD, Huxman TE, Adams HD, *et al.* 2008. Vegetation synchronously leans upslope as climate warms. *P Natl Acad Sci USA* **105**: 11591–92.

Brown JS and Kotler BP. 2004. Hazardous duty pay and the foraging cost of predation. *Ecol Lett* **7**: 999–1014.

Cahill AE, Aiello-Lammens ME, Fisher-Reid MC, *et al.* 2012. How does climate change cause extinction? *P Roy Soc B-Biol Sci* **280**: 1–9.

Caro T. 2015. Human responses to changing environments: a comment on Wong and Candolin. *Behav Ecol* **26**: 675–76.

Carter A, Goldizen A, and Heinsohn R. 2012. Personality and plasticity: temporal behavioural reaction norms in a lizard, the Namibian rock agama. *Anim Behav* **84**: 471–77.

Chalfoun AD and Martin TE. 2010. Facultative nest patch shifts in response to nest predation risk in the Brewer's sparrow: a "win-stay, lose-switch" strategy? *Oecologia* **163**: 885–92.

Charmantier A, McCleery RH, Cole LR, *et al.* 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science* **320**: 800–03.

Chevin LM, Lande R, and Mace GM. 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS Biol* **8**: e1000357.

Cleland EE, Chuine I, Menzel A, *et al.* 2007. Shifting plant phenology in response to global change. *Trends Ecol Evol* **22**: 357–65.

Corrigan LJ, Winfield IJ, Hoelzel AR, *et al.* 2011. Dietary plasticity in Arctic charr (*Salvelinus alpinus*) in response to long-term environmental change. *Ecol Freshwater Fish* **20**: 5–13.

da Silva EDB, Kuhn TMA, and Monteiro LB. 2011. Oviposition behavior of *Grapholita molesta* Busck (Lepidoptera: Tortricidae) at different temperatures. *Neotrop Entomol* **40**: 415–20.

DeSantis LRG and Haupt RJ. 2014. Cougars' key to survival through the Late Pleistocene extinction: insights from dental microwear texture analysis. *Biol Lett* **10**: 20140203.

Frost AJ, Thomson JS, Smith C, *et al.* 2013. Environmental change alters personality in the rainbow trout, *Oncorhynchus mykiss*. *Anim Behav* **85**: 1199–207.

Gambino P. 1991. Reproductive plasticity of *Vespula pensylvanica* (Hymenoptera, Vespidae) on Maui and Hawaii islands, USA. *NZ J Zool* **18**: 139–49.

Giroud S, Blanc S, Aujard F, *et al.* 2008. Chronic food shortage and seasonal modulations of daily torpor and locomotor activity in the grey mouse lemur (*Microcebus murinus*). *Amer J Physiol-Reg I* **294**: R1958–67.

Glick P, Stein BA, and Edelson NA. 2011. Scanning the conservation horizon: a guide to climate change vulnerability assessment. Washington, DC: National Wildlife Federation.

Goodenough AE, Hart AG, and Elliot SL. 2011. What prevents phenological adjustment to climate change in migrant bird species? Evidence against the "arrival constraint" hypothesis. *Intl J Biometeorol* **55**: 97–102.

Hadfield MG and Strathmann MF. 1996. Variability, flexibility and plasticity in life histories of marine invertebrates. *Oceanol Acta* **19**: 323–34.

Hall LE, Chalfoun AD, Beever EA, and Loosen AE. 2016. Microrefuges and the occurrence of thermal specialists: implications for wildlife persistence amidst changing temperatures. *Climate Change Responses* **3**: 8; doi.org/10.1186/s40665-016-0021-4.

Hansen BB, Aanes R, and Sæther B-E. 2010. Feeding-crater selection by high-arctic reindeer facing ice-blocked pastures. *Can J Zool* **88**: 170–77.

Hoffmann AA and Merilä J. 1999. Heritable variation and evolution under favourable and unfavourable conditions. *Trends Ecol Evol* **14**: 96–101.

Hupp JW, Schmutz JA, and Ely CR. 2006. The prelaying interval of emperor geese on the Yukon-Kuskokwim Delta, Alaska. *Condor* **108**: 912–24.

Kearney MR. 2013. Activity restriction and the mechanistic basis for extinctions under climate warming. *Ecol Lett* **16**: 1470–79.

Kearney M, Shine R, and Porter WP. 2009. The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. *P Natl Acad Sci USA* **106**: 3835–40.

Kilpi M. 1992. Responses of herring-gulls (*Larus argentatus*) and common gulls (*L canus*) to warm years – early migration and early breeding. *Omis Fennica* **69**: 82–87.

Mazerolle DF, Sealy SG, and Hobson KA. 2011. Interannual flexibility in breeding phenology of a Neotropical migrant songbird in response to weather conditions at breeding and wintering areas. *Ecoscience* **18**: 18–25.

Muñoz A-R, Marquez AL, and Real R. 2015. An approach to consider behavioral plasticity as a source of uncertainty when forecasting species' response to climate change. *Ecol Evol* **5**: 2359–73.

Murray IW and Smith FA. 2012. Estimating the influence of the thermal environment on activity patterns of the desert woodrat (*Neotoma lepida*) using temperature chronologies. *Can J Zool* **90**: 1171–80.

Parmesan C. 2006. Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Evol Syst* **37**: 637–69.

Pigliucci M. 2001. Phenotypic plasticity: beyond nature and nurture. Baltimore, MD: Johns Hopkins University Press.

Pitcher TJ. 2012. The behaviour of teleost fishes. Beckenham, UK: Croom Helm Ltd.

Reisen WK, Aslamkhan M, and Basio R. 1976. The effects of climatic patterns and agricultural practices on the population dynamics of *Cules-tritaeniorhynchus* in Asia. *SE Asian J Trop Med* **7**: 61–71.

Righton DA, Andersen KH, Neat F, *et al.* 2010. Thermal niche of Atlantic cod *Gadus morhua*: limits, tolerance and optima. *Mar Ecol-Prog Ser* **420**: 1–13.

Rosen PC. 1991. Comparative field study of thermal preferenda in garter snakes (*Thamnophis*). *J Herpetol* **25**: 301–12.

Ruiz-Aravena M, Gonzalez-Mendez A, Estay SA, *et al.* 2014. Impact of global warming at the range margins: phenotypic plasticity and behavioral thermoregulation will buffer an endemic amphibian. *Ecol Evol* **4**: 4467–75.

Sassi PL, Borghi CE, Dacar MA, *et al.* 2011. Geographic and seasonal variability in feeding behaviour of a small herbivorous rodent. *Acta Theriol* **56**: 35–43.

Schulte LM and Lötters S. 2013. The power of the seasons: rainfall triggers parental care in poison frogs. *Evol Ecol* **27**: 711–25.

Seebacher F, Sparrow J, and Thompson MB. 2004. Turtles (*Chelodina longicollis*) regulate muscle metabolic enzyme activity in response to seasonal variation in body temperature. *J Comp Physiol B* **174**: 205–10.

Sih A, Stamps J, Yang LH, *et al.* 2010. Behavior as a key component of integrative biology in a human-altered world. *Integr Comp Biol* **50**: 934–44.

Sinervo B, Mendez-de-la-Cruz F, Miles DB, *et al.* 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* **328**: 894–99.

Smith AT. 1974. The distribution and dispersal of pikas: influences of behavior and climate. *Ecology* **55**: 1368–76.

Smith JA and Erb LP. 2013. Patterns of selective caching behavior of a generalist herbivore, the American pika (*Ochotona princeps*). *Arct Antarct Alp Res* **45**: 396–403.

Snell-Rood EC. 2013. An overview of the evolutionary causes and consequences of behavioural plasticity. *Anim Behav* **85**: 1004–11.

Sol D and Maspons J. 2015. Integrating behavior into life-history theory: a comment on Wong and Candolin. *Behav Ecol* **26**: 677–78.

Staudinger MD, Carter SL, Cross MS, *et al.* 2013. Biodiversity in a changing climate: a synthesis of current and projected trends in the US. *Front Ecol Environ* **11**: 465–73.

Stuart SN, Chanson JS, Cox NA, *et al.* 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* **306**: 1783–86.

Thomas DL and McClintock JB. 1996. Aspects of the population dynamics and physiological ecology of the gastropod *Physella cubensis* (Pulmonata: Physidae) living in a warm-temperate stream and ephemeral pond habitat. *Malacologia* **37**: 333–48.

Tottrup AP, Rainio K, Coppack T, *et al.* 2010. Local temperature fine-tunes the timing of spring migration in birds. *Integr Comp Biol* **50**: 293–304.

Touchon JC. 2012. A treefrog with reproductive mode plasticity reveals a changing balance of selection for nonaquatic egg laying. *Am Nat* **180**: 733–43.

Valdecantos S, Martinez V, Lobo F, *et al*. 2013. Thermal biology of *Liolaemus* lizards from the high Andes: being efficient despite adversity. *J Thermal Biol* **38**: 126–34.

Van Buskirk J. 2012. Behavioural plasticity and environmental change. In: Candolin U and Wong BBM (Eds). Behavioral responses to a changing world: mechanisms and consequences. New York, NY: Oxford University Press.

Van Buskirk J, Mulvihill RS, and Leberman RC. 2012. Phenotypic plasticity alone cannot explain climate-induced change in avian migration timing. *Ecol Evol* **2**: 2430–37.

Varner J and Dearing MD. 2014a. The importance of biologically relevant microclimates in habitat suitability assessments. *PLoS ONE* **9**: e104648.

Varner J and Dearing MD. 2014b. Dietary plasticity in pikas as a strategy for atypical resource landscapes. *J Mammal* **95**: 72–81.

Villegas-Amtmann S and Costa DP. 2010. Oxygen stores plasticity linked to foraging behaviour and pregnancy in a diving predator, the Galapagos sea lion. *Funct Ecol* **24**: 785–95.

Weidinger K and Kral M. 2007. Climatic effects on arrival and laying dates in a long-distance migrant, the collared flycatcher (*Ficedula albicollis*). *Ibis* **149**: 836–47.

With KA. 2015. How fast do migratory songbirds have to adapt to keep pace with rapidly changing landscapes? *Landscape Ecol* **30**: 1351–61.

Wong BBM and Candolin U. 2015. Behavioral responses to changing environments. *Behav Ecol* **26**: 665–73.

Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.1502/suppinfo

---

[7] *Minerva Schools at KGI, San Francisco, CA*; [8] *University of New Mexico, Department of Biology, Albuquerque, NM*; [9] *University of Washington, School of Environmental and Forest Sciences, Seattle, WA*