



INVITED PAPER

Anthropogenic Change Alters Ecological Relationships via Interactive Changes in Stress Physiology and Behavior within and among Organisms

Talysin T. Hammond,^{1,*} Chelsea A. Ortiz-Jimenez[†] and Jennifer E. Smith[‡]

*San Diego Zoo Institute for Conservation Research, Escondido, CA 92027, USA; [†]Department of Environmental Science and Policy, University of California, Davis, CA 95616, USA; [‡]Department of Biology, Mills College, Oakland, CA 94613, USA

1E-mail: talisintess@gmail.com

Synopsis Anthropogenic change has well-documented impacts on stress physiology and behavior across diverse taxonomic groups. Within individual organisms, physiological and behavioral traits often covary at proximate and ultimate timescales. In the context of global change, this means that impacts on physiology can have downstream impacts on behavior, and vice versa. Because all organisms interact with members of their own species and other species within their communities, the effects of humans on one organism can impose indirect effects on one or more other organisms, resulting in cascading effects across interaction networks. Human-induced changes in the stress physiology of one species and the downstream impacts on behavior can therefore interact with the physiological and behavioral responses of other organisms to alter emergent ecological phenomena. Here, we highlight three scenarios in which the stress physiology and behavior of individuals on different sides of an ecological relationship are interactively impacted by anthropogenic change. We discuss host–parasite/pathogen dynamics, predator–prey relationships, and beneficial partnerships (mutualisms and cooperation) in this framework, considering cases in which the effect of stressors on each type of network may be attenuated or enhanced by interactive changes in behavior and physiology. These examples shed light on the ways that stressors imposed at the level of one individual can impact ecological relationships to trigger downstream consequences for behavioral and ecological dynamics. Ultimately, changes in stress physiology on one or both sides of an ecological interaction can mediate higher-level population and community changes due in part to their cascading impacts on behavior. This framework may prove useful for anticipating and potentially mitigating previously underappreciated ecological responses to anthropogenic perturbations in a rapidly changing world.

Introduction

Because all organisms interact with members of their own species and other species within their communities, the effects of human-related stressors on one organism can impose indirect effects on one or more other organisms, resulting in cascading changes across interaction networks. One mechanism by which individual organisms may respond to environmental change is through physiological responses to stressors. Stress can covary with behavior (Packard et al. 2016), meaning that it can affect how organisms interact with their biotic and abiotic surroundings. While relationships between stress physiology and behavior are inconsistent across species, stress–behavior associations of variable directions and

magnitudes are well-documented at short-term (plastic within the lifetime of an individual, e.g., response to chronic and acute stressors; Thaker et al. 2009; Adamo and Baker 2011; Allan et al. 2015) and longer-term timescales (e.g., evolutionarily selected co-variation in suites of stress- and behavior-related traits, Réale et al. 2010; Baugh et al. 2017; but see Royauté et al. 2018). The specific nature of these relationships may be context-dependent and difficult to predict, but within an individual, physiological and behavioral changes induced by anthropogenic change can covary and impact one another.

Interwoven changes in behavior and physiology often take place in parallel among individuals involved in ecological relationships. The consequences

of global change may differ from what would be expected if these factors are considered independently, with possible amplifying, stabilizing, and non-additive effects (Tylianakis et al. 2008; Ferrari et al. 2017; Gunderson et al. 2017b). Moreover, environmental stressors can alter relationships between physiological and behavioral traits (Killen et al. 2013). An integrative approach must be employed to understand and describe such relationships in the context of modified and altered environments.

Here, we highlight ecological scenarios in which changes in stress physiology and behavior in interacting individuals coping with anthropogenic stressors can trigger changes at higher levels of biological organization. We are not the first to call attention to the role that behavioral and physiological responses to global change may play in mediating community-level dynamics (e.g., Gunderson et al. 2017a; Warne et al. 2019). However, this perspective offers a mechanistic view, examining how changes in the stress physiology of two or more interacting “partner organisms” intermingle to induce vertical changes on higher levels of biological organization, thereby attenuating, amplifying, or otherwise altering the biological interaction. In contrast to previous work, we concentrate on three specific ecological interactions—host–pathogen/parasite dynamics, predator–prey relationships, and beneficial partnerships—to elucidate how responses to anthropogenic stressors may alter these interactions.

Stress is notoriously multifaceted and difficult to define. Here, we define it as a response that occurs when a physiological system is faced with an external or psychological challenge that pushes the system out of the scale of normal daily, circannual, or life-history-transition based variation (Wingfield et al. 1998; Romero et al. 2009). This often involves the sympathetic adrenomedullary system and the hypothalamic pituitary adrenocortical (HPA) axis. While we acknowledge that stress and glucocorticoids (GCs) are not equivalent (MacDougall-Shackleton et al. 2019), our perspective does rely heavily upon the large body of empirical evidence for behavioral responses to stressors via the HPA axis. However, we also point toward other, relevant components of the physiological stress response that may be important, particularly in non-vertebrate systems (e.g., heat shock proteins, oxidative stress; Ottaviani and Franceschi 1996; Gunderson et al. 2017a). We define anthropogenic change inclusively (i.e., climate change, invasive species, overexploitation, and habitat degradation/loss, including pollution and human presence). Each ecological interaction is likely impacted by multiple components of anthropogenic

change, but we first review the types most pertinent for each of our three ecological relationship foci (host–pathogen/parasite dynamics, predator–prey relationships, and beneficial partnerships). We then explore how changes in stress physiology and behavior within individuals on different sides of the relationship could impact larger ecological and evolutionary phenomena. These non-exhaustive examples contribute to a simplified framework with the aim of identifying common processes vulnerable to anthropogenic change across seemingly disparate areas of study.

Host–pathogen relationships

While many facets of anthropogenic change impact disease dynamics (Daszak et al. 2001), two particularly relevant drivers in host–pathogen/parasite relationships are habitat alteration (Pongsiri et al. 2009) and introduced/invasive species (Crowl et al. 2008). Habitat modification can impact disease dynamics via changes in resource availability and distribution, which have downstream consequences that alter disease exposure and transmission rates (Becker et al. 2015; Flint et al. 2016; Altizer et al. 2018). For instance, food provisioning has been associated with increased host densities, inter-individual contact rates, and endoparasite infections (Wright and Gompper 2005; Blanco et al. 2017). Humans also introduce pathogens into novel areas, often via domestic animals or commercial trade, thereby exposing organisms to pathogens with which they have no evolutionary history (Epstein et al. 2006; O’Hanlon et al. 2018). These and other human-related activities can impact a host’s likelihood of contracting a pathogen and, often less appreciated, a pathogen’s ability to infect.

Stress responses of individuals can mediate many of these emergent dynamics (Fig. 1A and Box 1A). For example, the recent onslaught of disease-related wildlife declines (Pongsiri et al. 2009) may be related to chronic stress in individuals exposed to multiple, simultaneous human-related stressors (Hing et al. 2016). Chronic stressors can reduce individual quality and cause immunosuppression, leading to increased disease susceptibility (Dhabhar and McEwen 1997; Apanius 1998; Gervasi et al. 2017). At the same time, individuals experiencing acute or chronic stress varying in stress reactivity (e.g., proactive vs. reactive personalities, Réale et al. 2010) can exhibit different behavioral traits, including altered foraging and risk-taking behaviors (Martins et al. 2007; Baugh et al. 2017; Vindas et al. 2017; Moyers et al. 2018a; but see Royauté et al. 2018; Westrick et al. 2019). In turn, certain behaviors

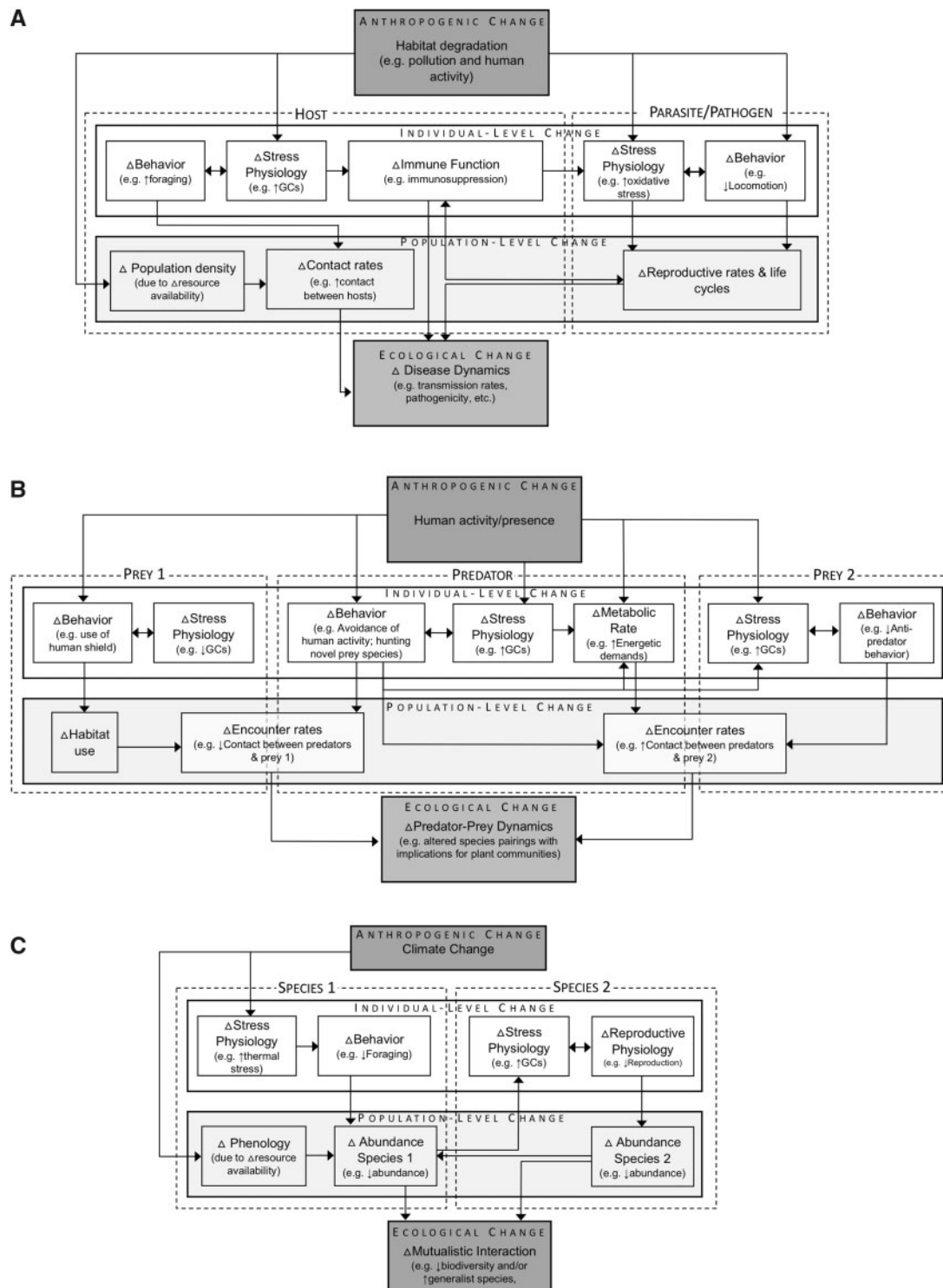


Fig. 1 Flowcharts exhibiting a set of possible relationships between anthropogenic change and interrelated changes in stress physiology and behavior in the context of three ecological interactions: (A) host–pathogen dynamics, (B) disease dynamics, and (C) beneficial relationships. Individual-level changes in physiology and behavior can have bidirectional, horizontal impacts and can contribute to higher, system-level changes, with potential consequences for populations, species interactions, and biodiversity.

are linked to population-level contact and disease transmission rates (Adelman et al. 2015; Adelman and Hawley 2017; Sih et al. 2018). Altogether, covarying behavioral and physiological traits may alter

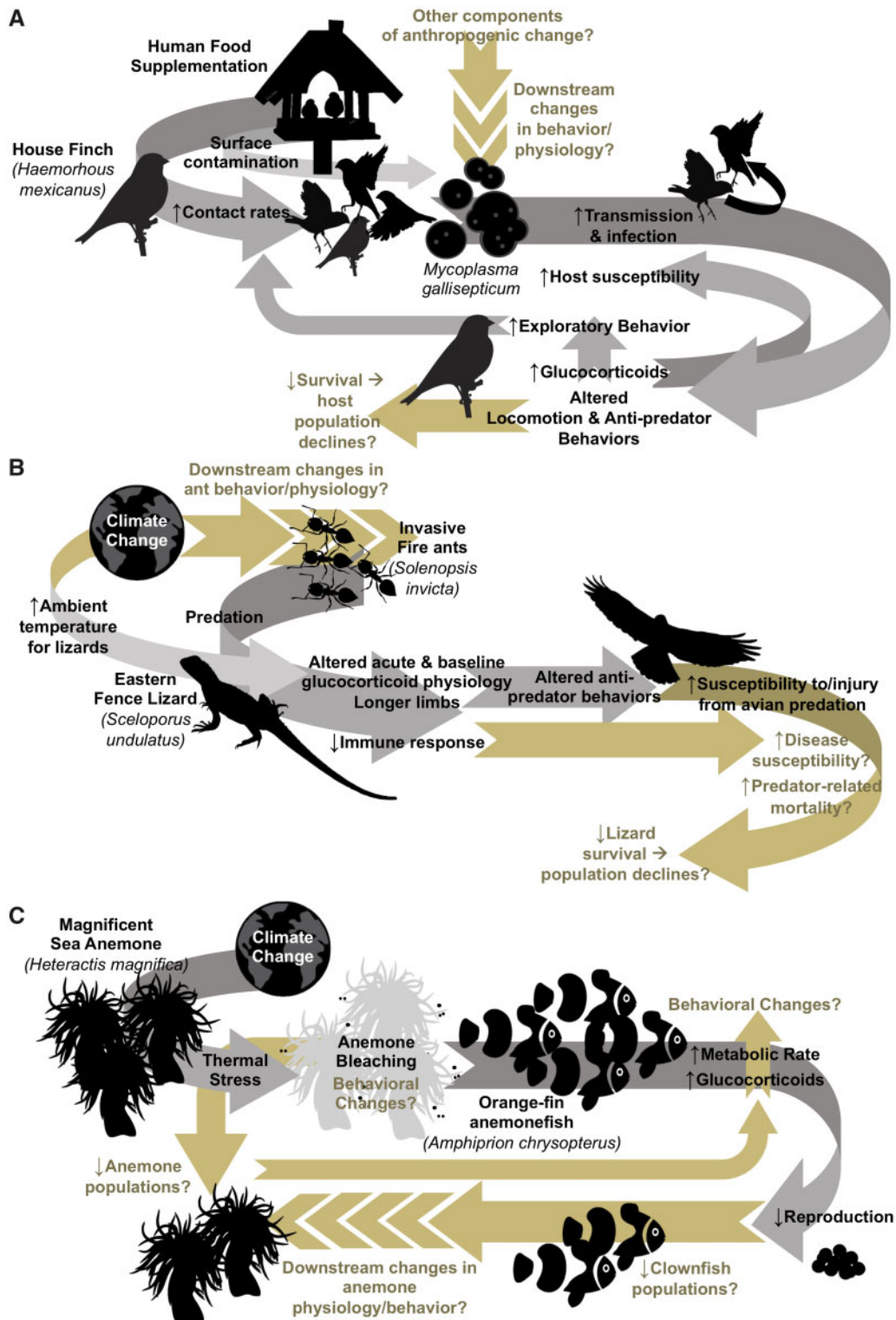
disease transmission via two linked mechanisms: altered susceptibility (often via physiological changes) and exposure (often via behavioral changes; Hawley et al. 2011), both of which respond to human

Box 1

Schematics illustrating relationships among anthropogenic change, stress physiology, behavior, and higher-level impacts on interspecific relationships. Relationships (casual or correlative) supported by empirical data are shown in gray/black; relationships not yet examined in the respective systems (but in some

cases with support in other related systems) and which could be focused on in future studies are shown in spotted rather than solid fill (online version: yellow instead of gray fill), with associated statements followed by question marks.

(A) Avian–*Mycoplasma* host–pathogen system: Human food supplementation can facilitate higher local densities of free-



living house finches (Mertz and Brittingham 2000), alter contact rates among house finches (Moyers et al. 2018b), and promote contaminated feeder surfaces (Adelman et al. 2015). These changes have consequences for transmission and infection rates of the bacterium *Mycoplasma gallisepticum* (Adelman et al. 2015; Fischer and Miller 2015). Infection with this pathogen can lead to increased GCs (Lindström et al. 2005; Love et al. 2016), decreased roost-site fidelity that may further increase contact rates (Dhondt et al. 2006), and can inhibit antipredator responses (Adelman et al. 2017). Moreover, in house finches, seasonal increases in GCs are correlated with periods of *Mycoplasma gallisepticum* outbreaks (Lindström et al. 2005), and individual differences in GCs are associated with increased exploratory behavior (Moyers et al. 2018a), which may further alter finch contact rates (Moyers et al. 2018a). The direct impacts of other aspects of anthropogenic change (e.g., climate change) on *M. gallisepticum*'s behavior and physiology have not yet been explored in this context, but ultimately these dynamics could lead to reductions in host populations.

(B) Fire Ant–Lizard Predator–Prey System: Invasive fire ants prey upon eastern fence lizards, resulting in changes to their GC physiology (Graham et al. 2012, 2017; McCormick et al. 2017; Sprayberry et al. 2019), immune responses (McCormick et al. 2019; Sprayberry et al. 2019), and limb morphology (Langkilde 2009). Changes in GC physiology and an evolutionary history of

exposure to fire ant predation in members of this species are also associated with altered anti-predator behaviors that are thought to reduce susceptibility to fire ant predation but to increase susceptibility to avian predation (Trompeter and Langkilde 2011; Thawley and Langkilde 2017). Although not yet explored, increased injury from avian predation (Thawley and Langkilde 2017) in combination with immune function changes related to fire ant exposure (Sprayberry et al. 2019) could make lizards more susceptible to certain diseases and mortality, with potential downstream consequences for population numbers. While the direct impacts of climate change on these dynamics have yet to be explored, recent work has suggested that increased temperatures can further contribute to changes in GC physiology in fence lizards (Telemeco et al. 2019), with unexplored consequences for/interactions with fire ants.

(C) Anemone–clownfish mutualism: Climate change causes thermal stress-induced bleaching in the magnificent sea anemone. Bleaching has been found to increase metabolic demands (Norin et al. 2018) and to induce a GC stress response in the anemones' associated anemonefish, the orange-fin anemonefish (Beldade et al. 2017). In turn, these changes have been associated with decreased reproduction in anemonefish (Beldade et al. 2017). The downstream consequences of these dynamics on anemone and anemonefish populations in this particular system and the role of anemone or anemonefish behavior in mediating these changes are not yet understood.

modifications of habitat structure and resource distributions.

Concurrent physiological and behavioral changes take place in the parasites and pathogens that infect human-impacted hosts. Relationships between anthropogenic change, stress, and behavior have largely been examined from the perspective of the host, but pathogens and parasites also have stress pathways (Vonlaufen et al. 2008; Keppel et al. 2016) and are susceptible to anthropogenic change (Carlson et al. 2017). Certain types of environmental change are known to directly impact their physiology and behavior. For example, in helminth parasites, pollution can inhibit reproductive (Gheorghiu et al. 2007) and encystment physiology (Morley et al. 2003) and can alter behavior by impairing locomotion and the ability to find hosts (Pietroock and Marcogliese 2003). Parasites and pathogens are also known to respond negatively to certain extreme environmental conditions (e.g., higher than usual temperatures, Stevenson et al. 2013; or lower than usual pH, Marcogliese and Cone 1996).

Studies examining hosts or parasites in isolation often conclude that anthropogenic stressors have negative impacts on fitness for each group, but the consequences of these changes for higher-level disease dynamics depend upon interactive effects (e.g.,

Ezenwa et al. 2016) and the relative susceptibilities of hosts versus parasites to environmental change (Rohr et al. 2008; Sonn et al. 2017; Decker et al. 2018). If pathogens or parasites incur higher costs than hosts, it is possible that environmental change could lead to unexpected benefits for host populations. For example, some parasites can act as “pollutant sinks” accumulating pollutants and thereby reducing the host's exposure (Sures et al. 2003, 2017). On the other hand, the ability of parasites and pathogens to use hosts as a buffer to their direct exposure to environmental change may allow these organisms to persist while taking advantage of immunocompromised hosts.

There is an urgent need for work characterizing the physiological and behavioral responses of pathogens and parasites to anthropogenic change, and how these responses interact with simultaneous impacts on infected hosts. Unsurprisingly, technological advances are opening doors for studies of disease ecology; proximity sensors, movement tracking, and passive integrated transponder (PIT) tags may be useful for mapping out contact/transmission dynamics. Studies of the house finch–mycoplasma system provide a particularly elegant, thoroughly explored case-study off of which future work could be modeled (Box 1A).

Predator–prey dynamics

Human activities are known to affect predator–prey dynamics directly, via human presence or direct killing, and indirectly via the introduction of invasive species and habitat alteration. Introduced species have had devastating impacts on native species with cascading effects on ecological communities (Nelson et al., 2010; Murphy et al. 2019). Habitat modification—particularly modification that involves changes in food availability (e.g., supplementation: Rodewald et al. 2011; overexploitation: Baum and Worm 2009; hunting: Ritchie and Johnson 2009)—has obvious impacts on predator–prey dynamics. More subtly, habitat modifications that impact sensory ecology—for example noise and light pollution—can alter susceptibility to predation and/or hunting ability (Siemers and Schaub 2011; Minnaar et al. 2015).

In comparison to other ecological interactions, there is a relatively large body of literature examining behavior- and stress-mediated impacts of humans on predator–prey dynamics. Predator–prey interactions are inherently behavioral, and there are clear impacts of humans on space use (Muhly et al. 2011; Ordiz et al. 2013; Suraci et al. 2019a), activity rhythms (Ordiz et al. 2017), and other behaviors relevant to predators and prey (Smith et al. 2015; Ortiz et al. 2019). Humans can also act or be perceived as direct predators, which can induce stress-mediated, non-consumptive impacts on animal physiology (Ellenberg et al. 2006; Pereira et al. 2006; Casas et al. 2016). Because humans are “super-predators” (Darimont et al. 2009; Suraci et al. 2019a), their activities can trigger stress–responses (Creel et al. 2002, 2013; Van Meter et al. 2009) in both prey and predator species. Such physiological changes can be linked to further downstream changes (e.g., Thaker et al. 2009), such as acting to inhibit anti-predator behaviors in prey (e.g., Allan et al. 2015; Hammond et al. 2019; but see Lawrence et al. 2017). Altogether, these physiological and behavioral changes could make already-stressed prey more susceptible to predation. It is difficult to predict the overall impacts of humans on predator–prey relationships without balancing the costs and benefits of human activity on each member of the relationship.

Interactions between changes in the physiology and behavior of predators and prey have cascading consequences that can mediate eco-system level changes (Hammond et al. 2007; Hawlena and Schmitz 2010; Guiden et al. 2019; Fig. 1B). For example, when predators avoid human settlements, the same areas can function as a shield for prey species,

providing a low-risk area for foraging and reproducing (Berger 2007; Muhly et al. 2011). This in turn alters dietary choices of prey, which can impact native plant communities (Schmitz et al. 1997; Killen et al. 2013; Suraci et al. 2019a). Altered prey availability in low-risk areas (Berger 2007; Muhly et al. 2011) may leave predators nutritionally stressed, forcing them to either hunt novel or non-preferred species, or to become willing to hunt in high-risk areas, thereby incurring further physiological costs. Alternatively, when prey perceive humans as predators, subsequent changes in stress physiology may lead to inhibition of anti-predator behaviors (Clinchy et al. 2013) and altered energy flow up the food chain (Hawlena and Schmitz 2010). When the performance curves of predator and prey species differ with respect to environmental traits, one species may be favored as the environment changes (Miller et al. 2017). Alternatively, fitness costs for both groups of animals may be amplified when chronically stressed predators hunt for poor-quality, declining prey.

Ultimately, anthropogenic stressors may drive selection for generalist and bold-type predators, which may be more successful in environments with scarce prey options (Terraube et al. 2011; Mella et al. 2015). Personality types in predators can alter predation rates and non-consumptive impacts on prey species (Sih et al. 2012; Toscano and Griffen 2014). Similarly, certain stress phenotypes in prey may be favored in modified environments, and if stress physiology is linked to behavioral phenotypes (Martins et al. 2007; Øverli et al. 2007; Atwell et al. 2012; Baugh et al. 2017; but see Royauté et al. 2018; Westrick et al. 2019), there may be parallel, selective impacts on prey temperament. Selection on animal temperaments can in turn influence community structure (Toscano et al. 2016; Moran et al. 2017; Sih et al. 2018).

Exploring stress- or behaviorally-mediated effects of anthropogenic change on both sides of predator–prey relationships is a difficult task, particularly for larger-bodied, longer-lived, and more far-ranging organisms like mammalian carnivores. Long-term datasets will likely be critical in this pursuit (Langkilde 2009; Smith et al. 2017b). Studies of invasive, predatory fire ants and fence lizards provide an elegant example that future work may benefit from emulating (Box 1B).

Beneficial partnerships

Certain types of anthropogenic change may be most likely to impact beneficial interaction networks, in

which the behavior and physiology of two or more individuals is linked through a mutualistic (between heterospecifics; Fig. 1C) or cooperative (between conspecifics) relationship. For example, climate change and invasive species can change species assemblages (Williams and Jackson 2007; Rogers et al. 2017) thereby altering the likelihood of mutualistic species interacting. In contrast, direct killing, which can remove key individuals from social groups (Packer et al. 2011) and human presence, which can alter grouping of conspecifics (Li et al. 2017), may impact cooperative networks. Theory and existing evidence suggest that humans may impose contrasting pressures on these relationships, acting to disrupt mutualisms (Tylianakis et al. 2008; Dunn et al. 2009; Aslan et al. 2013), but to promote cooperation (Raulo and Dantzer 2018).

While mutualistic relationships are thought to ameliorate environmental stressors for the involved species (Stachowicz 2001), there is little empirical research exploring how anthropogenic stressors imposed on one partner may indirectly act as a stressor upon an associated partner, thereby contributing to biodiversity loss because associated species are bound to common fates (Toby Kiers et al. 2010). One key example comes from the impacts of climate change on a marine mutualism. Temperature-induced anemone bleaching can indirectly harm anemones' associated anemonefish by increasing metabolic demands (Norin et al. 2018), triggering the fish's GC response, and ultimately significantly suppressing reproductive output (Beldade et al. 2017). This fascinating study system has been illustrated in Box 1C. Indirect effects of global change may also negatively affect cleaner mutualisms via the stress axis in other systems. Mutualistic relationships can be subject to cheating (Bshary and Grutter 2005), thus, if anthropogenically-mediated changes in stress are associated with certain behavioral types or responses, then selfish behaviors may change in frequency. Moreover, stress activation can have masking impacts on relationships between physiology and behavior, sometimes resulting in a homogeneity of behavioral types (Killen et al. 2013).

Relatively fewer studies have explored the potential for humans to trigger stress responses to modify patterns of cooperation within social species. Evidence for the role of the HPA-axis in promoting or inhibiting social behavior comes mainly from studies of reproduction (Montgomery et al. 2018; Raulo and Dantzer 2018). Mating behavior and parental care are generally inhibited by HPA activation (Wingfield et al. 1998; Kirby et al. 2009; but see Blumstein et al. 2016), including, potentially, human-induced HPA activation. However, stressors

can also promote coordinated, group-level cooperation (von Dawans et al. 2012; Schweda et al. 2019) and increase social network cohesion (Crockford et al. 2008), both of which can positively impact individual fitness of social animals (Silk 2007; Smith et al. 2017a). Such findings can be extended to generate hypotheses about the impacts of human-induced stressors on cooperative behaviors (e.g., cooperative hunting, group defense/vigilance). For example, human-induced disturbances can promote group-level vigilance in ungulates or birds (Hunter and Skinner 1998; Blumstein 2006). These effects may shape community processes by altering rates of herbivory or depredation by non-human predators. Although the strength of these effects likely varies with sex, species, and the intensity/duration of the stressor, human-induced stressors may promote group-level cooperation to alter population demography, spatial distributions, and persistence.

The extent to which social cooperation can buffer anthropogenic challenges remains poorly understood. Cooperatively breeding vertebrates do occur disproportionately in unpredictable environments (Guindre-Parker and Rubenstein 2018; Schradin et al. 2019), but the extent to which this flexibility in offspring care behavior reduces vulnerability to anthropogenic change is understudied. Even for non-cooperatively breeding animals, social bonds can shield the effects of everyday stressors (Young et al. 2014), suggesting that sociality may help animals to buffer some costs of global change. However, in other species, individuals sacrifice their personal thermal preferences to maintain social cohesion (Cooper et al. 2018), suggesting that sociality may constrain appropriate responses to warming global temperatures. Going forward, technological advances such as animal-worn sensors that monitor stress-reactivity in real-time (Young et al. 2014; Lee et al. 2016) in combination with data collected from long-term studies (Packer et al. 2011; Smith et al. 2017b) could offer insights into the effects of physiological and beneficial partnerships shaping higher-level processes.

Conclusions and future directions

The exposure of multiple parties in an ecological relationship to simultaneous anthropogenic stressors may be greater or less than the sum of its parts (Jackson et al. 2016). We focused on three, classic ecological relationships here, but many other interactions could be examined with a similar perspective (e.g., competition, pollination, animal-mediated seed dispersal, herbivory). We also did not touch upon the extensive ways that early life stress and maternal

stress may impact these dynamics (Pryce et al. 2002), nor upon higher-level interactions between interactions, for example, the impacts of predator–prey relationships on disease dynamics (Buss and Hua 2018; Sprayberry et al. 2019). Stress and stress-mediated changes are not inherently “bad,” and may facilitate wildlife persistence in the face of environmental change (Boonstra 2013). In some cases, anthropogenic change-induced stress responses may interact to facilitate or stabilize ecological dynamics. Still, while impacts of anthropogenic change on interacting organisms may sometimes counterbalance each other in a network, when multiple changes are made to a carefully tuned system disruption is more likely than stabilization (Tylianakis et al. 2008). These dynamics are context-dependent, and ideally should be studied against the backdrop of altered environments.

It is challenging and often logistically impossible to simultaneously study stress and behavior on multiple sides and/or levels of an ecological interaction. However, systematically studying species responses to environmental change in isolation from the ecological relationships and modified habitats they exist within may yield biased conclusions. When attempting to predict or characterize one species’ response to anthropogenic change, meta-analyses that integrate seemingly disparate literatures may be valuable in examining how that same type of environmental change impacts other species that are ecologically bound to the focal species (Winfree et al. 2009; Becker et al. 2015). HormoneBase, a new repository of vertebrate hormone levels, may be a useful online resource in this pursuit (Vitousek et al. 2018). Simulations and modeling may also be required (Gilman et al. 2010). Studies that experimentally manipulate physiological or environmental parameters (e.g., with hormone implants, or mesocosms) will be critical in teasing apart the causality of hormone–behavior–anthropogenic change relationships in modified habitats. Finally, while it is more easily suggested than done, another possible solution to this logistical challenge is for multiple research groups studying disparate sides or levels of the same ecological relationship to combine forces. This approach may be most useful when long term or museum-based datasets are also available, or when studies can be preemptively designed with both groups in mind. Moreover, it will be important to reach outside of comfort zones to pair seemingly diverse datasets (e.g., behavioral/movement datasets from telemetry, GPS, or accelerometers in combination with ecosystem function studies that integrate data on stable isotopes or nutrient flow; Nakamura and Sato 2014; Schmitz et al. 2018).

Stress-mediated ecological changes will have evolutionary consequences for wildlife communities. For example, species that have spent many generations in urbanized conditions can exhibit altered physiological and behavioral traits, potentially due to evolutionary change (Partecke et al. 2006; Donihue and Lambert 2015; Charmantier et al. 2017; Tennessen et al. 2018). In the face of environmental change, novel species assemblages (Williams and Jackson 2007), and altered phenology (Rafferty et al. 2015), the target species involved in pathogenic, predatory, or mutualistic relationships may change. Generalist species with flexible life histories may emerge as “winners” (Dunn et al. 2009; Le Viol et al. 2012; Hammond et al. 2018). The stress response may be one process at play in these shifting community dynamics, allowing species to modulate several mechanisms of response to novel conditions (e.g., behavior, reproduction, metabolic expenditure, etc.). Species exist within ecological interactions. When attempting to predict the impacts of anthropogenic change on one species, we must also consider the ways that it may directly or indirectly impact the physiology and behavior of partner species.

Funding

While working on this project T.T.H. was supported by a National Science Foundation (NSF) Postdoctoral Research Fellowship in Biology, C.A.O.-J. was supported by an NSF Graduate Research Fellowship, and J.E.S. was supported by the Letts-Villard Professorship in Natural Sciences at Mills College.

References

- Adamo SA, Baker JL. 2011. Conserved features of chronic stress across phyla: the effects of long-term stress on behavior and the concentration of the neurohormone octopamine in the cricket, *Gryllus texensis*. *Horm Behav* 60:478–83.
- Adelman JS, Mayer C, Hawley DM. 2017. Infection reduces anti-predator behaviors in house finches. *J Avian Biol* 48:519–28.
- Adelman JS, Moyers SC, Farine DR, Hawley DM. 2015. Feeder use predicts both acquisition and transmission of a contagious pathogen in a North American songbird. *Proc R Soc B* 282:20151429.
- Adelman JS, Hawley DM. 2017. Tolerance of infection: a role for animal behavior, potential immune mechanisms, and consequences for parasite transmission. *Horm Behav* 88:79–86.
- Allan BJ, Domenici P, Munday PL, McCormick MI. 2015. Feeling the heat: the effect of acute temperature changes on predator–prey interactions in coral reef fish. *Conserv Physiol* 3:cov011.

- Altizer S, Becker DJ, Epstein JH, Forbes KM, Gillespie TR, Hall RJ, Hawley DM, Hernandez SM, Martin LB, Plowright RK, et al. 2018. Food for contagion: synthesis and future directions for studying host–parasite responses to resource shifts in anthropogenic environments. *Philos Trans R Soc B* 373:20170102.
- Apanius V. 1998. Stress and immune defense. *Adv Stud Behav* 27:133–53.
- Aslan CE, Zavaleta ES, Tershy B, Croll D. 2013. Mutualism disruption threatens global plant biodiversity: a systematic review. *PLoS One* 8:e66993.
- Atwell JW, Cardoso GC, Whittaker DJ, Campbell-Nelson S, Robertson KW, Ketterson ED. 2012. Boldness behavior and stress physiology in a novel urban environment suggest rapid correlated evolutionary adaptation. *Behav Ecol* 23:960–9.
- Baugh AT, Senft RA, Firke M, Lauder A, Schroeder J, Meddle SL, van Oers K, Hau M. 2017. Risk-averse personalities have a systemically potentiated neuroendocrine stress axis: a multilevel experiment in *Parus major*. *Horm Behav* 93:99–108.
- Baum JK, Worm B. 2009. Cascading top-down effects of changing oceanic predator abundances. *J Anim Ecol* 78:699–714.
- Becker DJ, Streicker DG, Altizer S. 2015. Linking anthropogenic resources to wildlife–pathogen dynamics: a review and meta-analysis. *Ecol Lett* 18:483–95.
- Beldade R, Blandin A, O'Donnell R, Mills SC. 2017. Cascading effects of thermally-induced anemone bleaching on associated anemonefish hormonal stress response and reproduction. *Nat Commun* 8:716.
- Berger J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. *Biol Lett* 3:620–3.
- Blanco G, Cardells J, Garijo-Toledo MM. 2017. Supplementary feeding and endoparasites in threatened avian scavengers: Coprologic evidence from red kites in their wintering stronghold. *Environ Res* 155:22–30.
- Blumstein DT. 2006. Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. *Anim Behav* 71:389–99.
- Blumstein DT, Keeley KN, Smith JE. 2016. Fitness and hormonal correlates of social and ecological stressors of female yellow-bellied marmots. *Anim Behav* 112:1–11.
- Boonstra R. 2013. Reality as the leading cause of stress: rethinking the impact of chronic stress in nature. *Funct Ecol* 27:11–23.
- Bshary R, Grutter AS. 2005. Punishment and partner switching cause cooperative behaviour in a cleaning mutualism. *Biol Lett* 1:396–9.
- Buss N, Hua J. 2018. Parasite susceptibility in an amphibian host is modified by salinization and predators. *Environ Pollut* 236:754–63.
- Carlson CJ, Burgio KR, Dougherty ER, Phillips AJ, Bueno VM, Clements CF, Castaldo G, Dallas TA, Cizauskas CA, Cumming GS, et al. 2017. Parasite biodiversity faces extinction and redistribution in a changing climate. *Sci Adv* 3:e1602422.
- Casas F, Benítez-López A, Tarjuelo R, Barja I, Viñuela J, García JT, Morales MB, Mougeot F. 2016. Changes in behaviour and faecal glucocorticoid levels in response to increased human activities during weekends in the pin-tailed sandgrouse. *Sci Nat* 103:91.
- Charmantier A, Demeyrier V, Lambrechts M, Perret S, Grégoire A. 2017. Urbanization is associated with divergence in pace-of-life in great tits. *Front Ecol Evol* 5:53.
- Clinchy M, Sheriff MJ, Zanette LY. 2013. Predator-induced stress and the ecology of fear. *Funct Ecol* 27:56–65.
- Cooper B, Adriaenssens B, Killen SS. 2018. Individual variation in the compromise between social group membership and exposure to preferred temperatures. *Proc R Soc B* 285:20180884.
- Creel S, Fox JE, Hardy A, Sands J, Garrett B, Peterson RO. 2002. Snowmobile activity and glucocorticoid stress responses in wolves and elk. *Conserv Biol* 16:809–14.
- Creel S, Christianson D, Schuette P. 2013. Glucocorticoid stress responses of lions in relationship to group composition, human land use, and proximity to people. *Conserv Physiol* 1:1–9.
- Crockford C, Wittig RM, Whitten PL, Seyfarth RM, Cheney DL. 2008. Social stressors and coping mechanisms in wild female baboons (*Papio hamadryas ursinus*). *Horm Behav* 53:254–65.
- Crowl TA, Crist TO, Parmenter RR, Belovsky G, Lugo AE. 2008. The spread of invasive species and infectious disease as drivers of ecosystem change. *Front Ecol Environ* 6:238–46.
- Darimont CT, Carlson SM, Kinnison MT, Paquet PC, Reimchen TE, Wilmers CC. 2009. Human predators outpace other agents of trait change in the wild. *Proc Natl Acad Sci U S A* 106:952–4.
- Daszak P, Cunningham AA, Hyatt AD. 2001. Anthropogenic environmental change and the emergence of infectious diseases in wildlife. *Acta Trop* 78:103–16.
- Decker LE, de Roode JC, Hunter MD. 2018. Elevated atmospheric concentrations of carbon dioxide reduce monarch tolerance and increase parasite virulence by altering the medicinal properties of milkweeds. *Ecol Lett* 21:1353–63.
- Dhabhar FS, McEwen BS. 1997. Acute stress enhances while chronic stress suppresses cell-mediated immunity *in vivo*: a potential role for leukocyte trafficking. *Brain Behav Immun* 11:286–306.
- Dhondt AA, Driscoll MJ, Swarthout EC. 2006. House finch *Carpodacus mexicanus* roosting behaviour during the non-breeding season and possible effects of mycoplasmal conjunctivitis. *Ibis* 149:1–9.
- Donihue CM, Lambert MR. 2015. Adaptive evolution in urban ecosystems. *Ambio* 44:194–203.
- Dunn RR, Harris NC, Colwell RK, Koh LP, Sodhi NS. 2009. The sixth mass coextinction: are most endangered species parasites and mutualists?. *Proc R Soc B* 276:3037–45.
- Ellenberg U, Mattern T, Seddon PJ, Jorquera GL. 2006. Physiological and reproductive consequences of human disturbance in Humboldt penguins: the need for species-specific visitor management. *Biol Conserv* 133:95–106.
- Epstein JH, Field HE, Luby S, Pulliam JR, Daszak P. 2006. Nipah virus: impact, origins, and causes of emergence. *Curr Infect Dis Rep* 8:59–65.
- Ezenwa VO, Archie EA, Craft ME, Hawley DM, Martin LB, Moore J, White L. 2016. Host behaviour–parasite feedback:

- an essential link between animal behaviour and disease ecology. *Proc R Soc B* 283:20153078.
- Ferrari MC, McCormick MI, Watson SA, Meekan MG, Munday PL, Chivers DP. 2017. Predation in high CO₂ waters: prey fish from high-risk environments are less susceptible to ocean acidification. *Integr Comp Biol* 57:55–62.
- Fischer JD, Miller JR. 2015. Direct and indirect effects of anthropogenic bird food on population dynamics of a songbird. *Acta Oecol* 69:46–51.
- Flint BF, Hawley DM, Alexander KA. 2016. Do not feed the wildlife: associations between garbage use, aggression, and disease in banded mongooses (*Mungos mungo*). *Ecol Evol* 6:5932–9.
- Gervasi SS, Burgan SC, Hofmeister E, Unnasch TR, Martin LB. 2017. Stress hormones predict a host superspreader phenotype in the West Nile virus system. *Proc R Soc B* 284:20171090.
- Gheorghiu C, Cable J, Marcogliese DJ, Scott ME. 2007. Effects of waterborne zinc on reproduction, survival and morphometrics of *Gyrodactylus turnbulli* (Monogenea) on guppies (*Poecilia reticulata*). *Int J Parasitol* 37:375–81.
- Gilman SE, Urban MC, Tewksbury J, Gilchrist GW, Holt RD. 2010. A framework for community interactions under climate change. *Trends Ecol Evol* 25:325–31.
- Graham SP, Freidenfelds NA, McCormick GL, Langkilde T. 2012. The impacts of invaders: basal and acute stress glucocorticoid profiles and immune function in native lizards threatened by invasive ants. *Gen Comp Endocrinol* 176:400–8.
- Graham SP, Freidenfelds NA, Thawley CJ, Robbins TR, Langkilde T. 2017. Are invasive species stressful? The glucocorticoid profile of native lizards exposed to invasive fire ants depends on the context. *Physiol Biochem Zool* 90:328–37.
- Guiden PW, Bartel SL, Byer NW, Shipley AA, Orrrock JL. 2019. Predator–prey interactions in the Anthropocene: Reconciling multiple aspects of novelty. *Trends Ecol Evol* 34:616–27.
- Guindre-Parker S, Rubenstein DR. 2018. Multiple benefits of alloparental care in a fluctuating environment. *R Soc Open Sci* 5:172406.
- Gunderson AR, King EE, Boyer K, Tsukimura B, Stillman JH. 2017. Species as stressors: heterospecific interactions and the cellular stress response under global change. *Integr Comp Biol* 57:90–102.
- Gunderson AR, Tsukimura B, Stillman JH. 2017. Indirect effects of global change: from physiological and behavioral mechanisms to ecological consequences. *Integr Comp Biol* 57:48–54.
- Hammond JT, Luttbeg B, Sih A. 2007. Predator and prey space use: dragonflies and tadpoles in an interactive game. *Ecology* 88:1525–35.
- Hammond TT, Palme R, Lacey EA. 2018. Ecological specialization, variability in activity patterns and response to environmental change. *Biol Lett* 14:20180115.
- Hammond TT, Vo M, Burton CT, Surber LL, Lacey EA, Smith JE. 2019. Physiological and behavioral responses to anthropogenic stressors in a human-tolerant mammal. *J Mammal* 100:1928–40.
- Hawlana D, Schmitz OJ. 2010. Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. *Am Nat* 176:537–56.
- Hawley DM, Etienne RS, Ezenwa VO, Jolles AE. 2011. Does animal behavior underlie covariation between hosts' exposure to infectious agents and susceptibility to infection? Implications for disease dynamics. *Integr Comp Biol* 51:528–39.
- Hing S, Narayan EJ, Thompson RA, Godfrey SS. 2016. The relationship between physiological stress and wildlife disease: consequences for health and conservation. *Wildl Res* 43:51–60.
- Hunter LTB, Skinner JD. 1998. Vigilance behaviour in African ungulates: the role of predation pressure. *Behaviour* 135:195–211.
- Jackson MC, Loewen CJ, Vinebrooke RD, Chimimba CT. 2016. Net effects of multiple stressors in freshwater ecosystems: a meta-analysis. *Glob Change Biol* 22:180–9.
- Keppel M, Dangel KC, Sures B. 2016. The Hsp70 response of *Anguillicola* species to host-specific stressors. *Parasitol Res* 115:2149–54.
- Killen SS, Marras S, Metcalfe NB, McKenzie DJ, Domenici P. 2013. Environmental stressors alter relationships between physiology and behaviour. *Trends Ecol Evol* 28:651–8.
- Kirby ED, Geraghty AC, Ubuka T, Bentley GE, Kaufer D. 2009. Stress increases putative gonadotropin inhibitory hormone and decreases luteinizing hormone in male rats. *Proc Natl Acad Sci U S A* 106:11324–9.
- Langkilde T. 2009. Invasive fire ants alter behavior and morphology of native lizards. *Ecol* 90:208–17.
- Lawrence MJ, Eliason EJ, Brownscombe JW, Gilmour KM, Mandelman JW, Cooke SJ. 2017. An experimental evaluation of the role of the stress axis in mediating predator–prey interactions in wild marine fish. *Comp Biochem Physiol A* 207:21–9.
- Le Viol I, Jiguet F, Brotons L, Herrando S, Lindström Å, Pearce-Higgins JW, Reif J, Van Turnhout C, Devictor V. 2012. More and more generalists: two decades of changes in the European avifauna. *Biol Lett* 8:780–2.
- Lee MA, Bakh N, Bisker G, Brown EN, Strano MS. 2016. A pharmacokinetic model of a tissue implantable cortisol sensor. *Adv Healthc Mater* 5:3004–15.
- Li D, Liu Y, Sun X, Lloyd H, Zhu S, Zhang S, Wan D, Zhang Z. 2017. Habitat-dependent changes in vigilance behaviour of Red-crowned Crane influenced by wildlife tourism. *Sci Rep* 7:16614.
- Lindström KM, Hawley DM, Davis AK, Wikelski M. 2005. Stress responses and disease in three wintering house finch (*Carpodacus mexicanus*) populations along a latitudinal gradient. *Gen Comp Endocrinol* 143:231–9.
- Love AC, Foltz SL, Adelman JS, Moore IT, Hawley DM. 2016. Changes in corticosterone concentrations and behavior during *Mycoplasma gallisepticum* infection in house finches (*Haemorrhous mexicanus*). *Gen Comp Endocrinol* 235:70–7.
- MacDougall-Shackleton SA, Bonier F, Romero LM, Moore IT. 2019. Glucocorticoids and “stress” are not synonymous. *Integr Org Biol* published online (<https://doi.org/10.1093/iob/obz017>).
- Marcogliese DJ, Cone DK. 1996. On the distribution and abundance of eel parasites in Nova Scotia: influence of pH. *J Parasitol* 1:389–99.
- Martins TL, Roberts ML, Giblin I, Huxham R, Evans MR. 2007. Speed of exploration and risk-taking behavior are

- linked to corticosterone titres in zebra finches. *Horm Behav* 52:445–53.
- McCormick GL, Robbins TR, Cavigelli SA, Langkilde T. 2017. Ancestry trumps experience: Transgenerational but not early life stress affects the adult physiological stress response. *Horm Behav* 87:115–21.
- McCormick GL, Robbins TR, Cavigelli SA, Langkilde T. 2019. Population history with invasive predators predicts innate immune function response to early-life glucocorticoid exposure in lizards. *J Exp Biol* 222:jeb188359.
- Mella VS, Ward AJ, Banks PB, McArthur C. 2015. Personality affects the foraging response of a mammalian herbivore to the dual costs of food and fear. *Oecologia* 177:293–303.
- Mertz T, Brittingham MC. 2000. Habitat use by house finches in central Pennsylvania. *Northeast Wildl* 55:20–30.
- Miller CR, Barton BT, Zhu L, Radeloff VC, Oliver KM, Harmon JP, Ives AR. 2017. Combined effects of night warming and light pollution on predator–prey interactions. *Proc R Soc B* 284:20171195.
- Minnaar C, Boyles JG, Minnaar IA, Sole CL, McKechnie AE. 2015. Stacking the odds: light pollution may shift the balance in an ancient predator–prey arms race. *J Appl Ecol* 52:522–31.
- Montgomery TM, Pendleton EL, Smith JE. 2018. Physiological mechanisms mediating patterns of reproductive suppression and alloparental care in cooperatively breeding carnivores. *Physiol Behav* 193:167–78.
- Moran NP, Wong BB, Thompson RM. 2017. Weaving animal temperament into food webs: implications for biodiversity. *Oikos* 126:917–30.
- Morley NJ, Leung KM, Morritt D, Crane M. 2003. Toxicity of anti-fouling biocides to *Parorchis acanthus* (Digenea: Philophthalmidae) cercarial encystment. *Dis Aquat Organ* 54:55–60.
- Moyers SC, Adelman JS, Farine DR, Moore IT, Hawley DM. 2018. Exploratory behavior is linked to stress physiology and social network centrality in free-living house finches (*Haemorrhous mexicanus*). *Horm Behav* 102:105–13.
- Moyers SC, Adelman JS, Farine DR, Thomason CA, Hawley DM. 2018. Feeder density enhances house finch disease transmission in experimental epidemics. *Phil Trans R Soc B* 373:20170090.
- Muhly TB, Semeniuk C, Massolo A, Hickman L, Musiani M. 2011. Human activity helps prey win the predator–prey space race. *PLoS One* 6:e17050.
- Murphy BP, Woolley L-A, Geyle HM, Legge SM, Palmer R, Dickman CR, Augusteyn J, Brown SC, Comer S, Doherty TS, et al. 2019. Introduced cats (*Felis catus*) eating a continental fauna: the number of mammals killed in Australia. *Biol Conserv* 237:28–40.
- Nakamura I, Sato K. 2014. Ontogenetic shift in foraging habit of ocean sunfish *Mola mola* from dietary and behavioral studies. *Marine Biol* 161:1263–73.
- Nelson DW, Crossland MR, Shine R. 2010. Indirect ecological impacts of an invasive toad on predator–prey interactions among native species. *Biol Invasion* 12:3363–9.
- Norin T, Mills SC, Crespel A, Cortese D, Killen SS, Beldade R. 2018. Anemone bleaching increases the metabolic demands of symbiont anemonefish. *Proc R Soc B* 285:20180282.
- O’Hanlon SJ, Rieux A, Farrer RA, Rosa GM, Waldman B, Bataille A, Kosch TA, Murray KA, Brankovics B, Fumagalli M, et al. 2018. Recent Asian origin of chytrid fungi causing global amphibian declines. *Science* 360:621–7.
- Ottaviani E, Franceschi C. 1996. The neuroimmunology of stress from invertebrates to man. *Prog Neurobiol* 48:421–40.
- Ordiz A, Støen O-G, Saebø S, Sahlén V, Pedersen BE, Kindberg J, Swenson JE. 2013. Lasting behavioural responses of brown bears to experimental encounters with humans. *J Appl Ecol* 50:306–14.
- Ordiz A, Saebø S, Kindberg J, Swenson JE, Støen O-G. 2017. Seasonality and human disturbance alter brown bear activity patterns: implications for circumpolar carnivore conservation?. *Anim Conserv* 20:51–60.
- Ortiz CA, Pendleton EL, Newcomb KL, Smith JE. 2019. Conspecific presence and microhabitat features influence foraging decisions across ontogeny in a facultatively social mammal. *Behav Ecol Sociobiol* 73:42.
- Øverli Ø, Sørensen C, Pulman KG, Pottinger TG, Korzan W, Summers CH, Nilsson GE. 2007. Evolutionary background for stress-coping styles: relationships between physiological, behavioral, and cognitive traits in non-mammalian vertebrates. *Neurosci Biobehav Rev* 31:396–412.
- Packard AE, Egan AE, Ulrich-Lai YM. 2016. HPA axis interactions with behavioral systems. *Comp Physiol* 6:1897–934.
- Packer C, Brink H, Kissui BM, Maliti H, Kushnir H, Caro T. 2011. Effects of trophy hunting on lion and leopard populations in Tanzania. *Conserv Biol* 25:142–53.
- Partecke J, Schwabl I, Gwinner E. 2006. Stress and the city: urbanization and its effects on the stress physiology in European blackbirds. *Ecology* 87:1945–52.
- Pereira RJG, Duarte JMB, Negrão JA. 2006. Effects of environmental conditions, human activity, reproduction, antler cycle and grouping on fecal glucocorticoids of free-ranging Pampas deer stags (*Ozotoceros bezoarticus bezoarticus*). *Horm Behav* 49:114–22.
- Pietrocki M, Marcogliese DJ. 2003. Free-living endohelminth stages: at the mercy of environmental conditions. *Trends Parasitol* 19:293–9.
- Pongsiri MJ, Roman J, Ezenwa VO, Goldberg TL, Koren HS, Newbold SC, Ostfeld RS, Pattanayak SK, Salkeld DJ. 2009. Biodiversity loss affects global disease ecology. *Bioscience* 59:945–54.
- Pryce CR, Ruedi-Bettschen D, Dettling AC, Feldon J. 2002. Early life stress: long-term physiological impact in rodents and primates. *News Physiol Sci* 17:150–5.
- Rafferty NE, CaraDonna PJ, Bronstein JL. 2015. Phenological shifts and the fate of mutualisms. *Oikos* 124:14–21.
- Raulo A, Dantzer B. 2018. Associations between glucocorticoids and sociality across a continuum of vertebrate social behavior. *Ecol Evol* 8:7697–716.
- Réale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio PO. 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. *Phil Trans R Soc B* 365:4051–63.
- Ritchie EG, Johnson CN. 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecol Lett* 12:982–98.

- Rodewald AD, Kearns LJ, Shustack DP. 2011. Anthropogenic resource subsidies decouple predator–prey relationships. *Ecol Appl* 21:936–43.
- Rohr JR, Raffel TR, Sessions SK, Hudson PJ. 2008. Understanding the net effects of pesticides on amphibian trematode infections. *Ecol Appl* 18:1743–53.
- Romero LM, Dickens MJ, Cyr NE. 2009. The reactive scope model—a new model integrating homeostasis, allostasis, and stress. *Horm Behav* 55:375–89.
- Royauté R, Berdal MA, Garrison CR, Dochtermann NA. 2018. Paceless life? A meta-analysis of the pace-of-life syndrome hypothesis. *Behav Ecol Sociobiol* 72:64.
- Schmitz OJ, Beckerman AP, O'Brien KM. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecol* 78:1388–99.
- Schmitz OJ, Wilmers CC, Leroux SJ, Doughty CE, Atwood TB, Galetti M, Davies AB, Goetz SJ. 2018. Animals and the zoogeochemistry of the carbon cycle. *Science* 362:eaar3213.
- Schradin C, Pillay N, Bertelsmeier C. 2019. Social flexibility and environmental unpredictability in African striped mice. *Behav Ecol Sociobiol* 73:94.
- Schweda A, Faber NS, Crockett MJ, Kalenscher T. 2019. The effects of psychosocial stress on intergroup resource allocation. *Sci Rep* 9:1–12.
- Siemers BM, Schaub A. 2011. Hunting at the highway: traffic noise reduces foraging efficiency in acoustic predators. *Proc R Soc B* 278:1646–52.
- Sih A, Cote J, Evans M, Fogarty S, Pruitt J. 2012. Ecological implications of behavioural syndromes. *Ecol Lett* 15:278–89.
- Sih A, Spiegel O, Godfrey S, Leu S, Bull CM. 2018. Integrating social networks, animal personalities, movement ecology and parasites: a framework with examples from a lizard. *Anim Behav* 136:195–205.
- Silk JB. 2007. Social components of fitness in primate groups. *Science* 317:1347–51.
- Smith JA, Wang Y, Wilmers CC. 2015. Top carnivores increase their kill rates on prey as a response to human-induced fear. *Proc R Soc B* 282:20142711.
- Smith JE, Lacey EA, Hayes LD. 2017a. Sociality in non-primate mammals. In: Rubenstein DR, Abbot P, editors. *Comparative social evolution*. United Kingdom: Cambridge University Press. p. 284–319.
- Smith JE, Lehmann KDS, Montgomery TM, Strauss ED, Holekamp KE. 2017. Insights from long-term field studies of mammalian carnivores. *J Mammal* 98:631–41.
- Sonn JM, Berman S, Richards-Zawacki CL. 2017. The influence of temperature on chytridiomycosis in vivo. *EcoHealth* 14:762–70.
- Sprayberry K, Tylan C, Owen DA, Macleod KJ, Sheriff MJ, Langkilde T. 2019. History of predator exposure affects cell-mediated immunity in female eastern fence lizards, *Sceloporus undulatus* (Squamata: Phrynosomatidae). *Biol J Linn Soc* 128:944–51.
- Stachowicz JJ. 2001. Mutualism, facilitation, and the structure of ecological communities. *Bioscience* 51:235–46.
- Stevenson LA, Alford RA, Bell SC, Roznik EA, Berger L, Pike DA. 2013. Variation in thermal performance of a widespread pathogen, the amphibian chytrid fungus *Batrachochytrium dendrobatidis*. *PLoS One* 8:e73830.
- Suraci JP, Clinchy M, Zanette LY, Wilmers CC. 2019. Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecol Lett* 22:1578–86.
- Sures B, Dezfuli BS, Krug HF. 2003. The intestinal parasite *Pomphorhynchus laevis* (Acanthocephala) interferes with the uptake and accumulation of lead (210Pb) in its fish host chub (*Leuciscus cephalus*). *Int J Parasitol* 33:1617–22.
- Sures B, Nachev M, Selbach C, Marcogliese DJ. 2017. Parasite responses to pollution: what we know and where we go in 'Environmental Parasitology'. *Parasite Vector* 10:65.
- Telemeco RS, Simpson DY, Tylan C, Langkilde T, Schwartz TS. 2019. Contrasting responses of lizards to divergent ecological stressors across biological levels of organization. *Integr Comp Biol* 59:292–305.
- Tennessen JB, Parks SE, Swierk L, Reinert LK, Holden WM, Rollins-Smith LA, Walsh KA, Langkilde T. 2018. Frogs adapt to physiologically costly anthropogenic noise. *Proc R Soc B* 285:20182194.
- Terraube J, Arroyo B, Madders M, Mougeot F. 2011. Diet specialisation and foraging efficiency under fluctuating vole abundance: a comparison between generalist and specialist avian predators. *Oikos* 120:234–44.
- Thaker M, Lima SL, Hews DK. 2009. Acute corticosterone elevation enhances antipredator behaviors in male tree lizard morphs. *Horm Behav* 56:51–7.
- Thawley CJ, Langkilde T. 2017. Attracting unwanted attention: generalization of behavioural adaptation to an invasive predator carries costs. *Anim Behav* 123:285–91.
- Toby Kiers E, Palmer TM, Ives AR, Bruno JF, Bronstein JL. 2010. Mutualisms in a changing world: an evolutionary perspective. *Ecol Lett* 13:1459–74.
- Toscano BJ, Gownaris NJ, Heerhartz SM, Monaco CJ. 2016. Personality, foraging behavior and specialization: integrating behavioral and food web ecology at the individual level. *Oecologia* 182:55–69.
- Toscano BJ, Griffen BD. 2014. Trait-mediated functional responses: predator behavioural type mediates prey consumption. *J Anim Ecol* 83:1469–77.
- Trompeter WP, Langkilde T. 2011. Invader danger: lizards faced with novel predators exhibit an altered behavioral response to stress. *Horm Behav* 60:152–8.
- Tylianakis JM, Didham RK, Bascompte J, Wardle DA. 2008. Global change and species interactions in terrestrial ecosystems. *Ecol Lett* 11:1351–63.
- Van Meter PE, French JA, Dloniak SM, Watts HE, Kolowski JM, Holekamp KE. 2009. Fecal glucocorticoids reflect socio-ecological and anthropogenic stressors in the lives of wild spotted hyenas. *Horm Behav* 55:329–37.
- Vindas MA, Gorissen M, Höglund E, Flik G, Tronci V, Damsgård B, Thörnqvist PO, Nilsen TO, Winberg S, Øverli Ø, et al. 2017. How do individuals cope with stress? Behavioural, physiological and neuronal differences between proactive and reactive coping styles in fish. *J Exp Biol* 220:1524–32.
- Vitousek MN, Johnson MA, Donald JW, Francis CD, Fuxjager MJ, Goymann W, Hau M, Husak JF, Kircher BK, Knapp R, et al. 2018. HormoneBase, a population-level database of steroid hormone levels across vertebrates. *Sci Data* 5:180097.

- von Dawans B, Fischbacher U, Kirschbaum C, Fehr E, Heinrichs M. 2012. The social dimension of stress reactivity. *Psychol Sci* 23:651–60.
- Vonlaufen N, Kanzok SM, Wek RC, Sullivan WJ Jr. 2008. Stress response pathways in protozoan parasites. *Cell Microbiol* 10:2387–99.
- Warne RW, Baer SG, Boyles JG. 2019. Community physiological ecology. *Trends Ecol Evol* 34:510–8.
- Westrick SE, van Kesteren F, Palme R, Boonstra R, Lane JE, Boutin S, McAdam AG, Dantzer B. 2019. Stress activity is not predictive of coping style in North American red squirrels. *Behav Ecol Sociobiol* 73:113.
- Williams JW, Jackson ST. 2007. Novel climates, no-analog communities, and ecological surprises. *Front Ecol Environ* 5:475–82.
- Winfree R, Aguilar R, Vázquez DP, LeBuhn G, Aizen MA. 2009. A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology* 90:2068–76.
- Wingfield JC, Maney DL, Breuner CW, Jacobs JD, Lynn S, Ramenofsky M, Richardson RD. 1998. Ecological bases of hormone—behavior interactions: the “emergency life history stage”. *Am Zool* 38:191–206.
- Wright AN, Gompper ME. 2005. Altered parasite assemblages in raccoons in response to manipulated resource availability. *Oecologia* 144:148–56.
- Young C, Majolo B, Heistermann M, Schülke O, Ostner J. 2014. Responses to social and environmental stress are attenuated by strong male bonds in wild macaques. *Proc Natl Acad Sci U S A* 111:18195–200.