

https://dspace.org/

Biological mechanisms matter in contemporary wildlife conservation

Cooke, Steven J.; Madliger, Christine L.; Lennox, Robert J.; Olden, Julian D.; Eliason, Erika J. ...

2023-03
Cell Press
https://hdl.handle.net/10539/49696
Steven J. Cooke, Christine L. Madliger, Robert J. Lennox, Julian D. Olden, Erika J. Eliason, Rebecca L. Cramp, Andrea Fuller, Craig E. Franklin, Frank Seebacher, Biological mechanisms matter in contemporary wildlife conservation, iScience, Volume 26, Issue 3, 2023, 106192, ISSN 2589-0042, https://doi.org/10.1016/j.isci.2023.106192.

Downloaded from a DSpace repository. https://dspace.org/

iScience

CellPress
OPEN ACCESS

Review

Biological mechanisms matter in contemporary wildlife conservation

Steven J. Cooke,[1,*] Christine L. Madliger,[2] Robert J. Lennox,[3] Julian D. Olden,[4] Erika J. Eliason,[5] Rebecca L. Cramp,[6] Andrea Fuller,[7] Craig E. Franklin,[6] and Frank Seebacher[8]

SUMMARY

Given limited resources for wildlife conservation paired with an urgency to halt declines and rebuild populations, it is imperative that management actions are tactical and effective. Mechanisms are about how a system works and can inform threat identification and mitigation such that conservation actions that work can be identified. Here, we call for a more mechanistic approach to wildlife conservation and management where behavioral and physiological tools and knowledge are used to characterize drivers of decline, identify environmental thresholds, reveal strategies that would restore populations, and prioritize conservation actions. With a growing toolbox for doing mechanistic conservation research as well as a suite of decision-support tools (e.g., mechanistic models), the time is now to fully embrace the concept that mechanisms matter in conservation ensuring that management actions are tactical and focus on actions that have the potential to directly benefit and restore wildlife populations.

INTRODUCTION

Conservation managers and practitioners use diverse forms of evidence, including empirical studies, evidence syntheses, experiential understanding, and indigenous and stakeholder knowledge[1,2] to make decisions intended to protect or restore biodiversity.[3] Although biodiversity inherently encompasses all levels of biological organization—from the molecule to the biome[4]—the vast majority of conservation decisions and actions are informed from evidence collected at the population level.[5,6] Superficially, this conservation paradigm is appropriate in that populations represent somewhat discrete (often spatially and genetically[7]) and logical units for both assessing trends in abundance and guiding management in a strategic manner.[8] From a practical perspective, many wildlife populations can be assessed such that trend-through-time data yield useful information on population trajectories,[9] which serve as the basis for threat assessments (e.g., the International Union for Conservation of Nature [IUCN] Red Listing and associated regional analogues;[10]). Yet, data on population status may be meaningless without a robust understanding of the mechanisms driving demography (i.e., vital rates;[11]). In the absence of a mechanistic dimension (i.e., establishing causation), it is difficult to apply targeted conservation actions that are effective and focus on the appropriate mechanistic levers (i.e., cause-effect relationships) that are regulating population growth or persistence.[12]

In this paper, we argue that mechanisms matter to conservation. We posit that if conservation scientists, managers, and practitioners were to seek and incorporate more mechanistic understanding of biological organization, conservation decisions would be more effective in protecting and restoring populations and indeed all forms of biodiversity. We first define what we mean by "mechanisms". Next, we discuss why mechanisms matter in the context of connecting wildlife to their environment, identifying conservation problems, and generating conservation solutions. We then discuss mechanistic approaches to wildlife research (spanning experimental studies to modeling) relevant to conservation. Using diverse case studies, we highlight where mechanistic approaches to understand species declines have been applied and conclude with a candid assessment of what is needed to make conservation more mechanistic and, ultimately, more successful. We recognize that mechanisms are as relevant to plants and other taxa as they are to animals, yet for the purpose of this paper we restrict our discussions to animals (herein wildlife). The concept that mechanisms matter in conservation is not entirely new,[13–17] but despite previous efforts to mainstream this idea, the approach has yet to be fully embraced. Moreover, most of the previous treatments did not consider mechanisms the same way as we do here. Our treatment is more rooted in

[1]Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental and Interdisciplinary Science, Carleton University, 1125 Colonel By Dr., Ottawa, ON K1S 5B6, Canada

[2]Department of Biology, Algoma University, 1520 Queen St. East, Sault Ste. Marie, ON P6A 2G4, Canada

[3]Norwegian Research Centre (NORCE), Laboratory for Freshwater Ecology and Inland Fisheries, 5008 Bergen, Norway

[4]School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195-5020, USA

[5]Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, Santa Barbara, CA 93106, USA

[6]School of Biological Sciences, University of Queensland, Brisbane, QLD 4072, Australia

[7]Brain Function Research Group, School of Physiology, Faculty of Health Sciences, University of the Witwatersrand, Parktown 2193, South Africa

[8]School of Life and Environmental Sciences A08, University of Sydney, Sydney, NSW 2006, Australia

*Correspondence: steven_cooke@carleton.ca

https://doi.org/10.1016/j.isci.2023.106192

This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

organismal physiology and animal-environment interactions (see next section), which we argue is particularly salient and timely given the current biodiversity and climate crises. Here we center the concept of mechanisms being important for conservation and provide a clear and direct narrative regarding the value in doing so while providing explicit examples of how that can be achieved.

WHAT DO WE MEAN BY MECHANISMS?

There are many formal definitions of mechanisms (see reviews[18,19]), and one that works well with biological systems and conservation is from Bechtel and Abrahamsen[20]: "A mechanism is a structure performing a function in virtue of its component (causally interacting) parts, component operations, and their organization. The orchestrated functioning of the mechanism is responsible for one or more phenomena." Machamer et al.[21] defines mechanisms as "entities and activities organized such that they are productive of regular changes from start or set-up to finish or termination conditions." In ecology, we use mechanisms to help explain how a phenomenon occurred/occurs as a result of the causal chain(s) of its integrated parts (see Connolly et al.[22] for a detailed discussion of mechanisms and processes in ecology). For example, the past experiences of the organisms (across various temporal scales) and ecological interactions may be explained through the dissection of a series of events, the interplay of processes and causal chains. In short, mechanisms are about how a system works[19] with the assumption that they are relevant to understanding and establishing causal relationships that may transcend scales (e.g., levels of biological organization[23]).

Individual animals are themselves complex systems as are the populations they are part of, the assemblages they belong to, and the ecosystems in which they are embedded. At the level of the individual, biological mechanisms that span physiology and behavior (and are underpinned by genetics, evolutionary history, and selection[24,25]) are the first point of contact between organism and environment, and the mechanism-environment interaction influences organismal performance and fitness (including survival[26]). Animals are thereby linked to their environment so that, when environmental conditions are suboptimal, there can be consequences that, in extreme cases, may be lethal (as elegantly outlined in the Fry Paradigm; see Kerr[27]). Behavior and physiology are inherently connected in that physiology constrains and enables behavior, whereas behaviors (e.g., feeding, habitat selection, movement) have physiological consequences.[15,28]

Mechanistic relationships and interdependencies evolve to provide animals the means with which to cope with change and restore homeostasis when encountering challenges.[29] Given the interplay between environmental conditions and fitness, this mechanistic dimension scales up to the population and influences demography.[26,29] Mechanisms can also extend across domains. For example, conservation issues almost always have a human dimension, and failure to consider such drivers or impacts would be problematic.[30] Given the manifold benefits that humans derive from biodiversity, loss of biodiversity can have consequences that extend beyond reductions in, say, wildlife fitness. Understanding mechanisms and mechanistic pathways reveals causal relationships that can be pursued in conservation.[12] For the purpose of this paper, we focus on the mechanistic intersection of physiology, behavior, and environment with considerations of consequences that extend from the individual to higher levels of biological organization (Figure 1). We take a pragmatic approach to applying mechanisms to conservation challenges, acknowledging that some scenarios will benefit from considering the interconnectedness of multiple aspects of physiology and behavior, while others may only require measurement of one mechanistic component.

WHY DO MECHANISMS MATTER?

Mechanisms connect animals to their environment

Animal performance is intricately linked to the surrounding environment—for ectotherms[31] and endotherms.[32] Individual physiological responses and capacities to respond to environmental drivers determine performance, ecological relationships, and the persistence of populations and species across space and time.[26,33] It is physiology that acts as a filter between the environment and fitness-related functions and provides the mechanism that supports and underpins our understanding of the ecology of a species and connects animals to their environment.[26,34] Changes in environmental drivers and mechanisms are intertwined; identifying how causal factors lead to species decline must be elucidated for the purposes of conservation.[26,35] We acknowledge that there are other types of mechanisms relevant to conservation, but these are at a higher organizational level than the physiological mechanisms which are the focus of this paper. For example, understanding species interactions (e.g., predator-prey,[36] plant-herbivore,[37]

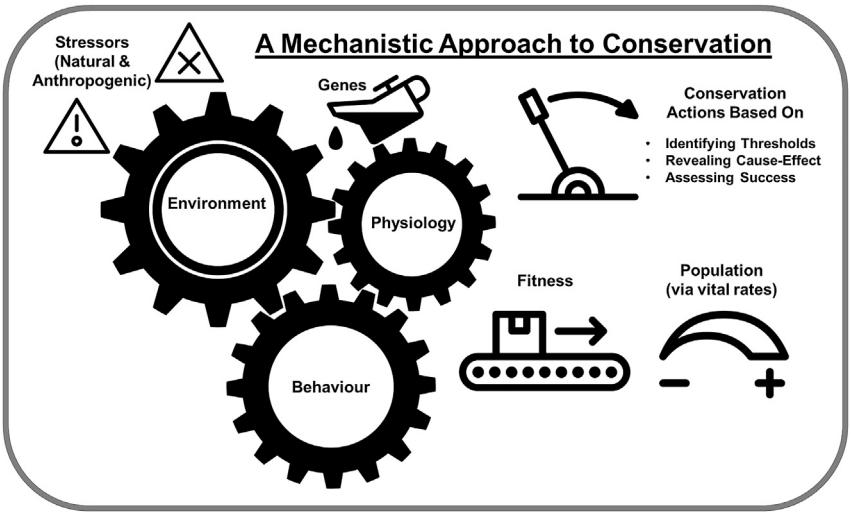


Figure 1. A mechanistic approach to conservation

Simple conceptual diagram visualizing ways in which environmental stressors (natural and anthropogenic) act on individuals (mediated by genes that underpin the connections between organism and environment) via behavioral and physiological pathways (often at their intersection) that have the potential to influence fitness at the level of the individual and contribute to population vital rates. Conservation actions represent levers that can be applied in various ways (e.g., to remove a stressor or to otherwise compensate for it by directly mediating behavior, physiology, and fitness) with a goal of altering population vital rates. Conservation actions are based on mechanistic knowledge related to thresholds, cause-effect relationships, and the assessment of conservation success.

and host-pathogen interactions[38]) has the potential to reveal mechanisms that are relevant to conservation. However, these interactions are one step removed in complexity from the direct interaction between environment and physiology, although not independent from environmental impacts on physiology (e.g., physiology underpins locomotion, which underpins predator-prey interactions).

Environmental change and conservation interventions both act on animal biology. Abiotic environmental changes, such as changes in temperature, typically elicit behavioral and physiological responses.[39] Changes in the biotic environment, such as interactions between individuals or their society, can affect physiology via endocrine-mediated processes. For example, social interactions can induce changes in metabolic function.[40,41] Conservation measures target biological processes by preserving or restoring particular habitats or aspects of the physical environment to improve individual fitness (reproductive outcomes and survival), assure population persistence, and maintain biodiversity.[42] For example, reforestation or pollution remediation alters the physical and chemical environments with beneficial outcomes for resident species.[43,44] However, unlike Newton's Third Law of action and reaction, the environmental or conservation inputs (action) do not necessarily produce a proportional biological output (reaction). Even simple thermodynamic effects of changes in acute temperature produce a non-linear output in physiological reaction rates. These relationships are complicated by evolutionary processes of adaptation and plasticity.

Adaptation, genetic drift, or gene flow can alter genotypes and phenotypes across multiple generations.[45] Genetic differences may thereby match species and populations to their environment and increase performance and fitness. For example, genetic divergence was the likely mechanism that conferred increased heat tolerance on urban ants (*Temnothorax curvispinosus*) compared to rural populations.[46] Insights into genetic divergence between populations and the link between genotype and physiological phenotype provide essential information for conservation decisions. In the case of ants above, the urban heat effect[47] would be offset by the greater heat tolerance of urban populations therefore lessening the urgency to implement conservation actions. Genetic diversity among populations can be important if it determined the sensitivity of individuals to environmental variability and their capacity to respond to change, and population genetics thereby play a major role in conservation.[48,49] However, particular genotypes are by no means fixed to perform well only within a narrow range of environments within which they have evolved. An environmental change may present a novel selective environment eliciting further genetic changes.[50] At a more rapid timescale and superimposed on these genetic changes are epigenetic modification of

gametes in parents that transmit environmentally induced modifications of gene expression pattern to the next generation.[51] In addition, environmental signals experienced within individuals early in development (developmental plasticity) or in adult organisms (reversible acclimation) can alter phenotypes in response to short-term environmental fluctuations.[52,53] Epigenetic effects in response to environmental signals are transmitted via molecular changes to DNA and proteins by DNA and histone methylation and acetylation of proteins.[54–57] Like a Fourier series in physics where oscillations with different periodicity are superimposed onto each other to produce complex responses, combinations of genetic and epigenetic change result in complex phenotypes that can respond to environmental change at different timescales. Understanding these dynamics is important for conservation because they define how quickly and at what magnitude individuals, populations, and species can respond to environmental change and potentially compensate for its effects. For example, an effective epigenetic response can induce plasticity that buffers physiological processes from an external change in temperature,[58] which would render the organism a low conservation priority in this particular case. On the other hand, in cases where plasticity is absent or ineffective a temperature increase may have strong detrimental effects so that immediate conservation action is necessary.[59] However, this complexity of mechanisms and temporal resolution also means that phenotypic responses are not easily predictable, thus pointing to the need for experimental physiological data to resolve these transient responses.

Intuitively, plastic responses are beneficial because they can offset potentially negative impacts of environmental change on physiological processes.[60] However, disadvantages may arise when there is a mismatch between the environmentally induced phenotype and the actual environment experienced.[61] In addition, beneficial plastic responses, such as compensation of swimming performance in fish for changing temperatures, may trade off against concurrent costs such as energetic cost of locomotion.[62] Greater energetic costs may cause an allocation trade-off within individuals so that energy is preferentially allocated to, for example, growth at the expense of reproduction.[62] It is crucial that evaluations and predictions of environmental impacts on natural systems, and conservation measures following these assessments, explicitly account for the temporal and mechanistic dimensions outlined above.[34,63,64]

Species distribution models (SDMs) are a useful tool to assess biodiversity in different geographic regions. Often, these models incorporate climate data to predict the potential distribution of species under current conditions and different scenarios of climate change.[65,66] At their most basic, SDMs (e.g., climate envelope models) use information about environmental conditions prevalent in current geographical ranges of species to model suitable geographical areas following an environmental change such as climate change.[67] Predictions by SDMs could be improved by incorporating key physiological processes,[68] demographic processes,[69] and the genetically and epigenetically modified response dynamics of these processes.[34] Accordingly, biophysical models add independently sourced data on environmental sensitivities of physiological processes to model potential species distributions in changing environments.[70] The most recent models explicitly include estimates of plasticity and adaptation to estimate species distributions and their vulnerability to environmental (climate) change.[71,72] Ultimately, the more information a model contains, the better its capacity to predict changing species distribution. The latter class of models that include plasticity and adaptation are still quite rare but are likely to provide the best estimates[71] particularly for physiological responses that are well known to be regulated epigenetically. Also noteworthy are recent developments in genomic offset estimates (prediction of maladaptation to future climate) that can be used alongside SDMs.[73]

Key physiological processes may vary between species, although there is some agreement of processes that are important in a conservation context.[63] Disruption of physiological processes that are essential for whole organism function (e.g., energy metabolism) is likely to compromise fitness, and these processes therefore represent a focus for conservation. Therefore, rather than focusing on downstream consequences of environmental change, it may be fruitful to consider the underlying regulatory pathways. For example, endocrine pathways are at the interface between the environment and organism behavior and function, and anthropogenically induced endocrine disruption can have a broad range of downstream effects.[74,75] A focus on the hormone rather than on its effect on individuals may therefore be an effective approach to identify and target specific remediation strategies.

Mechanisms can be used to elucidate problems

Environmental change introduces a myriad of challenges to animals in the wild, and a major tenet of conservation biology is to identify and resolve multiple stressors that are limiting the productivity of animal

populations.[64,76] Major stressors that interact mechanistically with individuals and cause a physiological and behavioral response can be isolated by experimentation. Mitigating the stressor or employing other conservation approaches that minimize the behavioral and physiological consequences on the animal can form the basis of effective management. Such interventions are contingent on an understanding of the mechanistic responses of animals to environmental change and on access to a conservation toolbox that assists scientists and practitioners in untangling the often-complex effects of multiple stressors. Where multiple stressors are operating on individuals, identifying problems and revealing mechanistic relationships between a single stressor and a response at the individual or sub-individual scale are more challenging, particularly where there are synergistic or antagonistic relationships between/among stressors.[77] Isolating stressors may include consideration of why and how animals die based on additive vs compensatory mortality frameworks or component-cause models. Failure to isolate mechanisms causing individual disturbance and impacting population demographics has been a major challenge for biodiversity conservation in a multi-stressor world, and conservation can benefit from experiments and null model testing.[78]

Working on realistic conservation timescales to identify stressors and mechanisms in the field when conservation action is needed may not always be possible and may not align with the timelines available for funding to address conservation issues, which are chronically resource limited (especially time). Laboratory manipulations or mesocosm experiments can identify mechanisms more rapidly and scale solutions to the field. In the future, simulations may be helpful to isolate mechanisms using probabilistic algorithms based on a comprehensive understanding of the action-reaction relationships that exist between animals and their environment. Operationalizing mechanisms as conservation tools requires frameworks for rapid assessment and off-ramps for general action to be taken when mechanisms are difficult to disentangle due to multiple stressors. Rapid assessment frameworks are necessary given that it is possible to get lost in the mechanisms. We are advocates of fundamental research, so engaging in detailed work is always intellectually useful; but for mission-oriented conservation research, it is important to focus on mechanisms and pathways relevant to a given threat, issue, or problem. For example, in the salmon case study below, simple reflex impairment assessments have been useful for assessing fish condition in the field after fisheries interactions and providing fishers and managers with tools to quantify and reduce bycatch mortality.

Mechanisms can be used to identify solutions

Physiological and behavioral mechanisms have become increasingly valued for detecting causes of disturbances to wildlife[79–81]; however, their combined use in delineating conservation solutions is still gaining momentum.[35] By identifying or confirming the environmental stressor responsible for disturbance and how it influences organismal function, integrated mechanistic approaches can formulate conservation solutions to address the underlying problem.[82,83] For example, recognizing that there is a mismatch in the thermal tolerance of some amphibian hosts and *Batrachochytrium dendrobatidis* (Bd; the fungal pathogen that causes chytridiomycosis), the creation of elevated temperature microhabitats where behavioral thermoregulation may assist in the management of pathogen infection intensity could be an effective conservation undertaking for some species.[84] An integrative behavioral and physiological approach can also facilitate improved monitoring of disturbances, thereby enabling faster detections of problems and providing more time to take conservation action. For instance, thermal physiology and behavioral measurements together lead to more informed ways to monitor *Pseudogymnoascus destructans* infection (i.e., white nose syndrome) in wild bat colonies.[85] Further, morphology, physiology, and behavior interact to permit or constrain performance within environmental contexts;[86] thus, considering this interconnectedness can provide information on critical habitat requirements and future vulnerability (e.g., to climate change[87–89]). Studying these form-function relationships can therefore determine areas for protection based on species' tolerances[83,90] or identify potential stocking or translocation locations incorporated, for example, into programs for imperiled fishes.[91,92] Considering the connections between behavior and physiology can also improve post-release survival following reintroductions, for example by informing predator-training programs and soft-release protocols.[93]

Simultaneously monitoring behavioral and physiological traits has improved identification of reproductive readiness[79,94] and overall welfare in captive programs (e.g., tigers[95]; elephants[96]). In terms of *in situ* conservation applications, determining the physiological underpinnings of migratory behavior can allow forecasting of migratory timing, allowing managers to put temporal and regional restrictions in place to minimize disturbance.[97] Similarly, by identifying the most energetically demanding parts of migratory routes, linking physiology and migratory behaviors can impart valuable knowledge for protecting key stopover

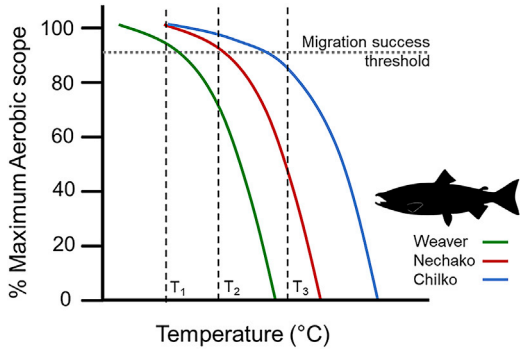


Figure 2. Pacific salmon performance

A conceptual figure showing the percentage of maximum aerobic scope as a function of temperature (cool to warm) is shown for three Fraser River, BC, Canada sockeye salmon populations: Weaver, Nechako and Chilko. Although it is unknown exactly how much aerobic scope is necessary to successfully migrate upstream, 90% is indicated as a likely threshold. At cooler river temperatures (T1), all populations have near-maximal aerobic scope at near-optimal migration temperatures. As temperatures warm (T2), Weaver salmon are unlikely to reach their spawning grounds while Chilko and Nechako salmon are within their optimal temperature range for migration. If river temperatures continue to rise (T3), even Chilko salmon are unlikely to reach their spawning grounds. Tagging studies revealed that Weaver salmon abnormally entering the Fraser River early encountered warm water temperatures (e.g., T2 and T3) exceeding their optimal threshold for aerobic scope which could partially explain migration failure.[103]

habitats or implementing supplementation programs.[97] Finally, understanding the physiological and behavioral responses of organisms to chemical and physical characteristics in their environment is leading to innovation in invasive species control (e.g., sea lamprey [*Petromyzon marinus*][98]) and the design of human infrastructure to keep native species from interacting with lights, dams, turbines, and fishing nets, among others.[16,99]

CASE STUDIES THAT DEMONSTRATE A MECHANISTIC APPROACH

We selected several case studies that highlight how a mechanistic approach has been applied to a variety of wildlife taxa (e.g., fish, amphibians, mammals) and issues (e.g., multiple stressors, disease, invasive species, climate change). Moreover, the case studies rely on various empirical and modeling methods that span physiology and behavior with some consideration of ecological mechanisms.

Pacific salmon management

The Fraser River of British Columbia (Canada) is home to sockeye salmon *Oncorhynchus nerka* which undertake iconic migrations from natal rivers to the high seas to feed and then back again to spawn. Because sockeye salmon are semelparous, failure to return to spawning grounds to reproduce means that lifetime fitness is zero. Although mortality occurs throughout all phases of the salmon life cycle, attention has predominantly focused on understanding adult upriver spawning migration given that in some years >90% of sockeye salmon that enter the river fail to make it to spawning grounds. Migration inherently connects behavior and physiology with environmental conditions such that adopting a mechanistic approach to understand reduced fitness is essential. Following several years of abnormal migration behavior (fish returning early) and exceedingly high rates of en route mortality, a large-scale mechanistic research program was initiated.[100] Both observational and experimental research revealed that early migrants were more reproductively advanced and ill-prepared for osmoregulatory transition upon their entry into fresh water.[101] Moreover, genomic studies revealed that early migrants were immunocompromised.[102] Because fish were entering the river early, they were exposed to water temperatures that were much higher than historic norms, which exacerbated disease progression and energy depletion.[101] Swimming performance and respirometry studies revealed population-specific variation in thermal optima, and, for some populations, the warmer temperatures exceeded their critical maxima leading to the collapse of metabolic and cardiac scope ending in death (Figure 2;[59]). Although some questions still remain, it is apparent from this body of research that water temperatures are major drivers of mortality for early migrants. Salmon also encounter fisheries, and there are instances when fish are released (e.g., regulations require release of given species as part of selecting fishing policies or conservation ethics of an angler or indigenous fisher). Simple reflex

indicators have been developed that provide rapid (and free) information on the vitality of fish that is predictive of survival (i.e., low reflex impairment = high survival, high reflex impairment = low survival[104]). After these tools were validated,[105] they provided fishers and managers with new tools to understand mechanisms impacting captured salmon and to adjust fishing practices to reduce impacts in real time. Although there was initial skepticism by fisheries managers about undertaking mechanistic research,[106] the creation of clear cause-effect pathways combined with the ability to explain population-specific mortality patterns has led to these approaches being embraced and incorporated into fisheries planning.[107] Moreover, the reflex assessments can be done by fishers, so they can adjust their fishing practices in real time.

Amphibian disease

Amphibians are at the forefront of the global biodiversity crisis due in large part to the emergence of the novel fungal skin disease chytridiomycosis, which has been linked to the decline or extinction of more than 500 amphibian species globally.[108] Mechanism is at the heart of understanding chytridiomycosis: its origins; how, why, when, and where it affects hosts; how individuals, populations, or species respond to infection; how ongoing or increasing environmental change alters disease risks for other populations and species; and how we manage disease risks to facilitate successful conservation. Like many diseases, the prevalence of chytridiomycosis is highly environment dependent as a result of impacts on both host physiological function and the thermal biology of the fungal pathogen. Anthropogenic environmental change likely contributed both to the emergence of the hypervirulent fungal lineage responsible for the disease chytridiomycosis and its ongoing impacts on global amphibian populations.[109] A mechanistic understanding of what constitutes optimal environmental conditions for pathogen survival and disease development in hosts has been pivotal in allowing researchers and conservation managers to model and predict the emergence[110] and spread of the pathogen under current and future climates,[111–113] the likely severity of disease,[114] and the seasonal dependence of outbreaks.[115] Elucidating the mechanisms underpinning host susceptibility to the pathogen and the pathology of the disease has revealed why some species and life stages are more susceptible to the pathogen.[116–119] Equally, an understanding of mechanism has been essential to interpret important host behavioral responses to infection such as increased skin shedding[120] and thermoregulatory changes[121] to manage pathogen loads and learned avoidance of the pathogen.[122] Importantly, an understanding of mechanism has been central to the development of effective treatments for infected frogs[117,123,124] and to the management of chytridiomycosis in conservation-significant amphibian populations worldwide.[125]

Invasive species control

Invasive species are responsible for profound, negative effects on biodiversity,[126] ecosystem functioning and services,[127] human health[128] and welfare,[129] and the economy.[130] Developing effective management strategies and policy to avoid or reduce the impacts of invasive species is of paramount importance. Mechanistic models represent indispensable tools for invasive species management as they allow scientists to estimate key vital rates such as spread rate, simulate the potential effects of invasive species, and explore implications of various control or eradication strategies.[131] These models can couple the temporal and/or spatial dynamics of invasive populations with the ability to simulate and evaluate management actions in terms of specified outcomes.[132] For example, Grechi et al.[133] integrated a multi-objective decision framework with mechanistic population growth models to predict the population dynamics and optimal management of buffelgrass (*Pennisetum ciliare*), a commercially valuable invasive species, in Australia.

Mechanistic models based on physiological data seek to capture system dynamics at larger spatiotemporal scales compared to those at which empirical data are typically available and field experimentation is possible, with the desire to better support management decisions.[134] Recently, new methods have been suggested to combine SDMs - which correlate species occurrence or abundance with environmental predictors—with physiological estimates of performance—such as temperature thresholds to delineate the range of environmental conditions within which the species can survive—to improve forecasts of species distributions when extrapolating to novel climate scenarios.[70] For example, the utility of physiology-SDMs has been demonstrated for predicting invasion risk of non-native marine species in the Mediterranean,[135] and if linked with economic analyses, mechanistic models can explore the costs of management and identify strategies that strike an optimal trade-off between management objectives such as suppression and cost.[136,137] The advantages of mechanistic SDMs, however, are tempered by the fact that species information, such as physiological data, is often limited and possibly biased, across

taxa at large scales.[138] This suggests that correlative SDMs may be more practical from an implementation perspective[139] and in some cases may be favored because of comparable predictive power to mechanistic models.[140]

Climate change and wildlife in warming and drying climates

Most predictive models of animal responses to climate change have focused on the direct effects of higher ambient temperatures. However, many terrestrial animals will have to contend with a concomitant reduction in food and water, which is likely to severely challenge their ability to maintain homeostasis.[141] Determining how chronic sub-lethal effects of climate change affect fitness requires an understanding of the behavioral trade-offs that animals make as well as the physiological plasticity available to them to buffer the changes.[141,142] For example, in the hot and arid Kalahari of southern Africa, there has been a decline in growth (body mass at 3-month) and survival rate in meerkat (*Suricata suricatta*) pups over time, which is associated with an increase in the daily maximum air temperature in the Kalahari over the last 20 years.[143] One might expect the underlying mechanism to be a reduction in energy intake, either because prey is less available or because prey has lower energy content. Alternatively, there may be reduced foraging as a result of higher air temperatures constraining activity or an increase in energy expenditure associated with a greater foraging effort to locate prey. However, the reduction in the body mass gain of pups on hotter days was unlikely to reflect a change in energy balance as the pups were fed by adults, and feeding rate increased with increasing maximum air temperatures. Instead, the mechanism may be related to the effects of repeated dehydration on growth,[143] an idea that requires further confirmation through both field and laboratory experimentation. Such mechanistic knowledge is crucial for determining whether appropriate conservation actions can be implemented for this species or whether the species distribution is likely to shrink with fewer suitable habitats available in future.

ACHIEVING MECHANISTIC CONSERVATION

Using four case studies, we highlighted diverse ways in which a mechanistic approach to conservation can be useful for understanding and solving conservation problems. A consistent theme arising from all case studies was that multiple tools and approaches were useful for obtaining comprehensive understanding. Those approaches may involve work in the lab, field or, in silico (e.g., modeling). Conservation problems and issues are diverse with some requiring mechanistic understanding that may have a physiological, behavioral, or ecological basis, and there may be instances in which knowledge of one of those domains is needed and others where all three are necessary. We also acknowledge that for some conservation problems (e.g., spatial protection prioritization), mechanistic knowledge may not be required. Nonetheless, outcomes from mechanistic work such as identifying thresholds or developing cause-effect relationships are almost always helpful when setting conservation targets and ensuring that the correct conservation levers are being applied.

The status quo relies on monitoring populations and preserving habitat—both essential features of conservation. However, a mechanistic understanding of how animals interact with their environment will provide a clearer understanding of the match between habitat characteristics and animal needs, and at the same time, a better understanding of the impact of altered environmental drivers on animal populations (including their demography[144]). Physiological and behavioral knowledge can provide a first-principles understanding of how animals respond to landscape characteristics that contain much greater predictive power than descriptions of presence and absence. Physiology and behavior therefore must become an integral part in landscape assessment for conservation and integrated landscape use,[145] in conjunction with evaluation of physical characteristics (e.g., hydromorphological and biophysical[146]) and species distribution modeling.[70] Although much progress has been made in all of these domains in the last few decades, there remains need for long-term studies/monitoring to generate robust empirical data that fully reflect spatiotemporal dynamics and relationships that presumably govern animal-environment interactions.

There is a philosophical divide between "conservation ecology" and "physiology" that may constrain our ability to achieve mechanistic conservation. Most conservation practitioners manage wildlife populations such that a mechanistic focus may be regarded as irrelevant[12]). Yet, failure to understand mechanisms can lead to misallocated resources and ultimately may delay or prevent the recovery of a population. There is a need for more "cultural integration" among different branches of research that can also be achieved

through broader training (that recognizes the value of mechanistic approaches in conservation) and the sharing of more success stories.[81] Fortunately, there are more examples of success stories as exemplified by the case studies presented here.

Mechanistic approaches to complex applied problems have been central in the realm of neuroscience (over reductionist thinking[19]). Given that conservation problems are equally complex, mechanistic thinking has much to offer. From urban ecology[147] to human-wildlife conflict[148] to invasive species management,[131] there have been numerous calls for making conservation more mechanistic. With a growing toolbox for doing mechanistic conservation research as well as a suite of decision-support tools (e.g., mechanistic models), the time is now to fully embrace the concept that mechanisms matter (where appropriate and relevant) in conservation. Approaching conservation from a mechanistic perspective (Figure 1) is not an academic exercise—it is about ensuring that management actions are tactical and focus on actions that have the potential to directly benefit and restore wildlife populations.

ACKNOWLEDGMENTS

Cooke is supported by the Natural Sciences and Engineering Research Council (NSERC) through a Discovery Grant and Genome Canada (through Gen-Fish). Madliger is supported by NSERC through the CREATE Fish-Cast program. We thank Gillian Zorn for assisting with formatting the paper and three anonymous referees for providing thoughtful comments on the manuscript.

AUTHOR CONTRIBUTIONS

All authors contributed to idea generation, writing, and revision.

DECLARATION OF INTERESTS

The authors declare no competing interests.

REFERENCES

1. Walsh, J.C., Dicks, L.V., and Sutherland, W.J. (2015). The effect of scientific evidence on conservation practitioners' management decisions. Conserv. Biol. *29*, 88–98.

2. Kadykalo, A.N., Cooke, S.J., and Young, N. (2021). The role of western-based scientific, Indigenous and local knowledge in wildlife management and conservation. People Nat. (Hoboken). *3*, 610–626.

3. Kareiva, P., and Marvier, M. (2012). What is conservation science? Bioscience *62*, 962–969.

4. DeLong, D.C., Jr. (1996). Defining biodiversity. Wildl. Soc. Bull. 738–749.

5. Shea, K.; NCEAS Working Group On Population Management (1998). Management of populations in conservation, harvesting and control. Trends Ecol. Evol. *13*, 371–375.

6. Mills, L.S. (2012). Conservation of Wildlife Populations: Demography, Genetics, and Management (John Wiley & Sons).

7. Moritz, C. (1994). Defining 'evolutionarily significant units' for conservation. Trends Ecol. Evol. *9*, 373–375.

8. A. Hastings, ed. (2013). Population biology: concepts and models (Springer Science & Business Media).

9. Witmer, G.W. (2005). Wildlife population monitoring: some practical considerations. Wildl. Res. *32*, 259–263.

10. Rodrigues, A.S.L., Pilgrim, J.D., Lamoreux, J.F., Hoffmann, M., and Brooks, T.M. (2006). The value of the IUCN Red List for conservation. Trends Ecol. Evol. *21*, 71–76.

11. Green, R.E. (2008). Diagnosing causes of bird population declines. Ibis *137*, S47–S55.

12. Cooke, S.J., and O'Connor, C.M. (2010). Making conservation physiology relevant to policy makers and conservation practitioners. Conserv. Lett. *3*, 159–166.

13. Gavin, T.A. (1991). Why ask" why": the importance of evolutionary biology in wildlife science. J. Wildl. Manage. *55*, 760–766.

14. Blumstein, D.T., and Fernández-Juricic, E. (2004). The emergence of conservation behavior. Conserv. Biol. *18*, 1175–1177.

15. Cooke, S.J., Blumstein, D.T., Buchholz, R., Caro, T., Fernández-Juricic, E., Franklin, C.E., Metcalfe, J., O'Connor, C.M., St Clair, C.C., Sutherland, W.J., and Wikelski, M. (2014). Physiology, behavior, and conservation. Physiol. Biochem. Zool. *87*, 1–14.

16. Dominoni, D.M., Halfwerk, W., Baird, E., Buxton, R.T., Fernández-Juricic, E., Fristrup, K.M., McKenna, M.F., Mennitt, D.J., Perkin, E.K., Seymoure, B.M., et al. (2020). Why conservation biology can benefit from sensory ecology. Nat. Ecol. Evol. *4*, 502–511.

17. Gabor, C.R., and Walls, S.C. (2020). Contributions of behavior and physiology to conservation biology. Front. Ecol. Evol. *8*, 33.

18. Illari, P.M., and Williamson, J. (2012). What is a mechanism? thinking about mechanisms across the sciences. Eur. J. Philos. Sci. *2*, 119–135.

19. Craver, C.F. (2005). Beyond reduction: mechanisms, multifield integration and the unity of neuroscience. Stud. Hist. Philos. Biol. Biomed. Sci. *36*, 373–395.

20. Bechtel, W., and Abrahamsen, A. (2005). Explanation: a mechanist alternative. Stud. Hist. Philos. Biol. Biomed. Sci. *36*, 421–441.

21. Machamer, P., Darden, L., and Craver, C.F. (2000). Thinking about mechanisms. Philos. Sci. *67*, 1–25.

22. Connolly, S.R., Keith, S.A., Colwell, R.K., and Rahbek, C. (2017). Process, mechanism, and modeling in macroecology. Trends Ecol. Evol. *32*, 835–844.

23. Bertolaso, M., and Buzzoni, M. (2017). Causality and levels of explanation in biology. In Philosophical and scientific perspectives on downward causation (Routledge), pp. 164–179.

24. Feder, M.E., Bennett, A.F., and Huey, R.B. (2000). Evolutionary physiology. Annu. Rev. Ecol. Syst. *31*, 315–341.

25. Irschick, D.J., Meyers, J.J., Husak, J.F., and Le Galliard, J.F. (2008). How does selection operate on whole-organism functional

performance capacities? a review and synthesis. Evol. Ecol. Res. *10*, 177–196.

26. Ricklefs, R.E., and Wikelski, M. (2002). The physiology/life-history nexus. Trends Ecol. Evol. *17*, 462–468.

27. Kerr, S.R. (1990). The fry paradigm: its significance for contemporary ecology. Trans. Am. Fish. Soc. *119*, 779–785.

28. Gilmour, K.M., Wilson, R.W., and Sloman, K.A. (2005). The integration of behaviour into comparative physiology. Physiol. Biochem. Zool. *78*, 669–678.

29. Spicer, J., and Gaston, K. (2009). Physiological Diversity: Ecological Implications (John Wiley & Sons).

30. Mascia, M.B., Brosius, J.P., Dobson, T.A., Forbes, B.C., Horowitz, L., McKean, M.A., and Turner, N.J. (2003). Conservation and the social sciences. Conserv. Biol. *17*, 649–650.

31. Fry, F.E.J. (1947). Effects of the environment on animal activity. In University of Toronto Studies Biological Series, *55* (Publications of the·Ontario Fisheries Research Laboratory), pp. 1–52.

32. Kronfeld-Schor, N., and Dayan, T. (2013). Thermal ecology, environments, communities, and global change: energy intake and expenditure in endotherms. Annu. Rev. Ecol. Evol. Syst. *44*, 461–480.

33. Kassahn, K.S., Crozier, R.H., Pörtner, H.O., and Caley, M.J. (2009). Animal performance and stress: responses and tolerance limits at different levels of biological organisation. Biol. Rev. Camb. Philos. Soc. *84*, 277–292.

34. Seebacher, F., and Franklin, C.E. (2012). Determining environmental causes of biological effects: the need for a mechanistic physiological dimension in conservation biology. Philos. Trans. R. Soc. Lond. B Biol. Sci. *367*, 1607–1614. https://doi.org/10.1098/rstb.2012.0036.

35. Cooke, S.J., Sack, L., Franklin, C.E., Farrell, A.P., Beardall, J., Wikelski, M., and Chown, S.L. (2013). What is conservation physiology? Perspectives on an increasingly integrated and essential science. Conserv. Physiol. *1*, cot001.

36. DeCesare, N.J., Hebblewhite, M., Robinson, H.S., and Musiani, M. (2010). Endangered, apparently: the role of apparent competition in endangered species conservation. Anim. Conserv. *13*, 353–362.

37. Bagchi, R., Brown, L.M., Elphick, C.S., Wagner, D.L., and Singer, M.S. (2018). Anthropogenic fragmentation of landscapes: mechanisms for eroding the specificity of plant–herbivore interactions. Oecologia *187*, 521–533.

38. Rizzoli, A., Tagliapietra, V., Cagnacci, F., Marini, G., Arnoldi, D., Rosso, F., and Rosà, R. (2019). Parasites and wildlife in a changing world: the vector-host-pathogen interaction as a learning case. Int. J. Parasitol. Parasites Wildl. *9*, 394–401.

39. Tattersall, G.J., Sinclair, B.J., Withers, P.C., Fields, P.A., Seebacher, F., Cooper, C.E., and Maloney, S.K. (2012). Coping with thermal challenges: physiological adaptations to environmental temperatures. Compr. Physiol. *2*, 2151–2202. https://doi.org/10.1002/cphy.c110055.

40. Kelly, A.M., and Vitousek, M.N. (2017). Dynamic modulation of sociality and aggression: an examination of plasticity within endocrine and neuroendocrine systems. Philos. Trans. R. Soc. Lond. B Biol. Sci. *372*, 20160243. https://doi.org/10.1098/rstb.2016.0243.

41. Seebacher, F., and Krause, J. (2019). Epigenetics of social behaviour. Trends Ecol. Evol. *34*, 818–830. https://doi.org/10.1016/j.tree.2019.04.017.

42. Smith, P., Arneth, A., Barnes, D.K.A., Ichii, K., Marquet, P.A., Popp, A., Pörtner, H.O., Rogers, A.D., Scholes, R.J., Strassburg, B., et al. (2022). How do we best synergize climate mitigation actions to co-benefit biodiversity? Glob. Chang. Biol. *28*, 2555–2577. https://doi.org/10.1111/gcb.16056.

43. Lamb, D., Erskine, P.D., and Parrotta, J.A. (2005). Restoration of degraded tropical forest landscapes. Science *310*, 1628–1632. https://doi.org/10.1126/science.1111773.

44. de Paula, F.R., Ruschel, A.R., Felizzola, J.F., Frauendorf, T.C., de Barros Ferraz, S.F., and Richardson, J.S. (2022). Seizing resilience windows to foster passive recovery in the forest-water interface in Amazonian lands. Sci. Total Environ. *828*, 154425. https://doi.org/10.1016/j.scitotenv.2022.154425.

45. Nielsen, R. (2009). Adaptionism - 30 years after gould and lewontin. Evolution *63*, 2487–2490. https://doi.org/10.1111/j.1558-5646.2009.00799.x.

46. Martin, R.A., Chick, L.D., Yilmaz, A.R., and Diamond, S.E. (2019). Evolution, not transgenerational plasticity, explains the adaptive divergence of acorn ant thermal tolerance across an urban–rural temperature cline. Evol. Appl. *12*, 1678–1687.

47. Tuholske, C., Caylor, K., Funk, C., Verdin, A., Sweeney, S., Grace, K., Peterson, P., and Evans, T. (2021). Global urban population exposure to extreme heat. Proc. Natl. Acad. Sci. USA *118*. e2024792118.

48. Lande, R. (1998). Anthropogenic, ecological and genetic factors in extinction and conservation. Popul. Ecol. *40*, 259–269.

49. Ouborg, N.J., Pertoldi, C., Loeschcke, V., Bijlsma, R.K., and Hedrick, P.W. (2010). Conservation genetics in transition to conservation genomics. Trends Genet. *26*, 177–187. https://doi.org/10.1016/j.tig.2010.01.001.

50. Hoffmann, A.A., and Willi, Y. (2008). Detecting genetic responses to environmental change. Nat. Rev. Genet. *9*, 421–432.

51. Perez, M.F., and Lehner, B. (2019). Intergenerational and transgenerational epigenetic inheritance in animals. Nat. Cell Biol. *21*, 143–151. https://doi.org/10.1038/s41556-018-0242-9.

52. Burggren, W. (2018). Developmental phenotypic plasticity helps bridge stochastic weather events associated with climate change. J. Exp. Biol. *221*, jeb161984–jeb161989. https://doi.org/10.1242/jeb.161984.

53. Guderley, H. (1990). Functional significance of metabolic responses to thermal acclimation in fish muscle. Am. J. Physiol. *259*, 245–252.

54. Allis, C.D., and Jenuwein, T. (2016). The molecular hallmarks of epigenetic control. Nat. Rev. Genet. *17*, 487–500.

55. Loughland, I., Little, A., and Seebacher, F. (2021). DNA methyltransferase 3a mediates developmental thermal plasticity. BMC Biol. *19*, 11.

56. Peserico, A., and Simone, C. (2011). Physical and functional HAT/HDAC interplay regulates protein acetylation balance. J. Biomed. Biotechnol. *2011*, 1–10. https://doi.org/10.1016/j.cell.2003.08.008.

57. Seebacher, F., and Simmonds, A.I.M. (2019). Histone deacetylase activity mediates thermal plasticity in zebrafish (Danio rerio). Sci. Rep. *9*, 8216. https://doi.org/10.1038/s41598-019-44726-x.

58. Beaman, J.E., White, C.R., and Seebacher, F. (2016). Evolution of plasticity: mechanistic link between development and reversible acclimation. Trends Ecol. Evol. *31*, 237–249.

59. Eliason, E.J., Clark, T.D., Hague, M.J., Hanson, L.M., Gallagher, Z.S., Jeffries, K.M., Gale, M.K., Patterson, D.A., Hinch, S.G., and Farrell, A.P. (2011). Differences in thermal tolerance among sockeye salmon populations. Science *332*, 109–112.

60. Wilson, R.S., and Franklin, C.E. (2002). Testing the beneficial acclimation hypothesis. Trends Ecol. Evol. *17*, 66–70. https://doi.org/10.1016/s0169-5347(01)02384-9.

61. Bateson, P., Gluckman, P., and Hanson, M. (2014). The biology of developmental plasticity and the Predictive Adaptive Response hypothesis. J. Physiol. *592*, 2357–2368. https://doi.org/10.1113/jphysiol.2014.271460.

62. Lailvaux, S.P., and Husak, J.F. (2017). Predicting life-history trade-offs with whole-organism performance. Integr. Comp. Biol. *57*, 325–332. https://doi.org/10.1093/icb/icx073.

63. Madliger, C.L., Love, O.P., Hultine, K.R., and Cooke, S.J. (2018). The conservation physiology toolbox: status and opportunities. Conserv. Physiol. *6*, coy029. https://doi.org/10.1093/conphys/coy029.

64. Wikelski, M., and Cooke, S.J. (2006). Conservation physiology. Trends Ecol. Evol.

21, 38–46. https://doi.org/10.1016/j.tree.2005.10.018.

65. Pecl, G.T., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.-C., Clark, T.D., Colwell, R.K., Danielsen, F., Evengård, B., et al. (2017). Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. Science *355*. eaai9214-11. https://doi.org/10.1126/science.aai9214.

66. Stuart-Smith, R.D., Edgar, G.J., and Bates, A.E. (2017). Thermal limits to the geographic distributions of shallow-water marine species. Nat. Ecol. Evol. *1*, 1846–1852. https://doi.org/10.1038/s41559-017-0353-x.

67. Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., De Siqueira, M.F., Grainger, A., Hannah, L., et al. (2004). Extinction risk from climate change. Nature *427*, 145–148.

68. Evans, T.G., Diamond, S.E., and Kelly, M.W. (2015). Mechanistic species distribution modelling as a link between physiology and conservation. Conserv. Physiol. *3*, cov056. https://doi.org/10.1093/conphys/cov056.

69. Ibáñez, I., Diez, J.M., Miller, L.P., Olden, J.D., Sorte, C.J.B., Blumenthal, D.M., Bradley, B.A., D'Antonio, C.M., Dukes, J.S., Early, R.I., et al. (2014). Integrated assessment of biological invasions. Ecol. Appl. *24*, 25–37.

70. Kearney, M., and Porter, W. (2009). Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecol. Lett. *12*, 334–350.

71. Benito Garzón, M., Robson, T.M., and Hampe, A. (2019). ΔTrait SDMs: species distribution models that account for local adaptation and phenotypic plasticity. New Phytol. *222*, 1757–1765.

72. Muñoz, A.R., Márquez, A.L., 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*, 2359–2373.

73. Capblancq, T., Fitzpatrick, M.C., Bay, R.A., Exposito-Alonso, M., and Keller, S.R. (2020). Genomic prediction of (mal)adaptation across current and future climatic landscapes. Annu. Rev. Ecol. Evol. Syst. *51*, 245–269.

74. Caporale, N., Leemans, M., Birgersson, L., Germain, P.-L., Cheroni, C., Borbély, G., Engdahl, E., Lindh, C., Bressan, R.B., Cavallo, F., et al. (2022). From cohorts to molecules: adverse impacts of endocrine disrupting mixtures. Science *375*, eabe8244. https://doi.org/10.1126/science.abe8244.

75. Wu, N.C., and Seebacher, F. (2020). Effect of the plastic pollutant bisphenol A on the biology of aquatic organisms: a meta-analysis. Glob. Chang. Biol. *26*, 3821–3833. https://doi.org/10.1111/gcb.15127.

76. Orr, J.A., Vinebrooke, R.D., Jackson, M.C., Kroeker, K.J., Kordas, R.L., Mantyka-Pringle, C., Van den Brink, P.J., De Laender, F., Stoks, R., Holmstrup, M., et al. (2020). Towards a unified study of multiple stressors: divisions and common goals across research disciplines. Proc. Biol. Sci. *287*, 20200421.

77. Côté, I.M., Darling, E.S., and Brown, C.J. (2016). Interactions among ecosystem stressors and their importance in conservation. Proc. Biol. Sci. *283*, 20152592.

78. Schäfer, R.B., and Piggott, J.J. (2018). Advancing understanding and prediction in multiple stressor research through a mechanistic basis for null models. Glob. Chang. Biol. *24*, 1817–1826.

79. Swaisgood, R.R. (2007). Current status and future directions of applied behavioral research for animal welfare and conservation. Appl. Anim. Behav. Sci. *102*, 139–162.

80. Berger-Tal, O., Polak, T., Oron, A., Lubin, Y., Kotler, B.P., and Saltz, D. (2011). Integrating animal behavior and conservation biology: a conceptual framework. Behav. Ecol. *22*, 236–239.

81. C.L. Madliger, C.E. Franklin, O.P. Love, and S.J. Cooke, eds. (2020). Conservation Physiology: Applications for Wildlife Conservation and Management (Oxford University Press).

82. Amiard-Triquet, C. (2009). Behavioral disturbances: the missing link between sub-organismal and supra-organismal responses to stress? prospects based on aquatic research. Hum. Ecol. Risk Assess. *15*, 87–110.

83. Madliger, C.L., Franklin, C.E., Chown, S.L., Fuller, A., Hultine, K.R., Costantini, D., Hopkins, W.A., Peck, M.A., Rummer, J.L., Sack, L., et al. (2021). The second warning to humanity: contributions and solutions from conservation physiology. Conserv. Physiol. *9*, coab038. https://doi.org/10.1093/conphys/coab038.

84. Hettyey, A., Ujszegi, J., Herczeg, D., Holly, D., Vörös, J., Schmidt, B.R., and Bosch, J. (2019). Mitigating disease impacts in amphibian populations: capitalizing on the thermal optimum mismatch between a pathogen and its host. Front. Ecol. Evol. *7*. https://doi.org/10.3389/fevo.2019.00254.

85. Willis, C.K.R. (2015). Conservation physiology and conservation pathogens: white-nose syndrome and integrative biology for host–pathogen systems. Integr. Comp. Biol. *55*, 631–641.

86. Green, S.J., Brookson, C.B., Hardy, N.A., and Crowder, L.B. (2022). Trait-based approaches to global change ecology: moving from description to prediction. Proc. Biol. Sci. *289*, 20220071. https://doi.org/10.1098/rspb.2022.0071.

87. Bernal, D., Brill, R.W., Dickson, K.A., and Shiels, H.A. (2017). Sharing the water column: physiological mechanisms underlying species-specific habitat use in tunas. Rev. Fish Biol. Fish. *27*, 843–880.

88. Madigan, D.J., Shipley, O.N., and Hussey, N.E. (2021). Applying isotopic clocks to identify prior migration patterns and critical habitats in mobile marine predators. In Conservation Physiology: Applications for Wildlife Conservation and Management, pp. 69–85.

89. Neel, L.K., Logan, M.L., Nicholson, D.J., Miller, C., Chung, A.K., Maayan, I., Degon, Z., DuBois, M., Curlis, J.D., Taylor, Q., et al. (2021). Habitat structure mediates vulnerability to climate change through its effects on thermoregulatory behavior. Biotropica *53*, 1121–1133.

90. Sunday, J.M., Bates, A.E., Kearney, M.R., Colwell, R.K., Dulvy, N.K., Longino, J.T., and Huey, R.B. (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. Proc. Natl. Acad. Sci. USA *111*, 5610–5615.

91. Moran, C.J., O'Neill, M., and Gibb, A.C. (2020). Integrating studies of anatomy, physiology, and behavior into conservation strategies for the imperiled cyprinid fishes of the southwestern United States. Integr. Comp. Biol. *60*, 487–496.

92. Turko, A.J., Leclair, A.T., Mandrak, N.E., Drake, D.A.R., Scott, G.R., and Pitcher, T.E. (2021). Choosing source populations for conservation reintroductions: lessons from variation in thermal tolerance among populations of the imperilled redside dace. Can. J. Fish. Aquat. Sci. *78*, 1347–1355.

93. Tetzlaff, S.J., Sperry, J.H., and DeGregorio, B.A. (2019). Effects of antipredator training, environmental enrichment, and soft release on wildlife translocations: a review and meta-analysis. Biol. Conserv. *236*, 324–331.

94. Wielebnowski, N., and Brown, J.L. (1998). Behavioral correlates of physiological estrus in cheetahs. Zoo Biol. *17*, 193–209.

95. Narayan, E., Baskaran, N., and Vaz, J. (2017). Conservation physiology of tigers in zoos: integrating stress physiology and behaviour to monitor their health and welfare. In Big Cats (IntechOpen), pp. 35–44.

96. Mason, G.J., and Veasey, J.S. (2010). How should the psychological well-being of zoo elephants be objectively investigated? Zoo Biol. *29*, 237–255.

97. Lennox, R.J., Chapman, J.M., Souliere, C.M., Tudorache, C., Wikelski, M., Metcalfe, J.D., and Cooke, S.J. (2016). Conservation physiology of animal migration. Conserv. Physiol. *4*, cov072. https://doi.org/10.1093/conphys/cov072.

98. Borowiec, B.G., Docker, M.F., Johnson, N.S., Moser, M.L., Zielinski, B., and Wilkie, M.P. (2021). Exploiting the physiology of lampreys to refine methods of control and conservation. J. Great Lakes Res. *47*, S723–S741.

99. Elmer, L.K., Madliger, C.L., Blumstein, D.T., Elvidge, C.K., Fernández-Juricic, E., Horodysky, A.Z., Johnson, N.S., McGuire, L.P., Swaisgood, R.R., and Cooke, S.J. (2021). Exploiting common senses: sensory ecology meets wildlife conservation and

management. Conserv. Physiol. *9*, coab002. https://doi.org/10.1093/conphys/coab002.

100. Cooke, S.J., Hinch, S.G., Farrell, A.P., Lapointe, M.F., Jones, S.R., Macdonald, J.S., Patterson, D.A., Healey, M., and Van Der Kraak, G. (2004). Abnormal migration timing and high en route mortality of sockeye salmon in the Fraser River, British Columbia. Fisheries *29*, 22–33.

101. Hinch, S.G., Cooke, S.J., Farrell, A.P., Miller, K.M., Lapointe, M., and Patterson, D.A. (2012). Dead fish swimming: a review of research on the early migration and high premature mortality in adult Fraser River sockeye salmon Oncorhynchus nerka. J. Fish. Biol. *81*, 576–599.

102. Miller, K.M., Li, S., Kaukinen, K.H., Ginther, N., Hammill, E., Curtis, J.M.R., Patterson, D.A., Sierocinski, T., Donnison, L., Pavlidis, P., et al. (2011). Genomic signatures predict migration and spawning failure in wild Canadian salmon. Science *331*, 214–217.

103. Farrell, A.P., Hinch, S.G., Cooke, S.J., Patterson, D.A., Crossin, G.T., Lapointe, M., and Mathes, M.T. (2008). Pacific salmon in hot water: applying aerobic scope models and biotelemetry to predict the success of spawning migrations. Physiol. Biochem. Zool. *81*, 697–708.

104. Davis, M.W. (2010). Fish stress and mortality can be predicted using reflex impairment. Fish Fish. *11*, 1–11.

105. Raby, G.D., Donaldson, M.R., Hinch, S.G., Patterson, D.A., Lotto, A.G., Robichaud, D., English, K.K., Willmore, W.G., Farrell, A.P., Davis, M.W., and Cooke, S.J. (2012). Validation of reflex indicators for measuring vitality and predicting the delayed mortality of wild coho salmon bycatch released from fishing gears. J. Appl. Ecol. *49*, 90–98.

106. Cooke, S.J., Hinch, S.G., Donaldson, M.R., Clark, T.D., Eliason, E.J., Crossin, G.T., Raby, G.D., Jeffries, K.M., Lapointe, M., Miller, K., et al. (2012). Conservation physiology in practice: how physiological knowledge has improved our ability to sustainably manage Pacific salmon during up-river migration. Philos. Trans. R. Soc. Lond. B Biol. Sci. *367*, 1757–1769.

107. Patterson, D.A., Cooke, S.J., Hinch, S.G., Robinson, K.A., Young, N., Farrell, A.P., and Miller, K.M. (2016). A perspective on physiological studies supporting the provision of scientific advice for the management of Fraser River sockeye salmon (Oncorhynchus nerka). Conserv. Physiol. *4*, cow026.

108. Scheele, B.C., Pasmans, F., Skerratt, L.F., Berger, L., Martel, A., Beukema, W., Acevedo, A.A., Burrowes, P.A., Carvalho, T., Catenazzi, A., et al. (2019). Amphibian fungal panzootic causes catastrophic and ongoing loss of biodiversity. Science *363*, 1459–1463. https://doi.org/10.1126/science.aav0379.

109. James, T.Y., Toledo, L.F., Rödder, D., da Silva Leite, D., Belasen, A.M., Betancourt-Román, C.M., Jenkinson, T.S., Soto-Azat, C., Lambertini, C., Longo, A.V., et al. (2015). Disentangling host, pathogen, and environmental determinants of a recently emerged wildlife disease: lessons from the first 15 years of amphibian chytridiomycosis research. Ecol. Evol. *5*, 4079–4097. https://doi.org/10.1002/ece3.1672.

110. Olson, D.H., Aanensen, D.M., Ronnenberg, K.L., Powell, C.I., Walker, S.F., Bielby, J., Garner, T.W.J., Weaver, G.; Bd Mapping Group, and Fisher, M.C. (2013). Mapping the global emergence of Batrachochytrium dendrobatidis, the amphibian chytrid fungus. PLoS One *8*, e56802. https://doi.org/10.1371/journal.pone.0056802.

111. Kriger, K.M., and Hero, J.-M. (2007). The chytrid fungus Batrachochytrium dendrobatidis is non-randomly distributed across amphibian breeding habitats. Divers. Distrib. *13*, 781–788. https://doi.org/10.1111/j.1472-4642.2007.00394.x.

112. Rödder, D., Kielgast, J., and Lötters, S. (2010). Future potential distribution of the emerging amphibian chytrid fungus under anthropogenic climate change. Dis. Aquat. Organ. *92*, 201–207. https://doi.org/10.3354/dao02197.

113. Miller, C.A., Tasse Taboue, G.C., Ekane, M.M.P., Robak, M., Sesink Clee, P.R., Richards-Zawacki, C., Fokam, E.B., Fuashi, N.A., and Anthony, N.M. (2018). Distribution modeling and lineage diversity of the chytrid fungus Batrachochytrium dendrobatidis (Bd) in a central African amphibian hotspot. PLoS One *13*, e0199288. https://doi.org/10.1371/journal.pone.0199288.

114. Murray, K.A., Retallick, R.W.R., Puschendorf, R., Skerratt, L.F., Rosauer, D., McCallum, H.I., Berger, L., Speare, R., and VanDerWal, J. (2011). Assessing spatial patterns of disease risk to biodiversity: implications for the management of the amphibian pathogen, Batrachochytrium dendrobatidis. J. Appl. Ecol. *48*, 163–173. https://doi.org/10.1111/j.1365-2664.2010.01890.x.

115. Savage, A.E., Sredl, M.J., and Zamudio, K.R. (2011). Disease dynamics vary spatially and temporally in a North American amphibian. Biol. Conserv. *144*, 1910–1915. https://doi.org/10.1016/j.biocon.2011.03.018.

116. Raffel, T.R., Michel, P.J., Sites, E.W., and Rohr, J.R. (2010). What drives chytrid infections in newt populations? Associations with substrate, temperature, and shade. EcoHealth *7*, 526–536.

117. Woodhams, D.C., Geiger, C.C., Reinert, L.K., Rollins-Smith, L.A., Lam, B., Harris, R.N., Briggs, C.J., Vredenburg, V.T., and Voyles, J. (2012). Treatment of amphibians infected with chytrid fungus: learning from failed trials with itraconazole, antimicrobial peptides, bacteria, and heat therapy. Dis. Aquat. Organ. *98*, 11–25. https://doi.org/10.3354/dao02429.

118. Wu, N.C., Cramp, R.L., and Franklin, C.E. (2018). Body size influences energetic and osmoregulatory costs in frogs infected with Batrachochytrium dendrobatidis. Sci. Rep. *8*, 3739. https://doi.org/10.1038/s41598-018-22002-8.

119. Ohmer, M.E.B., Cramp, R.L., White, C.R., Harlow, P.S., McFadden, M.S., Merino-Viteri, A., Pessier, A.P., Wu, N.C., Bishop, P.J., and Franklin, C.E. (2019). Phylogenetic investigation of skin sloughing rates in frogs: relationships with skin characteristics and disease-driven declines. Proc. Biol. Sci. *286*, 20182378. https://doi.org/10.1098/rspb.2018.2378.

120. Ohmer, M.E., Cramp, R.L., White, C.R., and Franklin, C.E. (2015). Skin sloughing rate increases with chytrid fungus infection load in a susceptible amphibian. Funct. Ecol. *29*, 674–682. https://doi.org/10.1111/1365-2435.12370.

121. Richards-Zawacki, C.L. (2010). Thermoregulatory behaviour affects prevalence of chytrid fungal infection in a wild population of Panamanian golden frogs. Proc. Biol. Sci. *277*, 519–528. https://doi.org/10.1098/rspb.2009.1656.

122. McMahon, T.A., Hill, M.N., Lentz, G.C., Scott, E.F., Tenouri, N.F., and Rohr, J.R. (2021). Amphibian species vary in their learned avoidance response to the deadly fungal pathogen Batrachochytrium dendrobatidis. J. Appl. Ecol. *58*, 1613–1620. https://doi.org/10.1111/1365-2664.13932.

123. Woodhams, D.C., Alford, R.A., and Marantelli, G. (2003). Emerging disease of amphibians cured by elevated body temperature. Dis. Aquat. Organ. *55*, 65–67. https://doi.org/10.3354/dao055065.

124. Bosch, J., Sanchez-Tomé, E., Fernández-Loras, A., Oliver, J.A., Fisher, M.C., and Garner, T.W.J. (2015). Successful elimination of a lethal wildlife infectious disease in nature. Biol. Lett. *11*, 20150874. https://doi.org/10.1098/rsbl.2015.0874.

125. Scheele, B.C., Hollanders, M., Hoffmann, E.P., Newell, D.A., Lindenmayer, D.B., McFadden, M., Gilbert, D.J., and Grogan, L.F. (2021). Conservation translocations for amphibian species threatened by chytrid fungus: a review, conceptual framework, and recommendations. Conserv. Sci. Pract. *3*, e524. https://doi.org/10.1111/csp2.524.

126. Doherty, T.S., Glen, A.S., Nimmo, D.G., Ritchie, E.G., and Dickman, C.R. (2016). Invasive predators and global biodiversity loss. Proc. Natl. Acad. Sci. USA *113*, 11261–11265.

127. Kumschick, S., Gaertner, M., Vilà, M., Essl, F., Jeschke, J.M., Pyšek, P., Ricciardi, A., Bacher, S., Blackburn, T.M., Dick, J.T., et al. (2015). Ecological impacts of alien species: quantification, scope, caveats, and recommendations. Bioscience *65*, 55–63.

128. Ogden, N.H., Wilson, J.R.U., Richardson, D.M., Hui, C., Davies, S.J., Kumschick, S., Le Roux, J.J., Measey, J., Saul, W.C., and Pulliam, J.R.C. (2019). Emerging infectious diseases and biological invasions: a call for a One Health collaboration in science and management. R. Soc. Open Sci. *6*, 181577.

129. Jones, B.A. (2017). Invasive species impacts on human well-being using the life satisfaction index. Ecol. Econ. *134*, 250–257.

130. Cuthbert, R.N., Pattison, Z., Taylor, N.G., Verbrugge, L., Diagne, C., Ahmed, D.A., Leroy, B., Angulo, E., Briski, E., Capinha, C., et al. (2021). Global economic costs of aquatic invasive alien species. Sci. Total Environ. *775*, 145238.

131. Thompson, B.K., Olden, J.D., and Converse, S.J. (2021). Mechanistic invasive species management models and their application in conservation. Conserv. Sci. Pract. *3*, e533.

132. Baker, C.M., and Bode, M. (2021). Recent advances of quantitative modeling to support invasive species eradication on islands. Conserv. Sci. Pract. *3*, e246.

133. Grechi, I., Chadès, I., Buckley, Y.M., Friedel, M.H., Grice, A.C., Possingham, H.P., van Klinken, R.D., and Martin, T.G. (2014). A decision framework for management of conflicting production and biodiversity goals for a commercially valuable invasive species. Agric. Syst. *125*, 1–11. https://doi.org/10.1016/j.agsy.

134. Schmolke, A., Thorbek, P., DeAngelis, D.L., and Grimm, V. (2010). Ecological models supporting environmental decision making: a strategy for the future. Trends Ecol. Evol. *25*, 479–486.

135. Gamliel, I., Buba, Y., Guy-Haim, T., Garval, T., Willette, D., Rilov, G., and Belmaker, J. (2020). Incorporating physiology into species distribution models moderates the projected impact of warming on selected Mediterranean marine species. Ecography *43*, 1090–1106.

136. Converse, S.J. (2020). Introduction to multi-criteria decision analysis. In Structured decision making: Case studies in natural resource management, M.C. Runge, S.J. Converse, and J.E. Lyons, eds. (Johns Hopkins University Press), pp. 51–61.

137. Pepin, K.M., Smyser, T.J., Davis, A.J., Miller, R.S., McKee, S., VerCauteren, K.C., Kendall, W., and Slootmaker, C. (2020). Optimal spatial prioritization of control resources for elimination of invasive species under demographic uncertainty. Ecol. Appl. *30*, e02126. https://doi.org/10.1002/eap.2126.

138. White, C.R., Marshall, D.J., Chown, S.L., Clusella-Trullas, S., Portugal, S.J., Franklin, C.E., and Seebacher, F. (2021). Geographical bias in physiological data limits predictions of global change impacts. Funct. Ecol. *35*, 1572–1578.

139. Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T., Regan, T.J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., et al. (2013). Predicting species distributions for conservation decisions. Ecol. Lett. *16*, 1424–1435.

140. Buckley, L.B., Urban, M.C., Angilletta, M.J., Crozier, L.G., Rissler, L.J., and Sears, M.W. (2010). Can mechanism inform species' distribution models? Ecol. Lett. *13*, 1041–1054.

141. Fuller, A., Mitchell, D., Maloney, S.K., Hetem, R.S., Fonsêca, V.F.C., Meyer, L.C.R., van de Ven, T.M.F.N., and Snelling, E.P. (2021). How dryland mammals will respond to climate change: the effects of body size, heat load, and a lack of food and water. J. Exp. Biol. *224*, jeb238113. https://doi.org/10.1242/jeb.238113.

142. Conradie, S.R., Woodborne, S.M., Cunningham, S.J., and McKechnie, A.E. (2019). Chronic, sublethal effects of high temperatures will cause severe declines in southern African arid-zone birds during the 21st century. Proc. Natl. Acad. Sci. USA *116*, 14065–14070. https://doi.org/10.1073/pnas.1821312116.

143. van de Ven, T.M.F.N., Fuller, A., and Clutton-Brock, T.H. (2020). Effects of climate change on pup growth and survival in a cooperative mammal, the meerkat. Funct. Ecol. *34*, 194–202. https://doi.org/10.1111/1365-2435.13468.

144. Ellis, R.D., McWhorter, T.J., and Maron, M. (2012). Integrating landscape ecology and conservation physiology. Landsc. Ecol. *27*, 1–12.

145. Pedroza-Arceo, N.M., Weber, N., and Ortega-Argueta, A. (2022). A knowledge review on integrated landscape approaches. Forests *13*, 312. https://doi.org/10.3390/f13020312.

146. Guerrero, P., Haase, D., and Albert, C. (2022). Identifying spatial patterns and ecosystem service delivery of nature-based solutions. Environ. Manage. *69*, 735–751. https://doi.org/10.1007/s00267-022-01613-y.

147. Shochat, E., Warren, P.S., Faeth, S.H., McIntyre, N.E., and Hope, D. (2006). From patterns to emerging processes in mechanistic urban ecology. Trends Ecol. Evol. *21*, 186–191.

148. Goswami, V.R., Medhi, K., Nichols, J.D., and Oli, M.K. (2015). Mechanistic understanding of human–wildlife conflict through a novel application of dynamic occupancy models. Conserv. Biol. *29*, 1100–1110.