CHAPTER 1

The history, goals, and application of conservation physiology

Christine L. Madliger, Oliver P. Love, Steven J. Cooke, and Craig E. Franklin

1.1 The history of combining animal physiology and conservation science

Although conservation physiology is often cited as one of the newest branches of conservation science (for an overview of conservation science writ large, see Soulé 1985), its foundation is formed by nearly 200 years of comparative animal physiology research. As that primarily laboratory-based discipline expanded into natural settings, the field of ecological (or environmental) physiology began to take shape. By the mid-1900s, scientists were characterizing how physiological adaptations allow organisms to prosper in extreme environments like deserts, the depths of the oceans, high altitudes, and the poles (Feder et al. 1997). Ecological physiology became increasingly interdisciplinary, drawing on molecular biology, evolutionary and life history theory, behavioural ecology, and natural history to characterize physiological diversity and adaptations across all environmental types and scales (Willmer et al. 2009). Given the capacity of this knowledge base, it is unsurprising that, as environmental movements gained traction in the 1960s, some scientists turned to physiology to discern the underlying mechanistic basis of widespread conservation issues. One prominent example is that of dichlorodiphenyltrichloroethane (DDT) causing reproductive failure in avian species, particularly large raptors such as bald eagles (*Haliaeetus leucocephalus*) and peregrine falcons (*Falco peregrinus*). It was the discovery of altered eggshell deposition dynamics—an interplay of reproductive physiology and toxicology (see Bitman et al. 1969; Jefferies 1969)—that provided some of the key evidence leading to pesticide bans in the United States, forming one of the earliest success stories in the field of conservation physiology.

Despite this success, it would be decades before researchers began to formally frame the process of integrating physiological tools into conservation science as a discipline in its own right. Much of the first published literature discussing the potential applications of physiology in conservation focused on endocrinology, in particular reproductive and stress physiology. For example, building off knowledge gained in captive breeding scenarios monitoring reproductive hormone levels, Berger et al. (1999) discussed the application of 'conservation endocrinology' for wild populations. By monitoring faecal progesterone levels, the authors determined that a low frequency of juvenile moose (*Alces alces*) in the Greater Yellowstone Ecosystem of the United States was not the result of increased predation by recolonizing wolves (*Canis lupus*) or grizzly bears (*Ursus arctus*), but instead was due to low pregnancy rates. It was therefore clear that physiology could help identify the underlying cause of population instability in a wild setting. In relatively close succession, Millspaugh and Washburn (2004), noting the increasing use of faecal glucocorticoid levels as indicators of 'stress' in wild animals, outlined numerous considerations for sample collection, processing, and interpretation that were specific to using this tool in conservation biology research. This work stressed just

Christine L. Madliger, Oliver P. Love, Steven J. Cooke, and Craig E. Franklin, *The history, goals, and application of conservation physiology*
In: *Conservation Physiology: Applications for Wildlife Conservation and Management*. Edited by: Christine L. Madliger, Craig E. Franklin, Oliver P. Love, and Steven J. Cooke, Oxford University Press (2021). © Oxford University Press. DOI: 10.1093/oso/9780198843610.003.0001

how important it is to have detailed knowledge of the role of any aspect of physiology in maintaining homeostasis (i.e. the value of validating tools for specific species and contexts) to employ a physiological metric as a conservation biomarker.

Conservation physiology became much more solidified in the mid-2000s as researchers came together to define its purpose and scope. In 2004, a symposium titled 'Ecophysiology and Conservation: The Contribution of Endocrinology and Immunology' at the Society for Integrative and Comparative Biology's annual meeting specifically showcased physiological research with conservation implications (Stevenson et al. 2005). Many of the associated papers from this symposium covered endocrine disruption in aquatic environments (Stevenson et al. 2005), reflecting the history of using physiological techniques to understand the effects of environmental toxins and pollutants. Soon after, Wikelski and Cooke (2006, p. 38) formally defined and described in detail the scope and goals of conservation physiology as an emerging, cogent discipline. Their definition stated that conservation physiology is, 'the study of physiological responses of organisms to human alteration of the environment that might cause or contribute to population declines'. Importantly, they stressed that one of the most valuable characteristics of conservation physiology is that it reaches beyond a description of patterns to provide information on the mechanism(s) underpinning a conservation issue.

The next major leap in the field came in 2013 with the launch of the dedicated journal *Conservation Physiology* by Oxford. For scientists sometimes facing difficulty fitting their research into the scope of existing journals, this became an outlet where studies could be published without having to tailor to either a solely physiological or conservation science-focused venue. The inaugural paper of the journal refined the definition of conservation physiology to be, 'an integrative scientific discipline applying physiological concepts, tools, and knowledge to characterizing biological diversity and its ecological implications; understanding and predicting how organisms, populations, and ecosystems respond to environmental change and stressors; and solving conservation problems across the broad range of taxa (i.e. including microbes, plants, and animals)' (Cooke et al. 2013, p. 2). This is an inherently broad definition that considers the diversity of physiological traits available, which span immunology/epidemiology, endocrinology, bioenergetics, cardiorespiratory physiology, physiological genomics, neuro- and sensory physiology, and toxicology (Cooke et al. 2013). The authors envisioned the discipline contributing to diverse conservation goals, including identifying strategies to rebuild populations, ecosystem restoration, conservation policy development, and

Table 1.1 The scope of conservation physiology. Adapted from Cooke et al. (2013).

Monitoring and identifying threats	Predicting change	Integrating with diverse disciplines	Achieving conservation success
Providing a mechanistic understanding of the effect of environmental change on organisms Understanding the influences of anthropogenic disturbance and variation in habitat quality on organism condition, health, and survival Understanding the physiological mechanisms involved in changes in community, ecosystem, and landscape structure, as well as individual species, in response to environmental change Evaluating stress responsiveness and environmental tolerances relative to environmental change (including climate change and ocean acidification) Applying physiological biomarkers as part of long-term environmental monitoring programmes	Developing mechanistic models for species distributions Developing mechanistic relationships between population declines and physiological processes Developing predictive models in conservation practices that include physiological parameters	Integration of physiology with conservation behaviour, conservation medicine, conservation toxicology, conservation genetics, and other relevant sub-disciplines Understanding the relevance of ecology and evolution of physiological diversity to conservation Understanding the relevance of acclimatization and adaptation of physiological processes to environmental variation to management and conservation Applications of contemporary genomic and post-genomic technologies to conservation physiology	Exploiting knowledge of organismal physiology to control invasive species and restore threatened habitats and populations Understanding the optimal environmental conditions for ex situ preservation of endangered species (e.g. captive breeding) Integrating physiological knowledge into ecosystem management and development of tools to solve complex conservation problems Evaluating and improving the success of various management and conservation interventions Understanding the policy implications of conservation physiology research

Figure 1.1 Conservation physiology successes cover a diversity of taxa, ecosystems, landscape scales, and physiological systems. (A) Birds of prey, such as osprey, have rebounded following regulations on DDT. (B) Plague is being combated in the endangered black-footed ferret via a targeted vaccination programme. (C) Caribou and wolf populations are being effectively managed via physiological monitoring of scat. (D) Nutrition programmes support successful breeding in the critically endangered kakapo. (E) Ecotourism feeding practices are regulated for stingrays in the Cayman Islands. (F) Sensory physiology has informed shoreline lighting regulations for nesting sea turtles. (G) Recovery chambers decrease the stress associated with bycatch in salmonids. (H) Physiological monitoring is improving translocation success in white rhino. Photo credits: (A) Randy Holland; (B) USGS NWHC; (C) Wayne Sawchuk, Samuel Wasser; (D) Kakapo Recovery; (E) Christina Semeniuk; (F) Sea Turtle Conservancy; (G) Cory Suski, Jude Isabella; and (H) Andrea Fuller. Reproduced with modification from Madliger et al. (2016).

natural resource management (Cooke et al. 2013; Table 1.1).

Over the past 15 years, conservation physiology has accrued measurable successes (Madliger et al. 2016, Cooke et al. 2020; Figure 1.1). It has not done so in isolation, but is often used in conjunction with tools and techniques from conservation behaviour, genetics, and/or social sciences. In this way, the discipline is becoming increasingly integrated into the broader conservation toolbox, enabling initiatives that support conservation actions for imperilled species (reactive approaches) and those that are part of sustainable management (proactive approaches) (Cooke et al. 2020). In the rest of this chapter, we briefly outline some of the benefits and applications conservation physiology has to offer, provide an overview of the current toolbox being used by researchers and practitioners, and discuss the layout and goals of the text.

1.2 What can conservation physiology offer?

1.2.1 An increasingly expanding and validated toolbox

The toolbox currently available to conservation physiologists is diverse and ever-expanding (Table 1.2). Endocrine tools have been the most heavily investigated in the context of conservation applications (Lennox et al. 2014; Madliger et al. 2018), with stress hormones (glucocorticoids such as cortisol and corticosterone) drawing the greatest attention. However, there has been a disconnect between the propensity with which stress hormones are measured for conservation purposes (e.g. inferring stress or disturbance in wild populations) and the number of resulting success stories (i.e. examples where measurement of the physiological trait resulted in a change in conservation policy, practice, or behaviour) (Madliger et al. 2016). As a result, we urge readers to consider conservation physiology in the most diverse manner possible, taking note that there are dozens of physiological traits in the toolbox (Madliger et al. 2018). To illustrate this diversity, Table 1.2 provides examples of many of the available tools partitioned by physiological sub-discipline, and the subsequent chapters in the text illustrate how many of these tools have been put into practice across a variety of animal taxa. Indeed, many metrics have the potential to fulfil a role in generating robust knowledge that can be integrated as decision-support tools for conservation science.

The potential for application of a vast array of traits becomes more realistic as researchers continue to validate tools across species and contexts and work to find techniques that are non-invasive or as minimally invasive as possible. For example, although the 'traditional' sample medium for a variety of reproductive, stress, and energetic hormones has been blood, there are now techniques to assess many hormone levels in saliva, urine, faeces, fur, feathers, claws, scales, shed skin, eggs, baleen, whale blow, ear wax, and water. Some of these sample types can be acquired without any handling or disturbance of an individual animal. For example, researchers obtained snags of hair from grizzly bears (*Ursus arctos*) to assess responses in reproductive and stress physiology to changing nutritional quality (Bryan et al. 2013). Faeces can similarly be collected entirely non-invasively from many organisms in the field. Hunninck et al. (2020) analysed glucocorticoid levels in faecal samples from wild ranging impala (*Aepyceros melampus*) paired with an indicator of forage quality (normalized difference vegetation index—NDVI) and determined that climate-induced changes in vegetation represent a larger disturbance than human-related land-use changes. Excitingly, some sample media also give us retrospective glimpses into physiological functioning long before the sample is collected; for example, whale baleen provides a cross-section of reproductive and stress hormone level changes across the decades in which it was grown (Hunt et al. 2014; Hunt et al., Chapter 12, this volume). This ability to reconstruct a species past history can even reveal where an animal has lived and its broad-scale movement patterns. Madigan et al. (Chapter 5, this volume) highlight the value of harnessing stable isotope analyses of various tissues (e.g. muscle, liver, erythrocytes, and plasma) that have different turnover rates and the geographical variation of isotopic signatures (i.e. isoscapes) to reveal migration patterns and habitat use of overexploited Pacific bluefin tuna (*Thunnus orientalis*).

Table 1.2 Physiological sub-disciplines, ways each can contribute to conservation science, and examples of common tools/techniques. Adapted from Cooke et al. (2013) and Madliger et al. (2018).

Physiological sub-discipline	Examples of contributions to conservation physiology	Examples of tools
Bioenergetics, metabolic, and nutritional physiology	Assessing whole-organism response to environmental change; improving captive breeding and rehabilitation through adequate nutrition; monitoring conservation management scenarios; identifying mechanisms behind population decline	Body condition indices Daily energy expenditure Lipid and fatty acid concentrations Metabolic rate Plasma glucose Plasma lactate Stable isotopes *U*crit (prolonged swimming speed) Vitellogenin
Cardiorespiratory physiology	Predicting and monitoring responses to environmental change; predicting invasive species spread; predicting species distributions under climate change scenarios	Aerobic scope Haematocrit Haemoglobin concentration Heart rate Respiratory rate EPOC (excess post-exercise oxygen consumption)
Immunology/epidemiology	Predicting spread of diseases; design of control and vaccination programmes; determining sub-lethal consequences of environmental change	Disease state (e.g. serum total protein) Humoral and cell-mediate immune response Cytokines
Neurophysiology/sensory biology	Determining guidelines/optimal designs to reduce human–wildlife conflicts; understanding mechanisms behind behavioural responses to environmental change	Neural activity Electrical excitability Pheromones Sensory sensitivity/tolerance
Reproductive physiology	Identifying mechanisms behind population declines; improving captive breeding success; monitoring success of reintroduction programmes	Developmental rate Fecundity Reproductive hormone levels (e.g. oestrogen, testosterone, progesterone) Sperm motility
Stress physiology	Predicting and monitoring responses to environmental change; monitoring success of restoration programmes; identifying best practices for translocation; improving welfare in captive scenarios	Electrolyte balance Glucocorticoids (e.g. cortisol, corticosterone) Oxidative status/stress pH Telomere shortening
Thermal physiology	Determining organismal capacity to respond to climate change (e.g. thermal plasticity, range expansion); determining thermal dependence of performance and tolerances across various environmental conditions; predicting potential limitations of invasive species spread	Thermal tolerance (e.g. CTMax, CTMin) Thermal performance curves Q_{10} Enzyme kinetics
Toxicology	Determining sources of population declines; delineating regulatory guidelines for chemicals/pollutants; designing remediation protocols	Pollutant/chemical contaminant concentration in various tissues Trace element/metal concentrations

There is also a great deal of capacity to assess stress, health, and physiological functioning at a variety of biological scales using the conservation physiology toolbox (Table 1.2), including 'gene expression (e.g. physiological genomics), gene products (e.g. physiological proteomics), cells (e.g. sperm physiology), individual tissues (e.g. muscle oxygenation), organs (e.g. heart rate) and the whole-organism (e.g. daily energy expenditure)' (Madliger et al. 2018, p. 5). As a result of the different scales that various physiological traits capture, their suitability for conservation questions and planning will also vary. For example, repeated individual measures of reproductive hormones can be useful for designing and improving captive breeding programmes focused around encouraging copulation, assessing reproductive potential, or improving artificial insemination practices in captivity (e.g. Swanson 2003; Dehnhard et al. 2008). Indeed, acquiring fundamental knowledge on reproductive physiology through non-invasive endocrine monitoring in killer whales (*Orcinus orca*) was necessary to develop the artificial insemination technology that resulted in the first successful conceptions (i.e. resulting in live offspring) in any cetacean species (Robeck et al. 2004). For highly vulnerable and endangered groups, like sea turtles, physiological biomarkers can also be used to understand physiological dysfunction and direct veterinary treatment options that aid in the rehabilitation of individuals (Innis and Dodge, Chapter 14, this volume; Narayan and Charalambous, Chapter 11, this volume). When conservation actions require capture and translocation of individual animals, the quantification of physiological biomarkers can ensure the health and safety of animals, such as the monitoring of arterial blood gases in white rhinos (*Ceratotherium simum*) that have been immobilized and anaesthetized (Haw et al., Chapter 17, this volume).

Other traits can be harnessed to understand conservation-relevant consequences within populations, such as how differences in immune function or energetics influence disease susceptibility and potential or realized population decline (e.g. Rohr et al. 2013; McCoy et al. 2017). Development and use of sensitive biomarkers and physiological approaches in the fight against emerging novel diseases is strongly advocated by Dzal and Willis (Chapter 9, this volume) and Ohmer et al. (Chapter 10, this volume). Determining the susceptibility of bats and amphibians to cutaneous fungal pathogens has been dependent on understanding the underlying physiology of the disease state, with applications for conservation strategy design to limit and treat disease spread within and across populations. Furthermore, other traits can be used for broader, macrophysiological applications (Chown and Gaston 2008). Assessments of metabolic scope have the power to determine environmental tolerance and therefore predict population ranges under climate change and/or the spread of invasive species across large spatial scales (e.g. Deutsch et al. 2015; Marras et al. 2015; Winwood-Smith et al. 2015).

In some conservation-relevant systems, researchers and practitioners can combine multiple physiological traits to solve problems across biological and spatial scales. In assessing the migration failure of Pacific salmon (*Oncorhynchus* genus), Cooke et al. (Chapter 3, this volume) highlight the value of the measurement of a suite of biomarkers that span levels of biological organization, from genomic to organismal, that are derived from both field- and laboratory-based studies. In this case, the measurement of multiple biomarkers provided a comprehensive understanding of physiological function and organismal performance, which in turn assists in better evaluating and predicting migration success or failure in salmon. The following sections and the chapters contained in this text will further illustrate many ways that physiology can provide both snapshots and longer-term assessments of animal stress, function, and health across biological, spatial, and temporal scales.

1.2.2 Sensitive biomarkers of organismal condition and health

Traditionally, physiological biomarkers have often been used as indicators of health, diagnosing the presence of a pathogen, and assessing severity of a disease state or pathological condition. Beyond this, physiological biomarkers are frequently used to determine the general welfare and condition of animals, with blood diagnostic tests quantifying immune function, endocrine function, oxygen transport capacity, nutritional/metabolic state, and electrolyte balance being common. As discussed above, conservation physiologists have developed an innovative and growing array of biomarkers to assess the health of organisms, identify threats, and ultimately aid in conservation efforts (Madliger et al. 2018; Cooke et al. 2020; Table 1.2). For biomarkers to be useful in evaluating the condition of animals, assessing and predicting how species perform in response to changing environmental conditions, or providing an indication of the health of an ecosystem, they must be sensitive to environmental changes of interest (Cooke et al. 2013, 2017a, 2020; Madliger et al. 2017). There are countless publications that investigate the sensitivity of various metrics of physiology to environmental conditions or the internal state of animals (e.g. reproductive status, development, age). Just in the most recent issue of the journal *Conservation Physiology* (Volume 8, 2020), we can find articles that link ocean acidification and warming to changes in the transcriptome of an Antarctic pteropod (*Limacina helicina antarctica*) (Johnson and Hofmann 2020); indicate zinc concentrations in walrus (*Odobenus rosmarus divergens*) teeth can reflect the onset of female reproductive maturity (Clark et al. 2020); show oxygen-carrying capacity is compromised under exposure to nitrate and low pH in perch (*Leiopotherapon unicolor*) (Gomez Isaza et al. 2020); and describe faecal cortisol and oestradiol concentrations varying with human disturbance in Asian elephants (*Elaphas maximus*) (Tang et al. 2020).

In every chapter of this book, sensitive biomarkers that assess physiological function, animal condition, and performance are described with concrete conservation applications. Specifically, biomarkers can help discriminate acute from chronic stress and identify specific stressors, with some of the more novel and ingenious techniques being able to assess physiological and health status of an organism in the absence of any physical sample taken from an animal. For example, Hunt et al. (Chapter 12, this volume) describe how droplets in the respiratory vapour of whales ('blow') can be collected by using a small aerial drone at the moment a whale exhales. The blow samples have been found to contain all major steroid and thyroid hormones, making them useful for health and reproductive monitoring across seasons and years.

Use of OMICS technologies (e.g. transcriptomics, gene expression) and generation of genomic/transcriptomic biomarkers can provide detailed mechanistic information that can cover an array of biological/physiological systems, including metabolic, digestive, and immune (Ge et al. 2013; McMahon et al. 2014; Bahamonde et al. 2016). In particular, information gained from genome-wide gene expression profiling (that generates large datasets) has been invaluable in diagnosing the health impacts of toxicants and chemical pollution (Trego et al., Chapter 7, this volume). These OMICS biomarkers can often be highly sensitive, detecting perturbations not easily revealed by more traditional biomarkers like stress hormones.

Sensitive physiological biomarkers can also provide red flags that show condition and reproductive health are changing in response to environmental variability. Crossin and Williams (Chapter 2, this volume) describe how yolk precursors, the primary sources of protein and lipid in egg yolk (e.g. vitellogenin), in the plasma of breeding birds can provide an assessment of the reproductive status of free-living birds. This approach is highly valuable in long-lived Arctic-breeding seabirds that would normally require large longitudinal datasets to ascertain a decline, resulting in delays that could make conservation approaches aimed at reversing declines much less effective. Further, because vitellogenin predictably and sensitively changes in relation to the environmental conditions that drive breeding decisions, a small blood sample can be taken prior to the commencement of egg laying and therefore avoid disturbing birds at times when they would abandon their nests. Alaux et al. (Chapter 4, this volume) further note that vitellogenin levels found in bees can provide an indication of tolerance to oxidative stress, an evaluation of immune defence, and ultimately could be used to provide an assessment of the effects of habitat enhancement and protection on bee health. These examples from birds and bees illustrate how a ubiquitous protein can provide useful conservation insights across vastly different taxonomic groups.

Organismal locomotor and performance traits (e.g. fish swimming speed, Wilson et al. 2001; Kern et al. 2018; frog jumping ability, Hudson & Franklin, 2002) are often not viewed as biomarkers, yet fundamentally they can provide an important measure of condition and health, but also locomotor capability. For example, Cramp et al. (Chapter 6, this volume) detail how measures of swimming performance can be effective in predicting the ability of fish to successfully transverse man-made structures, like culverts and fish ladders. Organismal performance traits can also elucidate impacts of environmental change. For example, determining the relationship between body temperature and performance in ectotherms can provide valuable insights into the impact of climate warming and the sensitivity of organisms to temperature increases, whether they are intertidal organisms (Helmuth, Chapter 13, this volume) or reptiles (Cree et al., Chapter 16, this volume).

1.2.3 Identification of underlying mechanisms of decline

Monitoring the abundance and vital rates of animal populations is fundamental to management and conservation (Krebs 1989). However, such information tends to only reveal that a problem exists (e.g. a population decline) rather than identifying the drivers or mechanistic basis for a decline. Associations (e.g. coincident with a decline in population was an increase in a given stressor) can be identified; yet, it is not possible to determine with any certainty if an association or correlation is spurious (Mayr 1961). In contrast, cause-and-effect relationships bring a level of certainty (Mayr 1961) that allows managers to identify optimal strategies and know that their efforts are focused on identifying threats that have a direct negative impact on organisms (Carey 2005; Cooke and O'Connor 2010; Seebacher and Franklin 2012). In this way, managers avoid mitigation strategies being put in place at later-than-optimal time points or wasting precious resources on efforts that will not result in any benefit to wildlife (Sutherland and Wordley 2017).

Conservation physiology is particularly well suited to understanding mechanisms and pathways of effect because, as also outlined above and throughout the subsequent chapters of this text, it sensitively links an organism's internal state with its external environment, providing an objective measure of how animals respond to or cope with changes (Wikelski and Cooke 2006; Tracy et al. 2006; Cooke and O'Connor 2010; Cooke et al. 2013). In particular, physiological studies focused on individual organisms allow scientists to use experimental approaches or comparisons across disturbed and undisturbed sites that can lead to the identification of cause-and-effect relationships (Cooke et al. 2017a) that can then be scaled up to the level of the population and even ecosystem (see Section 1.2.4). Such cause-and-effect relationships are so compelling that they are used as the gold standard in courts of law (Cooke and O'Connor 2010), and physiological measurements have been used to allow decision-makers to better target their conservation strategies. For example, monitoring multiple physiological traits (faecal reproductive, thyroid, and adrenal hormones) in Puget Sound killer whales allowed researchers to tease apart the impacts of boat traffic and nutritional stress, leading to the identification of protecting the whales' salmon prey as a more effective conservation strategy compared with limiting vessel disturbance (Ayres et al. 2012). Similarly, by combining faecal corticosterone and thyroid hormone monitoring in woodland caribou (*Rangifer tarandus caribou*), researchers have been able to determine how wolf predation and extraction of petroleum products from the Canadian oil sands development differentially impact a population, which has led to the deemphasizing of wolf removal programmes and greater effort in preservation of habitat that provides lichen as a food source (Wasser et al. 2011; Joly et al. 2015).

Being able to ascertain the mechanisms underlying conservation challenges can also provide compelling quantifiable measures for decision-makers, providing the evidence necessary to move forward with conservation action. For example, Semeniuk (Chapter 8, this volume) promotes the use of biomarkers of animal health in the management of wildlife provisioning tourism. Together with other physiological and biochemical indicators, non-esterified fatty acid profiles were used as a biomarker for assessing diet composition, lipid requirements, and nutritional status of tourist-fed stingrays to determine that tourism was imposing an ecological trap on the animals. This information provided concrete evidence to the Caymanian government that ecotourism guidelines should be updated. Beyond policy-makers, physiological mechanisms can also be effective tools in communicating conservation messages to stakeholders and the general public to draw support for conservation action (Bouyoucos and Rummer, Chapter 11, this volume; Laubenstein and Rummer, Chapter 18, this volume).

Finally, monitoring physiology to determine underlying mechanisms of decline can provide greater resolution on the complexity of some conservation challenges, which can in turn also benefit the development of evidence-informed mitigation strategies. Studying elk (*Cervus elaphus*) in the Greater Yellowstone Ecosystem, Creel et al. (2007) found that wolf predation pressure leads to greater vigilance, decreased foraging, and altered habitat selection and diet. These behavioural responses are associated with decreased levels of progesterone in adult females that is linked to lower calving rates and declining population size. By further measuring glucocorticoid (faecal cortisol) levels, Creel et al. (2009) showed that the negative influence of wolves on calf recruitment is not due to chronic stress, but is instead much more likely to be the result of the increased predation risk resulting in changes in foraging and nutrition. Declines in body mass and fat resources then result in a lowered ability of females to maintain pregnancies (Creel et al. 2009). From a management perspective, this type of information creates a clearer picture of the direct versus indirect effects of wolf predation, and how this can be intertwined with habitat change and availability.

1.2.4 Proactive and predictive capacity

Harnessing the predictive capacity to forecast the performance and fitness responses of organisms in complex systems is a primary motivation behind incorporating any mechanism (i.e. gene transcription, behaviour, physiology) into conservation studies (Madliger et al. 2015, 2018). Quantifying variation in physiological traits can allow us to link larger-scale abiotic processes to the organismal responses that influence fitness, population demography, and even ecosystem functioning (Bergman et al. 2019; Ames et al. 2020). With knowledge of the structure and strength of these linkages, we can then use predictive modelling techniques (McClane et al. 2011) to more effectively forecast expected outcomes for individuals and populations under expected future environmental scenarios (Semeniuk et al. 2012a; Cooke et al. 2013; Madliger et al. 2015). As outlined below, this type of scaled, predictive approach uses previous findings to cement mechanistic linkages to build strong predictive modelling capacity, and as a collective result has the power to better inform conservation decisions across a diversity of systems.

Since physiology links the organism to its environment, we can use a multitude of traits to quantify how both small-scale (e.g. variation in habitat/resource quality) and large-scale (e.g. variation in weather, climate) environmental variation influences organismal functioning (Madliger et al. 2015). Examples of emerging success stories range from the finer-scale examination of how human-induced increases in turbidity from sediment dredging in the Great Barrier Reef impact respiratory physiology and gill microbiome responses in larval reef fish (Hess et al. 2015, 2017; Illing and Rummer 2017), to using energetic physiology and stable isotopes in wide-ranging oceanic top predators such as seabirds, tuna, and sharks to monitor how global change is impacting resource acquisition and key biological processes (Hennin et al. 2016; Ferguson et al. 2017; Pethybridge et al. 2018; Descamps et al. 2019; Lorrain et al. 2020; Madigan et al., Chapter 5, this volume). Bringing this field together is the unified framework of 'macro-physiology'—the investigation of variation in physiological traits over large geographic and temporal scales and the ecological implications of this variation (Chown and Gaston 2016)—which is enabling researchers to predict and test a diversity of environment–physiology relationships (Lennox et al. 2018).

The next step is to quantify how environmentally related changes in centrally regulated physiological traits affect performance and fitness (Madliger and Love 2016b). Variation in breeding phenology/investment/success and survival are all being predicted by traits as diverse as energetic and glucocorticoid physiology (Madliger and Love 2014, 2015; Hennin et al. 2016, 2018, 2019; Sorenson et al. 2017; Minke-Martin et al. 2017; Crossin and Williams, Chapter 2, this volume), oxidative stress (Guindre-Parker et al. 2013; Costantini and Dell'Omo 2015), and cardiorespiratory physiology (Brownscombe et al. 2017). For example, Crossin and Williams (Chapter 2, this volume) outline how yolk precursors, the primary sources of protein and lipid in developing follicles and egg yolk, can predict breeding propensity and reproductive success in at-risk bird species. Although these types of linkages are often some of the most difficult to establish regardless of the system (Madliger et al. 2016), they are imperative for being able to scale these relationships up to quantify impacts on populations and ecosystems (Cooke and O'Connor 2010; Bergman et al. 2019; Ames et al. 2020).

Despite the expected management benefits of scaling individual variation in physiological traits up to predict population-level demographic responses to environmental variation or disturbance (Cooke and O'Connor, 2010; Madliger et al. 2018; Bergman et al. 2019), accomplishing this has been challenging in the wild (Bergman et al. 2019). However, recent successful case studies include using energetic traits to predict abrupt depopulation of managed honey bee colonies in Europe (Dainat et al. 2012; Alaux et al. 2017; López-Uribe et al. 2020; Alaux et al., Chapter 4, this volume); using resource-induced changes in glucocorticoids to predict population success in seabirds (Kitaysky et al. 2007); using environmentally induced changes in telomere length to predict negative changes in relative abundance and risk of extinction in lizard (*Zootoca vivipara*) populations across Europe (Dupoué et al. 2017); and using glucocorticoid and androgen hormones to link weather, habitat stressors, and altered social structure to predict declines in fecundity and population size in at-risk zebra (*Equus zebra zebra*) populations in South Africa (Lea et al. 2018). In other systems, a growing body of research is beginning to form a clearer picture of the links between environmental stressors, physiology, and fitness. For example, Dzal and Willis (Chapter 9, this volume) outline how a skin infection of hibernating bats (white-nose syndrome) leads to the disruption of physiological homeostasis and mortality. Research is also showing that the same degree of environmental change can result in different, individually flexible physiological decisions and therefore different fitness outcomes (Love et al. 2014; Madliger and Love 2016a), making our ability to predict larger-scale effects at the population level more complex. Ultimately, scaling processes up to determine ultimate impacts on ecosystem functioning is difficult, but progress is already being made (Schimel et al. 2007; Jungblut et al. 2017) and advances will increase with our ability to model this complexity effectively.

Indeed, the inclusion of physiological traits within the field of predictive modelling—the ability to model future outcomes of individuals, populations, and species based on variation in underlying phenotypic responses to environmental change—under future environmental scenarios is already a reality (e.g. Pirotta et al. 2018). Models spanning multiple physiological systems are being used to predict the tolerance and spread of invasive species (Kolbe et al. 2010; Seebacher and Franklin 2011; Higgins and Richardson 2014; Marras et al. 2015; Winwood-Smith et al. 2015), determine broad-scale host–parasite interactions (Rohr et al. 2013), predict the spread of novel diseases and disease dynamics (Legagneux et al. 2014; Ceccato et al. 2016; Becker et al. 2018), temporally and spatially define source vs. sink populations (Whitlock et al. 2015), examine how industrial activity will impact at-risk species (Muhly et al. 2011; Semeniuk et al. 2012a, b, 2014), and assess how the impacts of tourism and human decision-making will influence population viability (Semeniuk et al. 2010; Semeniuk, Chapter 8, this volume). Recently, studies using physiological traits across a diversity of taxa are helping to predict species responses to the effects of climate change (e.g. Farrell et al. 2008; Kearney and Porter 2009; Wilczek et al. 2010; Dey et al. 2017, 2018). The strengthening of this predictive capacity will enable practitioners to quantify how further changes to habitat, ecosystem, and climatic functioning will impact species continuance over vast spatiotemporal scales (Madliger et al. 2017).

1.3 Layout of the book: what to expect

We view this book as an opportunity to convey the current status of the field of conservation physiology, while also providing examples of research and practice that will be relevant into the future. We have structured the book as a series of 'case studies'—overviews of bodies of research that illustrate the variety of taxa, tools, and conservation issues that conservation physiologists are addressing. The case study chapters vary in their scope. Some cover topics that are relatively new to the discipline's research space or just gaining traction, such as the landscape ecology and physiology of bees (Alaux et al., Chapter 4, this volume) or the use of physiology in social-ecological models to mitigate human wildlife conflict (Semeniuk, Chapter 8, this volume). As a result, some chapters will detail a single case study, with developed sections on how to build the theory and implement the tools more extensively moving forwards. Other topics have been addressed using a conservation physiology approach more widely, and such chapters incorporate multiple case studies. For example, Crossin and Williams (Chapter 2, this volume) highlight work in four different avian systems to illustrate how physiological measurements can provide information on reproductive status that is otherwise nearly impossible to obtain. Cramp et al. (Chapter 6, this volume) similarly cover four case studies where physiology has contributed to understanding and rectifying barriers to fish passage in freshwater ecosystems. We believe this type of chapter structure is an ideal illustration of how the field of conservation physiology continues to build from a strong foundation of fundamental and applied work.

Through the 16 case study chapters, the text will cover a diversity of taxa (reptiles, amphibians, birds, fish, mammals, insects, crustaceans), ecosystems (terrestrial, freshwater, marine), and conservation questions (monitoring environmental stress, predicting the impact of climate change, understanding disease dynamics, improving captive breeding, reducing human–wildlife conflict). The tools and techniques included are also highly varied, spanning stress, energetic, immune, nutritional, cardiorespiratory, and reproductive physiology. They range from metrics that are considered relatively 'simple' (e.g. body condition assessed through photography) to those requiring more complex experimental set-ups (e.g. respirometry). They also vary in the degree to which an animal must be handled for collection, with some (like faecal samples for hormone analysis) being quite non-invasive, and others involving capture and handling (e.g. swabs to assess skin infection). We view the great variety of tools available in the conservation physiology toolbox as a benefit, as researchers and practitioners can choose the techniques that best suit their questions and constraints. By acting as practical roadmaps across a diversity of subdisciplines, we hope the case studies can serve to increase the accessibility of this discipline to new researchers, illustrate the far-reaching nature of the field, and allow readers to gain an appreciation of the purpose, value, and status of the field of conservation physiology. We would also like to draw readers' attention to the take-home messages that are included at the start of each chapter. These are designed to provide a one- or two-sentence overview of what the chapter will cover, but also to illustrate the broader goals that can be accomplished with a conservation physiology approach.

We acknowledge that the book is focused only on animals, as we felt that this arm of conservation physiology is the most established. Indeed, only 3 per cent of the papers published in the journal *Conservation Physiology* in the 5 years after its launch (2013–2018) focused on plants (Madliger et al. 2018). However, we recognize the value and success of such research (Madliger et al. 2016) and hope to see its continued growth.

Following the case studies in the main section of the book, we have included two concluding chapters. In the first, Laubenstein and Rummer (Chapter 18, this volume) cover some of the important goals of conservation physiology that extend beyond acquiring data and publishing results. Here, readers will find information on establishing relationships with stakeholders, carrying research through to application, and sharing their findings with the broader public. Finally, our synthesis and conclusion chapter (Cooke et al., Chapter 19, this volume) outlines 12 themes that came to light through the series of case studies, the challenges and gaps the discipline currently faces, and a final message of optimism for future growth and cohesion with the ultimate aim of ensuring the conservation of earth's remarkable biodiversity.

References

Alaux, C., Allier, F., Decourtye, A. et al., 2017. A 'Landscape physiology' approach for assessing bee health highlights the benefits of floral landscape enrichment and semi-natural habitats. *Scientific Reports*, *7*(1), 1–10.

Ames, E.M., Gade, M.R., Nieman, C.L. et al., 2020. Striving for population-level conservation: integrating physiology across the biological hierarchy. *Conservation Physiology*, *8*(1), coaa019.

Ayres, K.L., Booth, R.K., Hempelmann, J.A. et al., 2012. Distinguishing the impacts of inadequate prey and vessel traffic on an endangered killer whale (*Orcinus orca*) population. *PLoS ONE*, *7*(6), e36942.

Bahamonde, P.A., Feswick, A., Isaacs, M.A. et al., 2016. Defining the role of omics in assessing ecosystem health:

perspectives from the Canadian environmental monitoring program. *Environmental Toxicology and Chemistry*, *35*(1), 20–35.

Becker, D.J., Hall, R.J., Forbes, K.M. et al., 2018. Anthropogenic resource subsidies and host–parasite dynamics in wildlife. *Philosophical Transactions of the Royal Society of London*, *373*(1745), 20170086. 10.1098/rstb.2017.0086.

Berger, J., Testa, J.W., Roffe, T., and Monfort, S.L., 1999. Conservation endocrinology: a noninvasive tool to understand relationships between carnivore colonization and ecological carrying capacity. *Conservation Biology*, *13*(5), 980–9.

Bergman, J.N., Bennett, J.R., Binley, A.D. et al., 2019. Scaling from individual physiological measures to population-level demographic change: case studies and future directions for conservation management. *Biological Conservation*, *238*, 108242.

Bitman, J., Cecil, H.C., Harris, S.J., and Fries, G.F., 1969. DDT induces a decrease in eggshell calcium. *Nature*, *224*(5214), 44–6.

Brownscombe, J.W., Cooke, S.J., Algera, D.A. et al., 2017. Ecology of exercise in wild fish: integrating concepts of individual physiological capacity, behavior, and fitness through diverse case studies. *Integrative and Comparative Biology*, *57*, 281–92.

Bryan, H.M., Darimont, C.T., Paquet, P.C. et al., 2013. Stress and reproductive hormones in grizzly bears reflect nutritional benefits and social consequences of a salmon foraging niche. *PLoS ONE*, *8*(11), e80537.

Carey, C., 2005. How physiological methods and concepts can be useful in conservation biology. *Integrative and Comparative Biology*, *45*(1), 4–11.

Ceccato, E., Cramp, R.L., Seebacher, F., and Franklin, C.E., 2016. Early exposure to ultraviolet-B radiation decreases immune function later in life. *Conservation Physiology*, *4*, cow037.

Chown, S.L. and Gaston, K.J., 2008. Macrophysiology for a changing world. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1642), 1469–78.

Chown, S.L. and Gaston, K.J., 2016. Macrophysiology—progress and prospects. *Functional Ecology*, *30*, 330–44.

Clark, C.T., Horstmann, L., and Misarti, N., 2020. Zinc concentrations in teeth of female walruses reflect the onset of reproductive maturity. *Conservation Physiology*, *8*(1), coaa029.

Cooke, S.J. and O'Connor, C.M., 2010. Making conservation physiology relevant to policy makers and conservation practitioners. *Conservation Letters*, *3*, 159–66.

Cooke, S.J., Birnie-Gauvin, K., Lennox, R.J. et al, 2017a. How experimental biology and ecology can support evidence-based decision-making in conservation: avoiding pitfalls and enabling application. *Conservation Physiology*, *5*(1), cox043.

Cooke, S.J., Hultine, K.R., Rummer, J.L., and Franklin, C.E., 2017b. Reflections and progress in conservation physiology. *Conservation Physiology*, *5*(1), cow071.

Cooke, S.J., Madliger, C.L., Cramp, R.L. et al., 2020. Reframing conservation physiology to become more inclusive, integrative, relevant and forward-looking: reflections and a horizon scan. *Conservation Physiology*, *8*(1), coaa016.

Cooke, S.J., Sack, L., Franklin, C.E. et al., 2013. What is conservation physiology? Perspectives on an increasingly integrated and essential science. *Conservation Physiology*, *1*, cot001.

Costantini, D. and Dell'Omo. G., 2015. Oxidative stress predicts long-term resight probability and reproductive success in Scopoli's shearwater (*Calonectris diomedea*). *Conservation Physiology*, *3*(1), cov024.

Creel, S., Christianson, D., Liley, S., and Winnie, J.A., 2007. Predation risk affects reproductive physiology and demography of elk. *Science*, *315*(5814), 960.

Creel, S., Winnie, J.A., and Christianson, D., 2009. Glucocorticoid stress hormones and the effect of predation risk on elk reproduction. *Proceedings of the National Academy of Sciences*, *106*(30), 12388–93.

Dainat, B., Evans, J.D., Chen, Y.P. et al., 2012. Predictive markers of honey bee colony collapse. *PLoS ONE*, *7*, 10.1371.

Dehnhard, M., Naidenko, S., Frank, A. et al., 2008. Noninvasive monitoring of hormones: a tool to improve reproduction in captive breeding of the Eurasian lynx. *Reproduction in Domestic Animals*, *43*, 74–82.

Descamps, S., Ramírez, F., Benjaminsen, S. et al., 2019. Diverging phenological responses of Arctic seabirds to an earlier spring. *Global Change Biology*, *25*, 4081–91.

Deutsch, C., Ferrel, A., Seibel, B. et al., 2015. Climate change tightens a metabolic constraint on marine habitats. *Science*, *348*(6239), 1132–5.

Dey, C.J., Richardson, E., McGeachy, D. et al., 2017. Increasing nest predation will be insufficient to maintain polar bear body condition in the face of sea-ice loss. *Global Change Biology*, *23*, 1821–31.

Dey, C.J., Semeniuk, C.A., Iverson, S.A. et al., 2018. Forecasting the outcome of multiple effects of climate change on northern common eiders. *Biological Conservation*, *220*, 94–103.

Dupoué, A., Rutschmann, A., Le Galliard, J.F. et al., 2017. Shorter telomeres precede population extinction in wild lizards. *Scientific Reports*, *7*, 16976.

Farrell, A.P., Hinch, S.G., Cooke, S.J. et al., 2008. Pacific salmon in hot water: applying aerobic scope models and biotelemetry to predict the success of spawning migrations. *Physiological and Biochemical Zoology*, *81*(6), 697–708.

Feder, M.E., Bennett, A.F., Burggren, W.W., and Huey, R.B., 1987. *New Directions in Ecological Physiology*. Cambridge University Press, Cambridge.

Ferguson, S.H., Young, B.G., Yurkowski, D.J. et al., 2017. Demographic, ecological, and physiological responses of ringed seals to an abrupt decline in sea ice availability. *PeerJ*, *5*, e2957.

Ge, Y., Wang, D.Z., Chiu, J.F. et al, 2013. Environmental OMICS: current status and future directions. *Journal of Integrated OMICS*, *3*(2), 75–87.

Gomez Isaza, D.F., Cramp, R.L., and Franklin, C.E., 2020. Simultaneous exposure to nitrate and low pH reduces the blood oxygen-carrying capacity and functional performance of a freshwater fish. *Conservation Physiology*, *8*(1), coz092.

Guindre-Parker, S., Baldo, S., Gilchrist, H.G. et al., 2013. The oxidative costs of territory quality and offspring provisioning. *Journal of Evolutionary Biology*, *26*, 2558–65.

Hennin, H.L., Dey, C., Bety, J. et al., 2018. Higher rates of pre-breeding condition gain positively impacts clutch size: a mechanistic test of the condition-dependent individual optimization model. *Functional Ecology*, *32*, 2019–28.

Hennin, H.L., Legagneux, P., Bêty, J. et al., 2016. Energetic physiology mediates individual optimization of breeding phenology in a migratory Arctic seabird. *American Naturalist*, *188*, 434–45.

Hennin, H.L., Legagneux, P., Gilchrist, H.G. et al., 2019. Plasma mammalian leptin analogue predicts reproductive phenology, but not reproductive output in a capital-income breeding seaduck. *Ecology and Evolution*, *9*, 1512–22.

Hess, S., Prescott, L.J., Hoey, A.S. et al., 2017. Species-specific impacts of suspended sediments on gill structure and function in coral reef fishes. *Proceedings of the Royal Society of London*, *284*, 10.1098/rspb.2017.1279

Hess, S., Wenger, A.S., Ainsworth, T.D., and Rummer, J.L., 2015. Exposure of clownfish larvae to suspended sediment levels found on the Great Barrier Reef: impacts on gill structure and microbiome. *Scientific Reports*, *5*, 10561.

Higgins S.I. and Richardson, D.M., 2014. Invasive plants have broader physiological niches. *Proceedings of the National Academy of Sciences of the USA*, *111*, 10610–10614.

Hudson, N.J. and Franklin, C.E., 2002. Effect of aestivation on muscle characteristics and locomotor performance in the green-striped burrowing frog, *Cyclorana alboguttata*. *Journal of Comparative Physiology B—Biochemical Systemic and Environmental Physiology*, *172*, 177–82.

Hunninck, L., May, R., Jackson, C.R. et al., 2020. Consequences of climate-induced vegetation changes exceed those of human disturbance for wild impala in the Serengeti ecosystem. *Conservation Physiology*, *8*(1), coz117.

Hunt, K.E., Stimmelmayr, R., George, C. et al., 2014. Baleen hormones: a novel tool for retrospective assessment of stress and reproduction in bowhead whales (*Balaena mysticetus*). *Conservation Physiology*, *2*, cou030.

Illing, B. and Rummer, J.L., 2017. Physiology can contribute to better understanding, management, and conservation of coral reef fishes. *Conservation Physiology*, *5*, cox005.

Jefferies, D.J., 1969. Induction of apparent hyperthyroidism in birds fed DDT. *Nature*, *222*(5193), 578–9.

Johnson, K.M. and Hofmann, G.E., 2020. Combined stress of ocean acidification and warming influence survival and drives differential gene expression patterns in the Antarctic pteropod, *Limacina helicina antarctica*. *Conservation Physiology*, *8*(1), coaa013.

Joly, K., Wasser, S.K., and Booth, R., 2015. Non-invasive assessment of the interrelationships of diet, pregnancy rate, group composition, and physiological and nutritional stress of barren-ground caribou in late winter. *PLoS ONE*, *10*(6), e0127586.

Jungblut, S., Boos, K., McCarthy, M. et al., 2017. Respiration physiology and ecosystem impact of European and Asian shore crabs in a temperate European habitat. The Crustacean Society Mid-Year Meeting, Barcelona, Spain, 19–22 June 2017.

Kearney M. and Porter, W., 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, *12*, 334–50.

Kern P., Cramp R.L., Gordos M.A. et al., 2018. Measuring Ucrit and endurance: equipment choice influences estimates of fish swimming performance. *Journal of Fish Biology*, *92*(1), 237–47.

Kitaysky, A., Piatt, J., and Wingfield, J., 2007. Stress hormones link food availability and population processes in seabirds. *Marine Ecology Progress Series*, *352*, 245–58.

Kolbe, J.J., Kearney, M., and Shine, R., 2010. Modeling the consequences of thermal trait variation for the cane toad invasion of Australia. *Ecological Applications*, *20*, 2273–85.

Krebs, C.J., 1989. *Ecological Methodology*. Harper & Row, New York.

Lea, J.M.D., Walker, S.L., Kerley, G.I.H. et al., 2018. Noninvasive physiological markers demonstrate link between habitat quality, adult sex ratio and poor population growth rate in a vulnerable species, the Cape mountain zebra. *Functional Ecology*, *32*, 300–12.

Legagneux, P., Berzins, L.L., Forbes, M. et al., 2014. No selection on immunological markers in response to a highly virulent pathogen in an Arctic breeding bird. *Evolutionary Applications*, *7*(7), 765–73. 10.1111/eva.12180.

Lennox, R. and Cooke, S.J., 2014. State of the interface between conservation and physiology: a bibliometric analysis. *Conservation Physiology*, 2, cou003.

Lennox, R.J., Suski, C.D., and Cooke, S.J., 2018. A macrophysiology approach to watershed science and management. *Science of the Total Environment*, *626*, 434–40.

López-Uribe, M.M., Ricigliano, V.A., and Simone-Finstrom, M., 2020. Defining pollinator health: a holistic approach based on ecological, genetic, and physiological factors. *Annual Review of Animal Biosciences*, *8*, 269–94.

Lorrain, A., Pethybridge, H., Cassar, N. et al., 2020. Trends in tuna carbon isotopes suggest global changes in pelagic phytoplankton communities. *Global Change Biology*, *26*, 458–70.

Love, O.P., Madliger, C.L., Bourgeon, S. et al., 2014. Evidence for baseline glucocorticoids as mediators of reproductive investment in a wild bird. *General and Comparative Endocrinology*, *199*, 65–9.

Madliger, C.L., Cooke, S.J., Crespi, E.J. et al., 2016. Success stories and emerging themes in conservation physiology. *Conservation Physiology*, *4*, cov57.

Madliger, C.L. Franklin, C.E., Hultine, K.R. et al., 2017. Conservation physiology and the quest for a 'good' Anthropocene. *Conservation Physiology*, *15*, cox003.

Madliger, C.L. and Love, O.P., 2014. The need for a predictive, context-dependent approach to the application of stress hormones in conservation. *Conservation Biology*, *28*, 283–7.

Madliger, C.L. and Love, O.P., 2015. The power of physiology in changing landscapes: considerations for the continued integration of conservation and physiology. *Integrative and Comparative Biology*, *55*, 545–53.

Madliger, C.L. and Love, O.P., 2016a. Employing individual measures of baseline glucocorticoids as population-level conservation biomarkers: considering within-individual variation in a breeding passerine. *Conservation Physiology*, *4*, cow048.

Madliger, C.L. and Love, O.P., 2016b. Conservation implications of a lack of relationship between baseline glucocorticoids and fitness in a wild passerine. *Ecological Applications*, *26*, 2732–45.

Madliger, C.L., Love, O.P., Hultine, K., and Cooke, S.J., 2018. The conservation physiology toolbox: status and opportunities. *Conservation Physiology*, *6*, coy029.

Madliger, C.L., Semeniuk, C.A.D., Harris, C.M. and Love, O.P., 2015. Assessing baseline stress physiology as an integrator of environmental quality in a wild avian population: implications for use as a conservation biomarker. *Biological Conservation*, *192*, 409–17.

Marras, S., Cucco, A., Antognarelli, F. et al., 2015. Predicting future thermal habitat suitability of competing native and invasive fish species: from metabolic scope to oceanographic modelling. *Conservation Physiology*, *3*(1), cou059.

Mayr, E., 1961. Cause and effect in biology. *Science*, *134*(3489), 1501–6.

McClane, A.J., Semeniuk, C.A.D., and Marceau, D., 2011. The role of agent-based models in wildlife ecology and management: the importance of accommodating individual habitat-selection behaviours and spatially explicit movement for conservation planning. *Ecological Modelling*, *222*, 1544–56.

McCoy, C.M., Lind, C.M., and Farrell, T.M., 2017. Environmental and physiological correlates of the severity of clinical signs of snake fungal disease in a population of pigmy rattlesnakes, *Sistrurus miliarius*. *Conservation Physiology*, *5*(1), cow077.

McMahon, B.J., Teeling, E.C., and Höglund, J., 2014. How and why should we implement genomics into conservation? *Evolutionary Applications*, *7*(9), 999–1007.

Millspaugh, J.J. and Washburn, B.E., 2004. Use of fecal glucocorticoid metabolite measures in conservation biology research: considerations for application and interpretation. *General and Comparative Endocrinology*, *138*, 189–199.

Minke-Martin, V., Hinch, S.G., Braun, D.C. et al., 2017. Physiological condition and migratory experience affect fitness-related outcomes in adult female sockeye salmon. *Ecology of Freshwater Fish*, *27*, 296–309.

Muhly, T.B., Semeniuk, C.A.D., Massolo, A. et al., 2011. Human activity helps prey win the predator-prey space race. *PLoS ONE*, *6*, e17050.

Pethybridge, H., Choy, C.A., Logan, J.M. et al., 2018. A global meta-analysis of marine predator nitrogen stable isotopes: relationships between trophic structure and environmental conditions. *Global Ecology and Biogeography*, *27*, 1043–55.

Pirotta, E., Mangel, M., Costa, D.P. et al., 2018. A dynamic state model of migratory behavior and physiology to assess the consequences of environmental variation and anthropogenic disturbance on marine vertebrates. *American Naturalist*, *191*, E40–56.

Robeck, T.R., Steinman, K.J., Gearhart, S. et al., 2004. Reproductive physiology and development of artificial insemination technology in killer whales (*Orcinus orca*). *Biology of Reproduction*, *71*(2), 650–60.

Rohr, J.R., Raffel, T.R., Blaustein, A.R. et al., 2013. Using physiology to understand climate-driven changes in disease and their implications for conservation. *Conservation Physiology*, *1*(1), cot022.

Schimel, J., Balser, T.C., and Wallenstein, M., 2007. Microbial stress-response physiology and its implications for ecosystem function. *Ecology*, *88*, 1386–94.

Seebacher, F. and Franklin, C.E., 2011. Physiology of invasion: cane toads are constrained by thermal effects on physiological mechanisms that support locomotor performance. *Journal of Experimental Biology*, *214*(9), 1437–44.

Seebacher, F. and Franklin, C.E., 2012. Determining environmental causes of biological effects: the need for a mechanistic physiological dimension in conservation biology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1596), 1607–14.

Semeniuk, C.A.D., Haider, W., Cooper, A., and Rothley, K.D., 2010. A linked model of animal ecology and human behaviour for the management of wildlife tourism. *Ecological Modelling*, *221*, 2699–713.

Semeniuk, C.A.D., Musiani, M., Birkigt, D.A. et al., 2014. Identifying non-independent anthropogenic risks using a behavioral individual-based model. *Ecological Complexity*, *17*, 67–78.

Semeniuk, C.A.D., Musiani, M. Hebblewhite, M. et al., 2012a. Evaluating risk effects of industrial features on woodland caribou habitat selection in west central Alberta using agent-based modelling. *Procedia Environmental Sciences*, *13*, 698–714.

Semeniuk, C.A.D., Musiani, M., Hebblewhite, M. et al., 2012b. Incorporating behavioural-ecological strategies in pattern-oriented modelling of caribou habitat use in a highly industrialized landscape. *Ecological Modelling*, *243*, 18–32.

Sorenson, G.H., Dey, C., Madliger, C.L., and Love, O.P., 2017. Effectiveness of baseline corticosterone as a monitoring tool for fitness: a meta-analysis in seabirds. *Oecologia*, *183*, 353–65.

Soulé, M.E., 1985. What is conservation biology? *BioScience*, *35*(11), 727–34.

Sutherland, W.J. and Wordley, C.F., 2017. Evidence complacency hampers conservation. *Nature Ecology & Evolution*, *1*(9), 1215–16.

Stevenson, R.D., Tuberty, S.R., DeFur, P.L. and Wingfield, J.C., 2005. Ecophysiology and conservation: the contribution of endocrinology and immunology—introduction to the symposium. *Integrative and Comparative Biology*, *45*(1), 1–3.

Swanson, W.F., 2003. Research in nondomestic species: experiences in reproductive physiology research for conservation of endangered felids. *ILAR Journal*, *44*(4), 307–16.

Tang, R., Li, W., Zhu, D. et al., 2020. Raging elephants: effects of human disturbance on physiological stress and reproductive potential in wild Asian elephants. *Conservation Physiology*, *8*(1), coz106.

Tracy, C.R., Nussear, K.E., Esque, T.C. et al., 2006. The importance of physiological ecology in conservation biology. *Integrative and Comparative Biology*, *46*(6), 1191–205.

Wasser, S.K., Keim, J.L., Taper, M.L., and Lele, S.R., 2011. The influences of wolf predation, habitat loss, and human activity on caribou and moose in the Alberta oil sands. *Frontiers in Ecology and the Environment*, *9*(10), 546–51.

Whitlock, R.E., Hazen, E.L., Walli, A. et al., 2015. Direct quantification of energy intake in an apex marine predator suggests physiology is a key driver of migrations. *Science Advances*, *1*, e1400270.

Wikelski, M. and Cooke, S.J., 2006. Conservation physiology. *Trends in Ecology & Evolution*, *21*(1), 38–46.

Wilczek, A.M., Burghardt, L.T., Cobb, A.R. et al., 2010. Genetic and physiological bases for phenological responses to current and predicted climates. *Philosophical Transactions of the Royal Society of London Biological Sciences*, *365*, 3129–47.

Willmer, P., Stone, G., and Johnston, I., 2009. *Environmental Physiology of Animals*, second edition. Blackwell Science Ltd, Oxford.

Wilson, R.S., Franklin, C.E., Davison, W., and Kraft, P., 2001. Stenotherms at sub-zero temperatures: thermal dependence of swimming performance in Antarctic fish. *Journal of Comparative Physiology B—Biochemical Systemic and Environmental Physiology*, *171*, 263–9.

Winwood-Smith, H.S., Alton, L.A., Franklin, C.E., and White, C.R., 2015. Does greater thermal plasticity facilitate range expansion of an invasive terrestrial anuran into higher latitudes? *Conservation Physiology*, *3*(1), cov010.