

The second warning to humanity: contributions and solutions from conservation physiology

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In 1992, the Union of Concerned Scientists shared their 'World Scientists' Warning to Humanity' with governmental leaders worldwide, calling for immediate action to halt the environmental degradation that threatens the systems that support life on Earth. A follow-up 'Second Warning' was released in 2017, with over 15 000 scientists as signatories, describing the lack of progress in adopting the sustainable practices necessary to safeguard the biosphere. In their 'Second Warning', Ripple and colleagues provided 13 'diverse and effective steps humanity can take to transition to sustainability.' Here, we discuss how the field of conservation physiology can contribute to six of these goals: (i) prioritizing connected, well-managed reserves; (ii) halting the conversion of native habitats to maintain ecosystem services; (iii) restoring native plant communities; (iv) rewinding regions with native species; (v) developing policy instruments; and (vi) increasing outdoor education, societal engagement and reverence for nature. Throughout, we focus our recommendations on specific aspects of physiological function while acknowledging that the exact traits that will be useful in each context are often still being determined and refined. However, for each goal, we include a short case study to illustrate a specific physiological trait or group of traits that is already being utilized in that context. We conclude with suggestions for how conservation physiologists can broaden the impact of their science aimed at accomplishing the goals of the 'Second Warning'. Overall, we provide an overview of how conservation physiology can contribute to addressing the grand socio-environmental challenges of our time.

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The scientists' warning movement

In 2017, a group of international scientists published a 'Second Warning to Humanity', which called for a transition to more environmentally sustainable practices or humanity would risk widespread suffering and irreversible damage to the biosphere (Ripple *et al.*, 2017). The article considered the progress that had been made since the Union of Concerned Scientists, along with over 1700 independent scientists, released 'World Scientists' Warning to Humanity' 25 years prior (Union of Concerned Scientists, 1992). Over this period of time, stabilizing the ozone layer has been a considerable accomplishment through ratification and implementation of the Montreal Protocol. However, little progress has been made in meeting other environmental challenges such as climate change, deforestation and agricultural expansion, which are becoming far more pressing and contributing to the ongoing sixth mass extinction of life on Earth (Ceballos *et al.*, 2015; Ceballos *et al.*, 2017; Ripple *et al.*, 2017). Ripple *et al.* (2017) cited the rapid action on limiting ozone-depleting substances as an example of humanity's capacity for positive change through decisive action, and the paper outlined 13 steps that could lead to a transition to sustainability across the globe. Here, we highlight how conservation physiology can contribute in meaningful and measurable ways to six of those goals. We viewed the other steps outlined in Ripple *et al.* (2017) (e.g. reducing food waste through education, further reducing fertility rates, revising our economy to reduce wealth inequality) as better addressed by other arms of conservation science (i.e. we did not see a direct avenue for conservation physiology to assist).

We represent a group of conservation physiologists from around the world working across wide geographic regions and international jurisdictions on diverse taxa, systems and physiological traits. Some of our experiences span decades, while some of us are in the early stages of establishing careers. Although our expertise includes ecological, evolutionary and environmental physiology, we share common goals. We aim to determine how an understanding of physiological function and variation can be harnessed to better document, predict and ameliorate environmental damage to plants and animals in the Anthropocene. We also attempt to establish cause-and-effect relationships by elucidating mechanisms through the measurement of functional/physiological traits. This perspective aims to align the strengths of conservation physiology with the steps outlined in the 'Second Warning to Humanity' by providing an overview of potential undertakings and proven examples. We conclude with broad-scale advice, drawing on our own personal experiences and research goals, that we envision as a road map for fellow conservation physiologists to follow at any stage of their career. In doing so, we broadly aim to contribute to solving some of the grand socio-environmental challenges of the Anthropocene as part of a larger multi-disciplinary toolbox.

Avenues for leadership by conservation physiology

Since the discipline of conservation physiology was formally described in 2006 (Wikelski and Cooke, 2006), there have been many published perspectives on the potential value of physiological approaches to conservation science and its successes (e.g. Cooke and O'Connor, 2010; Ellis *et al.*, 2012; Cooke *et al.*, 2013; Madliger *et al.*, 2016; Madliger *et al.*, 2021a). As part of a diverse multi-disciplinary toolbox, conservation physiology emphasizes that an understanding of the mechanisms that govern how organisms respond to their environments is valuable for determining the nature, timing and severity of threats. Proponents of conservation physiology often emphasize that potential solutions can be targeted and assessed experimentally, providing evidence to support conservation spending and implementation schemes (Cooke *et al.*, 2017). Identifying and utilizing sensitive physiological metrics can also be essential for predicting responses of organisms to anthropogenic pressures, thereby providing a window into population distributions and dynamics that are otherwise difficult to model (Ames *et al.*, 2020; Bergman *et al.*, 2019; Evans *et al.*, 2015). Physiological perturbations (e.g. stress) can precede fitness consequences (e.g. reduced fecundity) and therefore allow prediction of population change. Physiological responses of individuals can therefore be scaled up using current models to provide population- and community-level predictions (Bergman *et al.*, 2019). Indeed, creating robust, physiologically based models is likely the best approach to predicting the responses of plants and animals to no-analog future conditions caused by climate change. Beyond these applications, physiology has well-defined potential and realized roles in improving the success and welfare of individuals in translocation (Tarszisz *et al.*, 2014), captive breeding and reintroduction (Kersey and Dehnhard, 2014) and restoration programmes (Cooke and Suski, 2008). As a whole, the discipline is increasingly poised to offer targeted, solution-oriented conservation responses and there is growing evidence of the ways that physiological approaches can be translated into action-based strategies (e.g. see Madliger *et al.*, 2021a).

We focus here on 6 of the 13 steps, as presented by Ripple *et al.* (2017) in their 'Second Warning', that we envision conservation physiology can help achieve (Fig. 1). In each case, we provide an overview of the potential roles of conservation physiology followed by a case study illustrating a physiological approach that is already helping to reach the goal (Fig. 2).

Prioritizing the design of connected and well-managed reserves

While there has been considerable debate throughout the history of conservation science about optimal reserve design, it is clear that terrestrial, marine, freshwater and aerial habitats can be protected through the establishment of well-managed

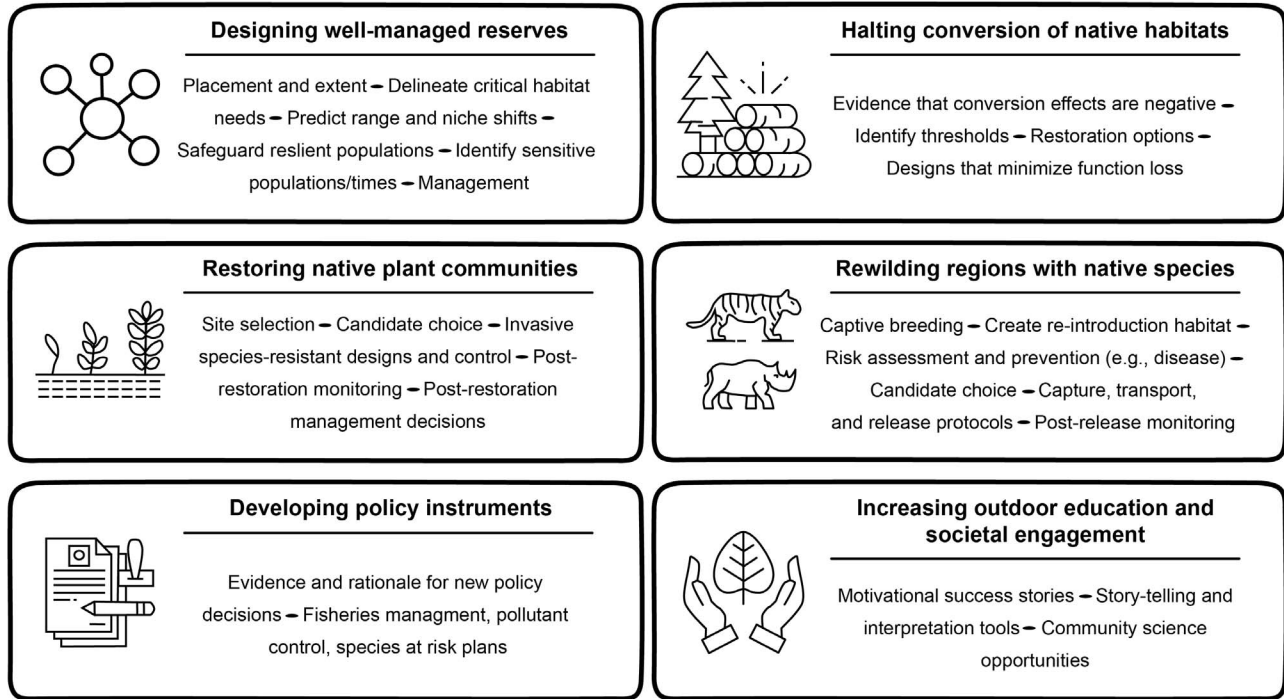


Figure 1: Overview of the ways that conservation physiology can contribute to six of the steps outlined in 'The Second Warning to Humanity' (Ripple *et al.*, 2017)

reserves that are inter-connected to the highest degree possible (Williams *et al.*, 2005). Physiology partly underlies dispersal capability/decisions (Zera and Brisson, 2012), migration timing and pace (Lennox *et al.*, 2016) and habitat requirements (e.g. Miller and Eadie, 2006). Therefore, physiological data could help guide some of the largest decisions associated with reserve design, such as the placement and necessary extent of reserves, as well as identifying reserves where organisms may suffer most from isolation. Under the ever-pressing influence of climate change, models that incorporate physiological information can predict range (Buckley, 2008) and niche shifts (Kearney and Porter, 2004; Helaouët and Beaugrand, 2009) as well as changes in primary productivity (Zhou *et al.*, 2017) within reserves that are necessary for future planning.

By helping to elucidate which populations, species and locations may have adaptive capacity (Somero, 2011), physiology can also assist in safeguarding resilient populations while identifying vulnerable populations that may need further conservation intervention. For example, due to differences in thermal sensitivity, it is predicted in marine ecosystems that benthic primary producers will be more vulnerable to climate change than higher trophic groups (Bennett *et al.*, 2019). In a more basic way, physiology can help reveal the critical habitat needs of organisms of interest (Miller and Eadie, 2006; Teal *et al.*, 2018), thus allowing the necessary components and extent of reserves to be better identified and integrated. Finally, monitoring physiology can determine whether additional interventions may be needed in reserves

at certain times of year when species may be more vulnerable (e.g. to disease, weather, human presence, food availability) (Bouyoucos and Rummer, 2021).

Case study: managing marine protected areas using physiological data

Protected areas are increasingly being used to ensure that marine life is safeguarded from human activities and exploitation. Yet, identifying where to locate protected areas remains a major challenge. It is now recognized that protected areas need to focus not only on structural aspects but also on ecosystem functioning (Parrish *et al.*, 2003). Physiology can provide insight into the functional aspects of ecosystems and thus can be used to help identify priority sites that will be resilient to stressors (McLeod *et al.*, 2009). Following the establishment of protected areas, physiological monitoring has been used to assess the environmental quality of the site, which is important in identifying the types of activities or restrictions that are consistent with their optimal function (i.e. by prohibiting activities that induce physiological stress; Smith *et al.*, 2008; Wright *et al.*, 2011). For example, using a panel of physiological traits (e.g. antioxidant responses, DNA damage, lipid peroxidation, metal burdens, total polycyclic aromatic hydrocarbons) from liver, kidney, gill and muscle samples of madamango sea catfish (*Cathorops spixii*) in the Environmental Protection Area of Cananéia-Iguape-Peruíbe, Brazil, Gusso-Choueri *et al.* (2015) identified spatial and

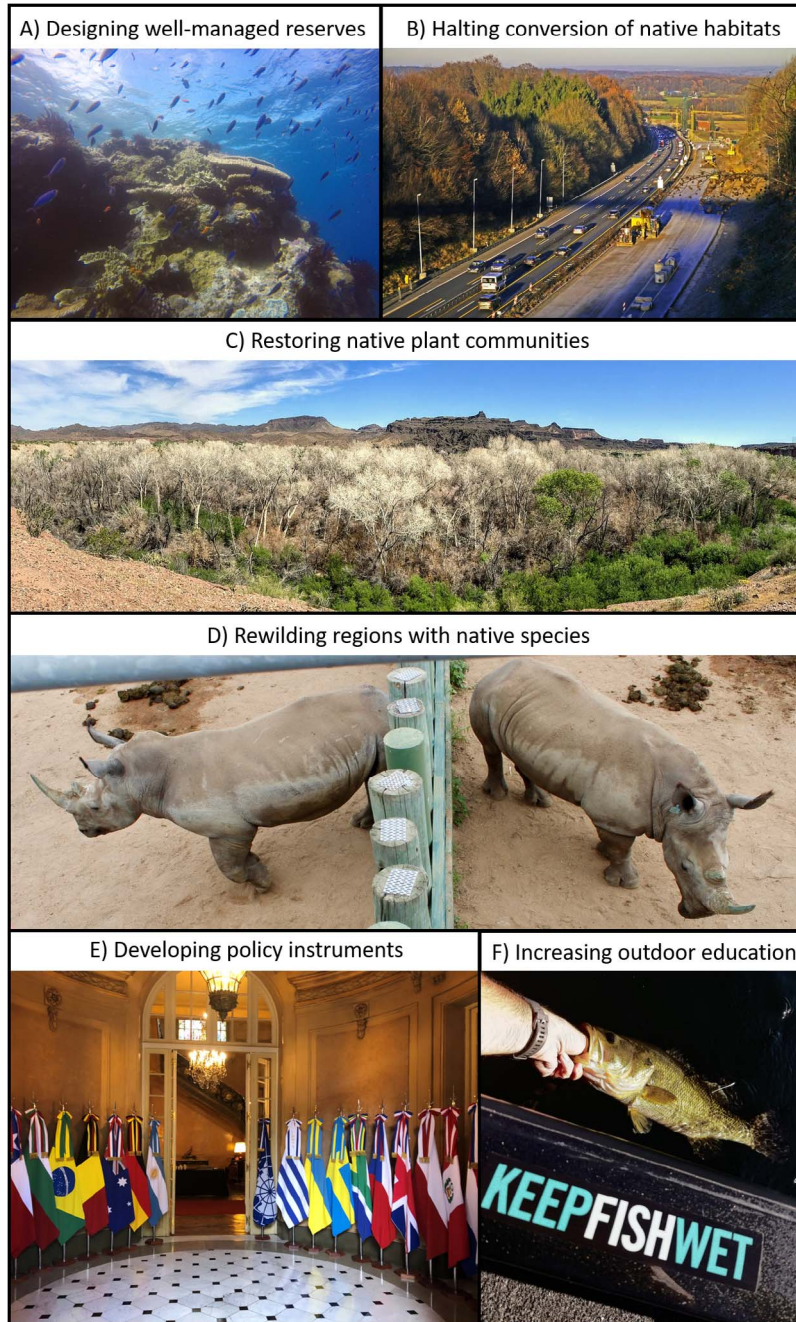


Figure 2: Case studies serving as examples of how conservation physiology is contributing to six of the steps outlined in ‘The Second Warning to Humanity’: (A) Physiological monitoring can identify spatial and temporal sources of pollution in MPAs, allowing for improved management (photo: J. Rummer); (B) Research on swimming performance can inform infrastructure design associated with highways, minimizing impacts of conversion on species and habitats (photo: hpgruesen, Pixabay License); (C) Cottonwood genotypes that are best suited to cope with future climate conditions, such as the heat and drought that killed the Fremont cottonwood trees pictured here in AZ, USA, are being identified for restoration of riparian ecosystems (photo: H. Cooper); (D) Physiological monitoring is leading to improved outcomes for translocated wildlife such as rhinoceros (photo: A. Fuller); (E) Physiological research is being incorporated into assessments, such as those by the multi-national Committee for Environmental Protection of the Antarctic Treaty, of the current and likely future impacts of invasive alien species (photo: S.L. Chown); and (F) Informed partly by research on the physiological consequences of air exposure, the ‘Keep Fish Wet’ movement encourages anglers to take part in better fish handling practices (photo: S. Cooke).

seasonal variation in pollution sources. This work provides evidence that a physiological biomarker approach can aid in identifying how, when and where stressors are acting on organisms within marine protected areas (MPAs), in turn allowing for decision-making targeted at minimizing or eliminating their effects.

Maintaining nature's ecosystem services by halting conversion of native habitats

Forests, grasslands, wetlands and marine and freshwater habitats provide essential ecosystem services for human well-being. Physiology can offer evidence for how conversion or degradation of these natural systems affects individuals, populations, species and communities, and therefore how it impacts overall ecosystem function and biodiversity. For example, relying on oxidative status markers, Messina *et al.* (2020) showed that some understorey birds are resilient to forest logging, strengthening the message that regenerating logged forests are of great conservation value. Moreover, physiological measurements of plants can identify the sensitivity of given species to stress associated with climate and land use changes, thus enabling prediction of vegetation responses to drought, fire or other disturbances (Scott *et al.*, 1999; Haber *et al.*, 2020). This type of assessment is critical for identifying potential loss of ecosystem services provided by intact vegetation, particularly under the effects of climate change (Wang and Polglase, 1995; Campbell *et al.*, 2009; Anderson-Teixeira *et al.*, 2013; McGregor *et al.*, 2020). Furthermore, and of relevance given the global COVID-19 pandemic, stress and immune physiology can provide evidence of the importance of healthy ecosystems in preventing land use-induced spill-over of zoonotic diseases (Plowright *et al.*, 2020; Cooke *et al.*, 2021c).

Physiological measurements can also represent robust indicators of population resilience, providing the evidence necessary to take conservation action (Bergman *et al.*, 2019). For example, by estimating optimal temperature of cardiac function in Baltic herring (*Clupea harengus*) larvae, Moyano *et al.* (2020) showed that the decline in annual productivity of this species, which provides a link between zooplankton and piscivorous fish and supports many fisheries, is connected to warming. Such physiological biomarkers therefore have great potential as assessment tools at timescales that are relevant to the fisheries industry (Moyano *et al.*, 2020).

In addition, physiological growth measurement of marine phytoplankton and plants can yield carbon sequestration rates that are important for mitigating the effects of climate change and nutrient uptake/incorporation required for controlling eutrophication (Beardall *et al.*, 1998; Beardall *et al.*, 2009; Basu and Mackey, 2018). Such projections can then be considered in spatial planning and management actions (e.g. MPAs) or habitat restoration projects aimed at maintaining or recreating these key ecosystem services using nature-based solutions. In other instances, physiological information can

help design human-made structures that will have less detrimental impacts on ecological function and better maintain ecosystem services in changed landscapes (e.g. design of culverts: Goodrich *et al.*, 2018; Watson *et al.*, 2018; Cramp *et al.*, 2021; or water diversion pipes: Mussen *et al.*, 2014; Poletto *et al.*, 2014a, Poletto *et al.*, 2014b).

Case study: physiological information improves infrastructure design to allow passage for native fishes

While there are examples of conservation physiology approaches helping to halt the conversion of natural habitats altogether [e.g. cessation of dam construction following physiological and behavioural monitoring of the endangered Mary River Turtle (*Elusor macrurus*); Clark *et al.*, 2009; see Madliger *et al.*, 2016 for a summary], more often, considering physiology has led to decision-making that lessens the impacts of environmental alterations that are deemed necessary. For example, to better inform upgrades for the Pacific Highway in Australia, researchers measured the swimming performance (critical swimming speeds— U_{crit} , burst swimming ability— U_{sprint} , endurance and traversability/passage success against water flow) of multiple native fish species in impacted rivers (Cramp *et al.*, 2021). These data provided the evidence necessary to allow the fisheries division of the New South Wales Government to insist that culverts would not be appropriate in areas where passage of certain species was necessary (Cramp *et al.*, 2021). Instead, bridge crossings were suggested as a better option, and researchers could recommend the aperture dimensions that were large enough to ensure the water velocity would allow transit by a key endangered species, Oxleyan pygmy perch (*Nannoperca oxleyana*) and other species of interest (Cramp *et al.*, 2021). This example illustrates that physiological data can assist in making management decisions that maximize ecological benefits and function in altered landscapes, in turn ensuring that essential ecosystem services can be maintained as much as possible.

Restoring native plant communities at large scales

Physiology can aid in nearly all aspects of the restoration process for plant communities (Cooke and Suski, 2008). At the site selection phase, characterizing the physiology of native plant species can determine the physical habitat and climate variables that must be present for successful restoration from seed or transplantation and subsequent growth (Kimball *et al.*, 2016). Furthermore, by evaluating the phenotypic expression of a variety of physiological traits related to phenology, carbon allocation, tolerance, etc., plant genotypes that are best suited to thrive under projected environmental changes can also be selected (Ehleringer and Sandquist, 2006; Kimball *et al.*, 2016). When invasive alien species must be combated to allow for successful restoration, physiology can be useful in determining vulnerabilities that can help with control and/or eradication (Sheley and Krueger-Mangold, 2003;

James *et al.*, 2010; Lennox *et al.*, 2015). Further, trait-based approaches can allow managers to design restoration communities that are resistant to invasion from the start (Funk *et al.*, 2008). For example, by assessing photosynthetic rate, growth and survival, Funk and McDaniel (2010) determined that establishing canopy species could limit growth of invasive grass species without adversely affecting native species that are ideal for restoration projects in Hawaii Volcanoes National Park.

Post-restoration, physiological monitoring can also quantify how plants are acclimatizing to a new environment (i.e. by providing health and function indices) to allow for adaptive management or intervention (e.g. fire and mowing) where necessary while also building an evidence base for future restoration initiatives (Funk *et al.*, 2008). For example, physiological measurements related to water balance, photosynthetic rate and annual aboveground productivity illustrated that the success of willow (*Salix* sp.) restoration efforts in areas with low water table may require simultaneously re-establishing beaver populations and limiting elk browsing (Johnston *et al.*, 2007). Physiological monitoring can further allow managers to choose between contrasting management treatments to enhance restoration success. For example, measuring leaf physiology allowed researchers to compare traditional and intensive silvicultural treatments following restoration with native tree species in Brazil, identifying the intensive silviculture practices as more beneficial for early establishment of natives (Campoe *et al.*, 2014).

Case study: informing restoration of the foundation tree species *Populus fremontii* with physiology

Populus fremontii, S. Wats. (Fremont cottonwood) is a dominant riparian tree that occupies a broad climatic range across the southwestern USA. It is also a critically important foundation species in the arid southwestern USA and northern Mexico because of its ability to structure communities across multiple trophic levels (Whitham *et al.*, 2008). Yet, altered stream flow regimes combined with changes in climate have resulted in a dramatic decline of pre-20th century habitat (Hultine *et al.*, 2020a). Restoring *P. fremontii* gallery forests that can thrive under current and future environmental conditions requires knowledge of physiological traits that could buffer individual genotypes against the forces of droughts and heatwaves. A recent common garden experiment revealed that chronic exposure to intense heatwaves could impose strong selection pressures on *P. fremontii* to maximize canopy thermal regulation via a suite of hydraulic strategies (Hultine *et al.*, 2020b; Blasini *et al.* 2021). Warm-adapted genotypes achieve greater evaporative canopy cooling during the summer, preventing potential thermal damage to leaves. However, an inevitable tradeoff is higher water use that could induce hydraulic failure during drought. Common garden studies are being used to identify *P. fremontii* genotypes that best optimize physiological traits to balance canopy thermal regulation with plant hydraulic limits. In turn, these studies are

identifying genotypes that can best thrive under future climate conditions that are predicted to bring more intense heatwaves and droughts to the arid regions of North America.

Rewilding regions with native species to restore ecological processes

Ripple *et al.* (2017) emphasized that apex predators will be especially important for restoring ecological processes and community dynamics. As a result, here we specifically include some examples related to the reintroduction of key predators; however, regardless of trophic level, physiology has avenues for integration at nearly all stages of the rewilding process (Tarszisz *et al.*, 2014), and the applications we discuss also include non-apex predator reintroduction scenarios.

For reintroduction programmes dependent on captive breeding, physiological monitoring can assess fertility, optimal reproductive windows and monitor pregnancy/gravidity to enhance the probability that offspring will be produced successfully. For example, monitoring urinary luteinizing hormone in combination with oestrogen or progestagen in giant pandas (*Ailuropda melanoleuca*) can better pinpoint the narrow window for successful mating and discriminate between pregnancies and miscarriages, respectively (Cai *et al.*, 2017). In female Asian elephants (*Elephas maximus*), manipulation of gonadotropin-releasing hormone (GnRH) can be used to induce ovulation at key timepoints of the reproductive cycle (Thitaram *et al.*, 2009) and monitoring serum progesterone can predict timing of oestrus to allow better coordination of breeding efforts (Carden *et al.*, 1998). Even in a much smaller species, the critically endangered Booroolong frog (*Litoria booroolongensis*), administration of GnRH can increase spermiation and the potential for captive breeding success (Silla *et al.*, 2020).

In cases where managers are creating new habitat in which animals will be translocated or reintroduced, physiology can help determine the abiotic and/or biotic features that may be necessary for persistence. Klop-Toker *et al.* (2016), with a knowledge of frog immune and nutritional physiology, were able to interpret that reduced breeding in male endangered green and golden bell frogs (*Litoria aurea*) was likely due to food limitation and exposure to chytrid fungus. They were therefore able to suggest diverse plantings to encourage invertebrate food sources, creation of ponds and recommendations to prevent disease prevalence for future projects (Klop-Toker *et al.*, 2016).

Physiological studies, often through measuring hormonal responses, can also be used to determine methods of capture, transport and release that are least likely to cause stress and/or post-release mortality (Teixeira *et al.*, 2007; Dickens *et al.*, 2010). Santos *et al.* (2017) paired a panel of physiological traits (haematocrit, leukocyte count, cardiac rate, body temperature, etc.) with telemetry data in wolves (*Canis lupus*) to determine the effects of trapping duration on stress and

post-capture movement. They concluded that adding technological solutions that decrease trapping duration, such as remote trap activation alarms, can lessen the physiological stress response and associated alterations to movement behaviour (Santos *et al.*, 2017). More broadly, measuring parameters related to stress physiology can allow managers to understand the consequences of different release methods (e.g. soft versus hard release), with soft release methods generally looking to be less detrimental to physiological function, behaviour and cognition (Teixeira *et al.*, 2007).

Physiology can also be helpful to identify other risks associated with reintroduction or translocation, such as alteration of host–pathogen interactions and disease. For individuals born and raised in captivity, physiological applications could include pre-release health monitoring, vaccinations or even ‘training’ the immune system via challenges (Tarszisz *et al.*, 2014). It has also been suggested that selection for host tolerance prior to release could be the best means of enhancing translocation or reintroduction success in the face of disease risk (Venesky *et al.*, 2012). Following release, health monitoring is also recommended (Sainsbury and Vaughan-Higgins 2012) and measuring thyroid status may be particularly useful for identifying sub-clinical diseases and evaluating overall health status (Tarszisz *et al.*, 2014). Indeed, monitoring a variety of physiological traits related to health, performance, tolerance and stress (e.g. glucocorticoids, thyroid hormones, nutritional physiology, health indices, body condition) can be used post-release to evaluate success and help determine other management actions that may be necessary (Tarszisz *et al.*, 2014). For example, reintroduction of tigers (*Panthera tigris*) to Sariska Tiger Reserve in India resulted in inadequate breeding success (Bhattacharjee *et al.*, 2015). To determine potential underlying causes, Bhattacharjee *et al.* (2015) measured faecal glucocorticoid levels and determined that encounters with humans, livestock and roads were likely causing disturbance for female tigers; this led to recommendations to relocate villages found in the core of the reserve and to restrict human activity throughout the reserve.

Finally, genetic techniques, such as transcriptional profiling of potential source populations, can provide information on physiological processes and responses to environmental stressors. Therefore, such techniques can represent a means to predict responses to reintroduction so that better candidates for release can ultimately be selected (He *et al.*, 2015). Physiology on its own (e.g. stress responsiveness, immune function) also has the potential to assist in determining reintroduction candidates. For example, Fanson (2009) found evidence that the magnitude of the stress response in Canada lynx (*Lynx canadensis*) was a predictor of post-release survival, with larger stress responses corresponding to shorter survival following reintroduction. The application of physiological tools for identifying ideal candidates for release is likely the area of reintroduction/translocation physiology that is currently least explored.

Case study: successfully rewilding megafauna through understanding their physiology

Careful rewilding or reintroduction of megafauna is crucial for restoring ecosystem function (Cromsigt *et al.*, 2018; Enquist *et al.*, 2020) and conserving species, sometimes in the face of heavy poaching (Ripple *et al.*, 2015). Successful translocation of large mammals requires their safe capture, holding, transport and release. Unfortunately, these interventions are associated with high levels of morbidity and mortality, as documented for rhinoceros (Miller *et al.*, 2016; Breed *et al.*, 2019). Etorphine, the standard drug used for capturing rhinoceros and many other herbivores, severely impairs cardiorespiratory function. However, recent trials using tools to study the physiological responses of immobilized rhinoceros have led to new protocols for chemical immobilization, resulting in improved physiological welfare (for example, Buss *et al.*, 2018; Haw *et al.*, 2014). During long-duration transport, measuring physiological variables has revealed that rhinoceros experience haemoconcentration, oxidative stress and stress-induced immunomodulation (Pohlin *et al.*, 2020). Anxiolytics that are used during transport to reduce stress responses may impair the immunological responses of rhinoceros, potentially leading to post-transport disease (Pohlin *et al.*, 2020). While improved chemical capture methods have been developed, the continued application of tools to understand physiological responses during and after translocation (Tarszisz *et al.*, 2014) is essential for successful rewilding programmes, not only for rhinoceros but also for other megafauna.

Developing and adopting policy instruments

Physiology can improve the evidentiary weight of conservation research and therefore provide the rationale for new policy decisions and bolster existing policies designed to remedy defaunation, the poaching crisis, pollution and the exploitation of threatened species (Cooke and O’Connor, 2010; Coristine *et al.*, 2014). By providing mechanistic insights into the causes of population decline and other conservation issues, physiology can confer the levels of reliability often considered necessary for policy development (Coristine *et al.*, 2014).

The most likely avenues for conservation physiology to intersect policy will grow from existing connections between scientists and practitioners. For example, while many researchers focusing on fish physiology do not have a direct line of contact with policymakers, collaboration with fisheries biologists can provide such a link (McKenzie *et al.*, 2016). Indeed, one of the earliest documented examples of conservation physiology influencing on-the-ground management is for Pacific salmon. Research on energetic and metabolic physiology, health monitoring and biotelemetry have led to better methods for recovering fish exhausted by fisheries interactions, increased the success of passage at fishways, helped managers make pre-season decisions on harvest rates, led to the installation of fish screens,

altered relocation efforts and reinforced the limitations on fishing effort when river temperatures exceed certain values (Cooke *et al.*, 2012; Cooke *et al.*, 2021a). There are also many examples in the realm of fisheries where considering physiology has improved bycatch avoidance or survival of marine mammals (e.g. Barlow and Cameron, 2003; Carretta *et al.*, 2008; Palka *et al.*, 2008) and non-target fishes (e.g. Young *et al.*, 2006; Jordan *et al.*, 2013; Lomeli *et al.*, 2021). Given that the channels for research co-production and influence of policy already exist in a fisheries context, there is great potential for conservation physiology to limit mortality from discards in many other fisheries, influence the design of MPAs (see above), predict potential invasions and spread by non-native species and understand how management actions should adapt under climate change (McKenzie *et al.*, 2016).

There is also great potential for conservation physiology research to inform policy related to pollutants, as it is well documented that physiology can be altered by chemical, physical (e.g. electromagnetic fields), particulate, thermal, light and noise pollution. Monitoring how physiology changes in the presence of different concentrations or types of pollutants can, therefore, provide the evidence necessary for restrictions based on specific threshold values to safeguard organismal health. For example, McKenzie *et al.* (2007) estimated metabolism of chub (*Leuciscus cephalus*) using portable swimming respirometers to determine the sub-lethal effects of heavy metals and organics in rivers. Swimming performance (the ability to raise metabolic rate and allocate oxygen towards exercise) was a reliable biomarker of the sub-lethal toxic effects of pollutant exposure (McKenzie *et al.*, 2007). Moreover, physiological responses to pollutants are often more sensitive indicators of adverse effects than some organism- or population-level responses. For example, Natural Resource Damage Assessments following oil spills often rely on point counts of heavily oiled birds showing visual symptoms of morbidity. However, Fallon *et al.* (2017, 2020) demonstrated that multiple species of birds with trace amounts of visible oiling exhibited a suite of symptoms related to haemolytic anaemia following the Deepwater Horizon spill. Such findings fundamentally change calculations of ecological damage from oil spills and, thus, influence the dialogue regarding environmentally protective policies.

Plant physiology also offers opportunities for understanding susceptibility to pollutants, and measures of growth and physiology have been used to identify concentration thresholds of effects for decades (McLaughlin, 1985). For example, alterations to stomatal behaviour, changes to carbon and nitrogen assimilation and interference with winter hardening processes can reflect tolerance and susceptibility to air pollution (Wolfenden and Mansfield, 1990). As a result of clear mechanistic connections between pollution and adverse physiological responses of plants and animals, some large regulatory bodies use physiological evidence to inform their policies (Rhind, 2009). For example, the European Commission enacted REACH legislation (EC 2006) that registers, evaluates, authorizes and restricts chemicals, and risks are

partially determined by drawing on physiological evidence in wildlife and humans, particularly for endocrine disruptors (European Commission, 2021).

Finally, we also see opportunities for physiological approaches to inform policies for species at risk. Incorporating physiology into species at risk plans has generally been limited and often is only present in the background information of recovery plans (e.g. US endangered species act recovery plans; Mahoney *et al.*, 2018). However, with the continued growth of the conservation physiology toolbox (Madliger *et al.*, 2018), there are greater opportunities in threatened and endangered populations to mechanistically link threats to physiological effects, formulate action plans and monitor conservation interventions (Mahoney *et al.*, 2018). Birnie-Gauvin *et al.* (2017) outline that a variety of physiological tools (sensory, cardiorespiratory, immunological, bioenergetics, reproductive, stress, etc.) can be useful in determining threat level under International Union for Conservation of Nature (IUCN) criteria by assisting with determining stressors, understanding species-habitat interactions and inferring or projecting population decline and its underlying cause(s). Overall, physiological information can improve the scientific basis behind threat status assignment using most criteria and, in turn, increase the likelihood that the formulated recovery plans will be successful (Birnie-Gauvin *et al.*, 2017). Indeed, knowledge of reproductive physiology in kiwi (*Apteryx* spp.) paired with genetic and behavioural techniques led to a successful translocation protocol and reclassification for three kiwi species in New Zealand (Birnie-Gauvin *et al.*, 2017). Measures of faecal glucocorticoids and reproductive hormones are also helping to refine management policies for the endangered white rhinoceros (*Ceratotherium simum*), indicating that dehorning procedures as an anti-poaching tactic can be used without long-term consequences for stress and reproductive function (Penny *et al.*, 2020). As new techniques for measuring physiological state in non-invasive ways are validated (e.g. glucocorticoids, reproductive hormones, thyroid hormones, stable isotopes for diet analysis), more capacity will be created for working in at risk populations where capture and handling currently pose a hindrance to use of more invasive physiological tools (Kersey and Dehnhard, 2014).

For this goal, we present three case studies below. The discipline of conservation physiology, being relatively new in formulation compared to many arms of conservation science, has been criticized for contributing more to threat assessment than enacting policy-based change and therefore is sometimes underappreciated by managers and policymakers. As a result, we use this opportunity to showcase how conservation physiology research can translate into policy decisions.

Case study: research on climate change impacts from heat and thermal extremes inform the Intergovernmental Panel on Climate Change

Large-scale, macrophysiological assessments of physiological tolerances have revealed that upper thermal tolerances—both

temperatures at which organisms can survive and those which limit activity—are remarkably similar across latitude in many terrestrial taxa. Early work demonstrating such constrained tolerances in insects (Addo-Bediako *et al.*, 2000) was followed by broader demonstrations of limited spatial variation in tolerances across multiple terrestrial groups (e.g. Hoffmann *et al.*, 2013; Araújo *et al.*, 2013; Lancaster and Humphreys, 2020). More critically, several analyses showed that owing to the spatial variation of environmental maximum temperatures, tropical organisms have a limited thermal safety margin (and/or a limited tolerance to warming) (Deutsch *et al.*, 2008; Huey *et al.*, 2009; Diamond *et al.*, 2012), despite warming associated with climate change not proceeding as rapidly in the tropics as elsewhere. Population-level work suggested that the impacts of limited warming tolerance and changing global temperatures were already discernible in some groups (Sinervo *et al.*, 2010). These critical analyses were incorporated into the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, through Working Group II on Impacts, Adaptation and Vulnerability (IPCC, 2014). The argument of tropical terrestrial organismal vulnerability to warming was clearly made on this basis. Subsequent research has started to explore the way in which terrestrial and marine species differ in their vulnerability to warming, the impacts of thermoregulation, the significance of heat extremes in the mid-latitudes and how tolerance differences among groups are likely to affect both population decline and range changes (Sunday *et al.*, 2012; Duffy *et al.*, 2015; Kingsolver and Buckley, 2017; Pinsky *et al.*, 2019), at least in part prompted by the need to better understand impacts and mitigate them through the policy process.

Case study: greater physiological tolerances in invasive alien than indigenous species lead to improved biosecurity policies

An early comparison of marine invasive and indigenous ascidians revealed that warming temperatures associated with climate change may give invasive species a significant advantage over indigenous species (Stachowicz *et al.*, 2002). This work was essentially reprising, in the context of global climate change expectations, two major hypotheses developed decades previously in plant invasion biology: the ideal weed hypothesis and the phenotypic plasticity hypothesis (Enders *et al.*, 2020). The first proposes that invasive alien species have some trait values that enable them to outcompete indigenous species (e.g. faster growth rates). The second proposes that phenotypic plasticity is most pronounced in invasive species. Although some complexity exists to these ideas (van Kleunen *et al.*, 2010; Hulme, 2017), support for such consistent differences, especially in basal trait values, is growing (Allen *et al.*, 2017; Capellini *et al.*, 2015; Van Kleunen *et al.*, 2018; Díaz de León Guerrero *et al.*, 2020). Among terrestrial invertebrates, for example, on average, invasive alien species appear to have greater thermal tolerances, more pronounced desiccation resistance and faster growth rates than their native counterparts

(Janion-Scheepers *et al.*, 2018; Phillips *et al.*, 2020; da Silva *et al.*, 2021). These research outcomes are being incorporated into assessments of the current and likely future impacts of invasive alien species through the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services Invasive Alien Species Assessment (IPBES, 2021). They have also been introduced into the work of the Committee on Environmental Protection (CEP) of the Antarctic Treaty, responsible for environmental governance of the Antarctic. Here, non-native species, as they are referred to in the CEP's language, are a priority concern.

Case study: embedding physiology into climate vulnerability and risk assessments

Climate vulnerability/risk assessments (CVAs) are conducted to help policymakers prioritize climate adaptation actions. Although the terminology has shifted from vulnerability to risk, similar components are included: exposure, sensitivity and adaptive capacity, with physiological traits playing an important role in the latter two. Several examples of CVAs have included physiological tolerance to single or multiple stressors when ranking the sensitivity of species to climate change. In one example, Hunter *et al.* (2014) integrated knowledge on thermal tolerance windows and thermal safety margins to calculate the sensitivity of commercially important fish to climate-driven warming in Pacific coastal waters off Canada. In a second example, Ekstrom *et al.* (2015) ranked the vulnerability of shellfish farms in the USA based on projected climate-driven shifts in the saturation of aragonite, a mineral needed for shell growth, of coastal waters due to ocean acidification as well as physiological impacts of eutrophication. That physiological knowledge on shellfish was combined with socioeconomic factors impacting dependent human communities. In a final example, Payne *et al.* (2020) combined thermal performance curves to demonstrate how different populations of the same species, such as Atlantic cod (*Gadus morhua*) in the North Sea, Irish Sea and Barents Sea, have markedly different climate risks. When that physiological knowledge was combined with other species traits and economic data on local fishing fleets, targeted climate adaptation advice could be produced for policymakers. A next critical step forward for CVAs is to increase our understanding of the physiological adaptive capacity of local populations as this element is poorly understood in even well-studied, commercially important fish and shellfish (Catalán *et al.* 2019) and is needed to plan climate adaptation strategies for food security.

Increasing outdoor education and overall societal engagement and reverence for nature

The prospects of success can be important for engaging individuals in any environmental movement (McAfee *et al.*, 2019). Conservation physiology offers many success stories that demonstrate how conservation issues can be tackled

(Madliger *et al.*, 2016; Madliger *et al.*, 2021b), rather than just assessed to determine threats or document declines. These successes provide examples that can motivate further work and provide researchers, practitioners and even the public with more confidence that positive changes are occurring. Further, physiological measurements can provide windows to observe the resilience of many organisms (Huey *et al.*, 2012; Gobler and Talmage, 2014; Seebacher *et al.*, 2015), which can illustrate that we still have time to make positive changes that will allow some species to recover.

Conservation physiology can also provide great storytelling tools because many of the adaptations that make animals or plants fascinating or unique are based in physiological functioning. For example, physiological feats (e.g. long-distance migration, hibernation and aestivation, growth and survival in harsh environments, deep diving) can be part of educational opportunities (e.g. zoo/aquarium or museum exhibits, curriculums, guided nature experiences) that can encourage appreciation of the natural world and a desire to strive for human–wildlife coexistence (Ernst, 2018; Godinez and Fernandez, 2019; Collins *et al.*, 2020). Finally, conservation physiology can also present direct opportunities for members of the public to engage in data collection, which can generate new connections to local wildlife and ecosystems. For example, participants in the ‘Neighbourhood Bat Watch’ community science programme in Canada assist in the identification of habitats important for thermoregulatory physiology and reproduction of little brown bats (*Myotis lucifugus*) (<http://www.willisbatlab.org/bat-watch.html>).

Case study: physiology informs the ‘Keep Fish Wet’ movement

Recreational anglers interact with the fish that they capture. To comply with regulations or as a result of conservation ethic, many fish are released. The ‘Keep Fish Wet’ movement (Danylchuk *et al.*, 2018) is a grass-roots social branding movement that recognizes that air exposure does not benefit fish. In fact, there is a wide body of science-based literature documenting the manifold negative consequences of air exposure on fish, many of which draw on physiological data (reviewed in Cook *et al.*, 2015). The #keepfishwet movement is all about simple messaging that encourages anglers to embrace better fish handling. This is one example of how empowering people and elevating important voices in stakeholder communities can be used to achieve outcomes that benefit the environment, drawing on physiological evidence.

Advice for initiating and driving change

We close with some additional advice based on personal experiences that can broaden the impact of science aimed at accomplishing the steps of the ‘Second Warning’ (Fig. 3). The list is by no means exhaustive but, instead, focuses on

small approaches that can be taken by any conservation physiologist, regardless of their research topic or career stage.

(i) *Publish the best science possible, applied or otherwise, and consider and discuss in as many publications as possible the conservation implications of the results:* Many conservation physiologists are multi-faceted in their research programmes, publishing in ecology, physiology, conservation science and taxa-specific journals simultaneously. The strongest conservation physiology work will be grounded in an underlying understanding of the physiological systems being measured, and attention to context-dependency and inter- and intra-individual variation in physiological metrics will raise the profile of the field and increase the applicability of the evidence it provides (Madliger and Love, 2015). For example, considering covariates that are necessary to understand the physiological variation measured, such as sex, age, location, time of year, etc., will improve the conclusions that can be drawn for whole populations. Likewise, including proper quality controls and sufficient methodological details will increase the work’s reproducibility and defensibility, which is particularly important to make the work useful in policy and management decisions. When possible, stating the conservation applications of the work clearly, even in those papers focused mainly on ‘pure science’, and including its potential use by practitioners or policymakers will have great impacts in the future (Mahoney *et al.*, 2018).

(ii) *Design studies with the use of the data for conservation and management decisions in mind:* Collaborating with scientists and practitioners at the onset of projects (i.e. engaging in co-production) will improve the likelihood that the collected physiological data will be useful to those poised to make on-the-ground decisions (Patterson *et al.*, 2016; Laubenstein and Rummer, 2021). Local communities can have ecological knowledge that is essential to interpreting physiological data and planning monitoring or experimental designs that will be successful. Similarly, staying up to date with new technology, particularly minimally invasive or non-invasive options, is expected to encourage up-take by conservation practitioners, who are often working with small or sensitive populations that cannot be manipulated extensively.

(iii) *Maintain a holistic view of conservation problems by removing yourself from your research silo:* Conservation physiology approaches may need to be integrated into solutions that are based not just on scientific evidence, but also in cultural and political contexts that could involve barriers, connections to local communities, multiple stakeholders with opposing views and considerations of economic impacts. By taking part in research agenda and knowledge co-production, conservation physiologists can work hand-in-hand with communities and stakeholders to design and collect data that will have the greatest applicability to all involved (Laubenstein and Rummer, 2021). A wide field of view can also be accomplished by attending diverse meetings and conferences, reading literature outside of one’s own main research focus, attending and giving talks to local naturalist and conservation

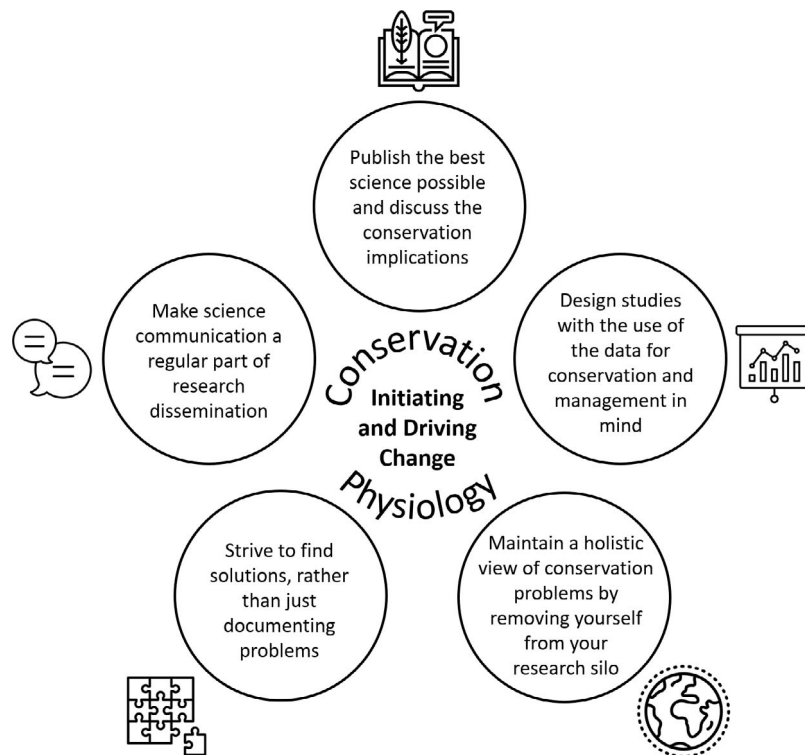


Figure 3: Summary of the five approaches that conservation physiologists can undertake to broaden the impact of science aimed at accomplishing the goals of 'The Second Warning to Humanity', based on the authors' personal experiences.

organizations and building new collaborations across disciplines within and outside of academia.

(iv) *Strive to find solutions, rather than just documenting problems:* Conservation physiology techniques have often been used to determine whether certain environmental changes are stressful or otherwise deleterious. This application is incredibly useful within the context of monitoring and managing populations; however, physiology imparts the added value of identifying *why* an alteration presents a challenge to organisms and in what way. Through this mechanistic insight, physiological information has the power to inform managers and practitioners about how to best address the consequences of environmental change (Cooke and O'Connor, 2010). Considering how different physiological traits could be measured to help identify cause-effect relationships and maintaining a solutions-oriented mindset when designing and disseminating research can only strengthen the applicability of conservation physiology. Solution-oriented work that is co-produced is also inherently more engaging and empowering to stakeholders, practitioners and policy makers than simply documenting yet another environmental problem.

5) *Make science communication a regular part of research dissemination:* Conducting research comes with an academic responsibility to disseminate results in the peer-

reviewed literature. Engagement in public discourse about scientific findings, their contribution to reliable knowledge and the role of science in society has long also been an important social responsibility of those conducting research. In the face of disinformation and pseudoscience, unfounded conspiracy theories, denialism and the politicization of scientific evidence, effective scientific communication with the public has taken on even greater importance. Conservation physiologists can engage with society by embracing the power of social media, imagery and film, by registering with and contributing to mainstream media centres, by drafting accurate press releases and by taking advantage of carefully worded institutional promotional resources (Laubenstein and Rummer, 2021). Public engagement requires less jargon, an assessment (but not underestimation) of the audience, and welcoming language that invites individuals into the science and the science process (Laubenstein and Rummer, 2021). At the undergraduate and graduate student level, the next generation of scientists can be encouraged and supported to take advantage of training opportunities in science communication. Conservation physiologists can also work directly with their local communities. Interactions with schools to infuse more science into local classrooms will inspire passion about the natural world in young learners who are often disconnected from their environment (Soga and Gaston, 2016). Local school boards frequently have opportunities for engagement with teachers, but there are

also global initiatives that link scientists with classrooms (e.g. ‘Letters to a Pre-Scientist’: <https://www.prescientist.org/>; ‘Skype a Scientist’: <https://www.skypeascientist.com/>). Simply talking with neighbours and at local community groups is similarly valuable.

While some conservation physiologists will be comfortable with and skilled at science communication, others will either have little time to do so given other demands or may be reluctant to do so for a variety of reasons. Alternative avenues are available to share research without having to undertake all of this work as an individual. Conservation physiologists can make and maintain connections to science journalists, and support them, by providing story ideas, by developing sound working relationships and by emphasizing the value of having science journalists in news and other media outlets, as well as within their institutions. Science journalists are not only adept at the interpretation and presentation of science for different audiences, but they also already have established long-standing relationships with those audiences. Although the productivity of researchers is still largely gauged by metrics related to academic publishing, assessments of public engagement are taking on greater significance (Gruzd *et al.*, 2011). Regardless of how these communication goals are accomplished, they should be viewed more widely as a valuable translational outcome of research and should be supported by institutional policies to promote science communication and reward individuals who take part in the process either directly or indirectly (Sugimoto, 2016).

Conclusions

With the goals outlined above, the role of physiology in addressing conservation issues is best situated as part of a multi-disciplinary toolbox that spans the natural and physical sciences, social sciences, humanities and economics. Our goal here has been to showcase that physiological tools and techniques have great potential in addressing 6 of the 13 steps that Ripple *et al.* (2017) outlined as important for humanity’s transition to sustainability (Fig. 1). This complements other recent efforts, including a horizon scan of how conservation physiology can help to address grand challenges (Cooke *et al.*, 2020) and the generation of a list of pressing research questions for conservation physiology (Cooke *et al.*, 2021b). Moreover, the ‘Second Warning from Scientists’ emerged prior to the COVID-19 global pandemic, which has led to many discussions about the role of science (including conservation physiology; Cooke *et al.*, 2021c) in the post-pandemic transition and recovery in addressing long-standing environmental problems (Nhamo and Ndlela, 2021; Sandbrook *et al.*, 2020). By providing examples here, we hope that conservation physiologists are inspired to take up or continue working on these broad goals as diverse teams across the globe. The final advice we provided was based on our own experiences, and we hope it is useful to those, especially early career conservation physiologists, working

to increase the reach, relevance and applicability of their research (Fig. 3). There are other steps outlined by Ripple *et al.* (2017) where conservation physiology may not directly contribute (e.g. reducing food waste, revising our economy to reduce wealth inequality), but this speaks to the multi-disciplinary nature of environmental problem solving. We see conservation physiology as just one of many arms of conservation practice that, when applied collaboratively and in partnership with other disciplines and stakeholders, will contribute meaningfully to addressing complex conservation challenges.

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