Introduction

Determining environmental causes of biological effects: the need for a mechanistic physiological dimension in conservation biology

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The emerging field of Conservation Physiology links environmental change and ecological success by the application of physiological theory, approaches and tools to elucidate and address conservation problems. Human activity has changed the natural environment to a point where the viability of many ecosystems is now under threat. There are already many descriptions of how changes in biological patterns are correlated with environmental changes. The next important step is to determine the causative relationship between environmental variability and biological systems. Physiology provides the mechanistic link between environmental change and ecological patterns. Physiological research, therefore, should be integrated into conservation to predict the biological consequences of human activity, and to identify those species or populations that are most vulnerable.

Keywords: global change; climate change; land clearing; adaptation; acclimation; ecological success

Conservation Physiology may be defined as the application of physiological theory, approaches and tools to elucidate and address conservation problems with the aim to provide a mechanistic understanding of how environmental disturbances and threatening processes impact physiological responses and thereby ecological function, population persistence, and species survival.

1. INTRODUCTION

The importance of addressing conservation issues, such as climate change, emerging diseases and habitat loss, lies in preserving the integrity of ecosystems at local and global scales. Biodiversity is essential to provide utilitarian ecosystems that can sustain human subsistence, as well as cultural values that confer a sense of identity. A well-functioning natural environment and maintenance of biodiversity are thus fundamental to human well-being [1]. Climate change and environmental degradation has already resulted in negative consequences for human subsistence and health and, hence, economic success [2,3]. The regional decline of agriculture [4] and of some fisheries [5–8] are examples of environmental and ecological problems that can be attributed directly to human activity. The most crucial issue is to slow anthropogenic impacts on natural systems and thereby maintain functioning ecosystems. There is good evidence that conservation can work [1,9], and our aim here is to help improve the effectiveness of conservation measures by linking physiology and ecology in a mechanistic framework, thereby providing a stronger knowledge base for decision-making.

Any conservation measure requires sound scientific information of the effects that habitat alterations resulting from human activity have on natural systems [10]. Even if the political will existed to curtail all human impact, this is logistically impossible. Conservation must therefore be selective and pragmatic. Decisions must be based on an understanding of the impacts that particular human activities have on ecosystems, so that the benefits of remedial actions can be maximized, while the costs to society are minimized. In other words, there is an urgent need to understand the link between the cause (i.e. human activity) and its effect on biological function from individuals to ecosystems. We argue here that in many if not most cases, the physiology of individuals provides this link between cause and effect, and can thereby explain ecological patterns. Physiological capacities and responses act as a filter between environmental change and ecological performance of individuals and, hence, populations and species [11,12] (figure 1).

2. HUMAN ACTIVITY MODIFIES THE ABIOTIC AND BIOTIC ENVIRONMENTS

Environmental change is natural and occurs at different time scales. For example, natural forcing can cause
Regional climate change at time scales of 1–10 years [13], and palaeoclimate records around the globe show that regional climate fluctuation of as much as 8–16°C occurred repeatedly at periods of less than 10 years [14]. These regional climate changes have had a direct impact on human societies [2]. Importantly, forcing by human activity accelerates climate change at regional and global scales. Human activity such as extensive deforestation may have affected climate since prehistoric times in Europe [15]. However, the recent climate change induced by increased CO₂ emissions starting in the late twentieth century remains unprecedented [15,16]. The resulting increases in temperature and acidification of marine systems are global [16], although temperature increases can be much more pronounced in climate change ‘hotspots’. For example, sea temperatures in southeastern Australia have increased much more rapidly (by 2–3°C since the mid-twentieth century) than the global average [17]. Regional and small-scale changes in the environment are also driven by local land-use practices [18]. Deforestation and land clearing affect biodiversity by direct removal of species. Direct removal of species, either as a result of land clearing or of exploitation for human use, alters resource availability, such as shelter and food, for higher trophic levels. Land clearing causes climate warming by adding CO₂ to the atmosphere and decreasing evaporation, but it may also have a cooling effect by changing the surface albedo [18]. Removal of vegetation cover affects the hydrologic dynamics of the soil and may contribute to increased salinization of freshwater systems [19,20].

Other major impacts on the physical environment at global or regional scales result from pollution. Dumping or spillage of industrial chemicals has a direct impact on the environment. Examples of negative effects on biodiversity are chemical spillages from mine tailing dams, such as in the otherwise relatively pristine rivers of New Guinea [21]. The military strategy of defoliation, whereby American forces dumped hundreds of thousands of tonnes of herbicides on forests in Vietnam in the 1960s and 1970s, has caused large-scale deforestation and pollution, the effects of which are still present today [22]. At a global scale, the increase in ultra-violet (UV) radiation as a result of hydrofluorocarbon release can affect ecosystems by disrupting different life-history stages of vulnerable species, and its effect may be compounded by other stressors such as pollution [23,24].

3. ECOLOGICAL SUCCESS IS COUPLED TO ENVIRONMENTAL CONDITIONS VIA THE SENSITIVITY OF PHYSIOLOGICAL SYSTEMS

It is well established that changes in the abiotic environment affect the physiology of organisms at multiple levels. A large proportion of reproductive success and individual fitness is determined by physiology, so that environmental change affects fitness by its effect on physiology. Time to sexual maturity depends on growth rate and therefore on the capacity of energy assimilation and metabolism [25]. Foraging, competition and reproductive behaviour of animals are a function of locomotor performance and therefore of muscle physiology and metabolism [26,27].

The efficacy of metabolism and muscle physiology as well as most other physiological systems depends...
on the cellular environment (temperature, pH, acid–base balance, etc.), which is influenced by the external environment. Changes in body temperature, for example, affect biochemical reaction rates and most organisms function best within a relatively narrow range of body temperatures. Because the thermal sensitivities of individual reaction rates vary, the challenge for organisms lies in maintaining the stoichiometry of their complex cellular biochemistry, which will be disrupted by a change in the thermal environment. Increases or decreases in means or variability of operative environmental temperatures change body temperature directly in those organisms that do not thermoregulate, or change the environmental context within which animals thermoregulate [28]. In endotherms, a decrease in environmental temperatures will elicit an increase in metabolic heat production and, conversely, increases in temperature decrease metabolic heat production. Ectotherms may respond to changes in environmental temperature by selecting different microhabitats, such as increased shelter use to minimize absorption of solar radiation in warming environments [29]. In addition to behavioral responses, many ectotherms modulate their cellular biochemistry to compensate for thermal effects by, for example, quantitatively or qualitatively changing the expression of rate-limiting enzymes [30,31]. In all cases, the change in physiological need that ensues from a change in the environment will alter the resource use of individuals. In the examples above, energy requirements and the utilization of the structural environment change, both of which have important ecological consequences by changing foraging and predation, and competition for particular microhabitats. Similar relationships as discussed briefly above for temperature exist for changes in other abiotic environmental variables, such as UV-B radiation, CO₂ levels, rainfall and dehydration, hypoxia and salinity. Hence, physiological requirements are at the interface between environmental change and ecology (figure 1).

Importantly, physiology also mediates biotic interactions. These interactions may be nested within the effect of abiotic drivers as in the example above where energetic needs for thermoregulation change in different environmental contexts. Nutrition, with respect to both energetic and macronutrient requirements, in particular determines interactions between organisms [32,33]. At a quantitative level, density of prey will determine predator numbers [34], but this relationship will change with environmentally driven changes in energy requirements, such as for thermoregulation. Different abiotic contexts can also change the macronutrient requirements of individuals and therefore change the need for prey quality in addition to quantity. For example, temperature affects the relative macronutrient requirements in trout, and fish at warm temperatures require relatively more protein than at cooler temperatures [35]. As a result, foraging behaviour must be adjusted to meet intake targets, and predation pressures shift to different prey species, potentially leading to a change in community structure and interactions [33].

Similarly, decreases in aquatic oxygen levels in freshwater river systems can impact on the diving ecology of bimodally respiring turtles, requiring them to expend greater energy to surface more frequently to acquire oxygen from the air, but also increasing the risk of predation, especially in hatchlings as they swim through the water column [36]. Changes in salinity of freshwater systems also change the activities of ATPases for ion regulation [37] and therefore regulate energy intake, and thereby the impact that individuals have on their ecological community.

Most species possess a degree of plasticity that permits persistence across a range of environmental conditions. However, there is a limit to physiological compensation for environmental variability [38,39]. If environmental conditions become too extreme, direct cellular damage may ensue and animals will become more susceptible to disease [40], and ultimately extinctions will occur.

4. PHYSIOLOGICAL SYSTEMS CAN COMPENSATE FOR ENVIRONMENTAL CHANGE—UP TO A POINT

The effect of environmental variation on physiological function (phenotype) may be modulated by compensatory responses. Such responses can occur at different time scales: between generations (genetic adaptation) [41], during development (developmental plasticity) [42,43] so that phenotypes are matched to prevailing environmental conditions, and within the adult lifespan as reversible plasticity (acclimation and acclimatization) [44–46] and migration [47,48].

The optimal ‘adaptive strategy’ of organisms depends on the patchiness or ‘grain’ of the environment [49]. A coarse-grained environment fluctuates between distinct states, and an individual is exposed to only one. Performance and fitness in a coarse-grained environment may be maximized by genetic adaptation if environmental conditions remain stable across generations, and by developmental plasticity if the environment remains stable during the lifetime of the organism [49,50]. In a fine-grained environment, an individual experiences numerous patches, so that total fitness will be the sum of the individual fitness components of each patch, and reversible acclimation would enhance performance and fitness [30,51]. In theory [49,52], coarse-grained environments will produce phenotypes that are specialized (adapted) to the relatively stable conditions experienced, while fine-grained environments produce generalists that perform well over a wider range of environmental conditions albeit at a reduced level; in other words, generalists trade-off maximal performance for performance breadth. However, this need not be the case if reversible acclimation can compensate for environmental variation experienced during the lifetime, effectively leading to ‘specialized generalists’ in which the conditions at which performance optima occur track changes in environmental conditions without loss of performance [51,53].

Most species experience both fine- and coarse-grained variation at several temporal (e.g. day, season and geological) and spatial (e.g. microhabitat and latitude) dimensions, as well as the interaction of the two resulting from animal movement within habitats [54], between geographically separated habitats [48], or as a consequence of life-history stages occupying different
habits [55]. Hence, fine-scale patchiness at a short temporal scale is added to coarse scale variation at longer periods. Patchiness of the environment changes naturally, for example, with season or latitude. However, conservation issues may arise when human activities alter patchiness and thereby disrupt evolutionary strategies. Local land-use patterns such as deforestation and agricultural activities, and anthropogenic climate change, for example, can alter fine- and coarse-grained patchiness of the environment, respectively.

The relative importance of plasticity and adaptation will depend firstly on the relationship between lifespan and rate of environmental change and, secondly, on the rate of phenotypic change relative to environmental change. The importance of lifespan is that species with very short lifespans may experience only one distinct (coarse-grained) environment, so that genetic adaptation between generations and possibly developmental plasticity will be the most important responses. Many species, however, will also experience at least some variation within their lifetime. In this case, the optimal adaptive strategy will be a plastic phenotype that can acclimate to each of the predictable extremes, in addition to genetic adaptation to latitudinal and altitudinal gradients [12,56,57].

Ideally, fitness is maximized when organisms can perform at a constant level despite environmental variability. It is impossible, however, that the phenotype can change at the same time as the environment, if the environmental change provides the signal for phenotypic change. Hence, there will always be a lag between the two. The lag in the phenotypic response may preclude plasticity, when the rate of environmental change is greater than the potential for phenotypic change. Hence, an environmental fluctuation with a period that is much shorter than the physiological response time could not act as a stimulus for phenotypic change. For example, it will take several weeks for changes in metabolic gene expression and enzyme activities to compensate for a chronic change in temperature [58,59] so that daily temperature fluctuation will not affect metabolic capacity. Generally, acute changes in temperature resulting from movement through different microclimates, weather changes and diurnal fluctuations may affect real-time physiological rates, but do not affect capacities. Similarly, genetic adaptation will occur only when the rate of environmental change is slower than that of genotypic change. Human activity is often rapid relative to the rate of adaptive processes and even relative to the lifespan of many organisms. Hence, genetic adaptation may play a lesser role in responding to human-induced environmental changes than developmental- and reversible plasticity. This means that capacity for acclimation will play a predominant role in determining the vulnerability of organisms to environmental change. Human activity will affect species within the same habitat differentially, depending on their capacity for physiological plasticity and lifespan; the latter characteristics alone can provide valuable background data informing conservation decisions.

Even in the most plastic organisms, however, the capacity to compensate for environmental change has its limits [38]. These limits may be set by inadequate environmental resources such as energy and nutrient supply, which may curtail growth, locomotion and other energy-consuming processes [32,60,61]. Limits may also be set by biochemical constraints such as an increased inefficiency of mitochondria in producing chemical energy (ATP), or by the production of reactive oxygen species, which cause damage to membranes and proteins [31,62,63]. Beyond these limits, fitness will decrease as a result of declining performance, and accumulated damage and disease. Successful conservation must predict these limits and, if possible, maintain the range of environmental fluctuations within the limits of effective organismal responses. An understanding of the capacity for individual plasticity that may compensate for human-induced changes is of particular importance in the light of rapidly changing environments. It is unlikely that all species or populations within a region will have the same capacities and limitations. However, knowing the limits of physiological responses to environmental perturbations will make it possible to identify the elements of the ecosystem that are most vulnerable to particular human activities.

5. PHYSIOLOGY CAN DETECT CAUSE AND EFFECT TO DETERMINE VULNERABILITIES TO ENVIRONMENTAL CHANGE

To date, most information regarding biological responses to anthropogenic environmental changes, and in particular to climate change, consists of correlations between environmental and biological variables [64,65]. For example, northward shifts in the distributions of marine and terrestrial organisms in the Northern Hemisphere have been associated with the avoidance of increasing temperatures at lower latitudes caused by anthropogenic climate change [66,67]. Shorter winters and mild springs resulting from global warming have been correlated with the earlier flowering of plants and other shifts in phenology [68]. These correlational data are essential to understanding the potential impact of climate change on biological systems. However, correlations are not sufficient to determine whether climate change has caused the observed changes in distribution or phenology. Invariably, any biological pattern will be correlated with a large number of abiotic and biotic patterns—some known, many unknown. To determine whether or not a change in the environment can cause the observed change in pattern requires experimental evidence [69]. It would be necessary to demonstrate experimentally, with adequate controls, replication and elucidation of the underlying pathways, that the environmental variable in question can affect the observed biological changes.

For example, in one of the first studies that related global warming to a change in distribution, Parmesan et al. [66] showed a northward shift in distribution of butterflies in Britain between 1910 and 1997. However, over that time frame, there were many changes in the British landscape, and one very obvious one was the decline and collapse of the coal industry in northern England and Scotland (figure 2). Plotting the abundance of butterflies in Scotland (i.e. the northermost
distribution) given in fig. 1 of Parmesan et al. [66] against the number of coalmines in the area (data from the UK Coal Authority) gives a perfect correlation of $r = 1$ (figure 2). Apart from the inherent limitation of only three data-points, figure 2 clearly presents an alternative hypothesis explaining distributional range shifts of butterflies in the UK in the last century. Which explanation is correct, global warming or coal pollution, if any? The only way to determine the correct answer is by experimentation. Another example is the perceived northward shift of fish in the North Sea [67] as a result of mean water temperature increases in the southern North Sea. At least for some species such as cod ($Gadus morhua$), published data [70–72] show that the fish are well able to acclimate to temperatures over the observed temperature increase in mean surface temperature from 11.7°C to 13.0°C in the North Sea between 1980 and 2006. In fact, the fish are more likely to be limited by cold at those temperatures than to be heat stressed. Hence, what is known about the physiology of the fish does not support the conclusions drawn from the correlational study that temperature per se caused shifts in distribution. Plausible alternative explanations that could explain the changed distribution pattern include overfishing, and a decline in copepod abundance which is the main food source of larval cod [73]. Cod are a good example of the challenges facing marine conservation, because the complex responses to environmental variability within individuals and between populations [8] make it difficult to manage the resource. Conservation physiology can make a significant contribution, because understanding the plasticity of physiological responses of the species will permit modelling of ecological responses [8] and predictions of the impact of future environmental change. Finally, correlations between climate change and bird distribution patterns lack predictive power and are unlikely to reveal the mechanistic basis of changes in distribution [74].

Correlations are essential to propose hypotheses that could explain the observed patterns. Hence, the studies cited above and many other correlational studies are extremely important. Over-interpretations of correlations, however, are detrimental to conservation because a misrepresentation of the cause underlying a biological pattern means that conservation efforts are misguided. This is where the importance of physiology lies: it can detect the cause. Even in the absence of a positive result, fairly standard physiological studies can eliminate possible explanations. In the cod example above, physiological studies have shown that locomotor performance [72], metabolism and growth of larvae [70,72], and even food supply [75] are not negatively affected by the observed temperature increase. Hence, temperature increases per se can be ruled out in explaining the observed distributional shift. It is now clear that overfishing is the most likely candidate to have caused the pattern [5]. We would like to emphasize that we do not wish to downplay the importance of climate change. Instead, we advocate a more stringent assessment of its effects to increase the efficacy of conservation measures. Physiological research provides a tool to identify causes of biological change, and to eliminate others that may be correlated but not causative.

The environment interacts with physiological capacities of individuals. Growth rates, as well as other fitness-related functions such as locomotion [76], are directly dependent on individual physiological capacities such as for aerobic metabolic energy production. Population growth—either positive or negative—is the sum total of the growth and performance of individuals. A shift in the environment that causes a mismatch between environmental conditions and optimal temperatures for individual physiological

![Figure 2. Correlation between butterfly distribution and coal mining. Butterfly distributions (from Parmesan et al. [66]) in Scotland were plotted against the number of coalmines in the area during the same time periods (inset). The strong correlation presents the alternative hypothesis that butterfly distributions are constrained by coal pollution rather than by climate change as suggested by Parmesan et al. [66]).](http://rstb.royalsocietypublishing.org/)

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performance can therefore cause population declines and extinctions if performance optima are fixed within populations. Hence, there is a need to understand individual responses to changing environments and then translate these to populations, species and communities [8,11,12].

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