Review TRENDS in Ecology and Evolution Vol.21 No.2 January 2006

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Conservation physiology

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Conservation biologists increasingly face the need to provide legislators, courts and conservation managers with data on causal mechanisms underlying conservation problems such as species decline. To develop and monitor solutions, conservation biologists are progressively using more techniques that are physiological. Here, we review the emerging discipline of conservation physiology and suggest that, for conservation strategies to be successful, it is important to understand the physiological responses of organisms to their changed environment. New physiological techniques can enable a rapid assessment of the causes of conservation problems and the consequences of conservation actions.

Conservation physiology: a trusted approach evolving into its own discipline

Physiological tools have been used in conservation science for many years. A hallmark example is the discovery of the effects of dichloro-diphenyl-trichloroethane (DDT) on the reproductive biology of top predators [1]. Once the causal connection between DDT and reproductive failure was established, the use of DDT-like substances was prohibited in large parts of the world. The DDT tragedy reinforced that physiological investigations of wild animals are important for conservation, not only to establish cause and effect and to provide baseline background data, but also to monitor the efficacy of management strategies. Physiological methods are also often the only tools available to assay the perception by an animal of its environment [2] and many minimally invasive techniques are now readily available for use in field studies.

Here, we review the emerging discipline of conservation physiology, which we define as the study of physiological responses of organisms to human alteration of the environment that might cause or contribute to population declines. Conservation physiology is an important field because it goes beyond a description of patterns to include a detailed mechanistic understanding of what causes conservation problems [3]. The physiology we are referring to usually includes whole-organism function such as metabolism, thermal relationships, nutrition, endocrine responses to environmental changes and changes in immune parameters [4].

We focus on animals, but conservation physiology is also relevant to other organisms. Among plants for example, Pywell *et al.* [5] used physiological traits as predictors of performance in grassland restoration and Orth *et al.* [6] applied knowledge of seed dormancy and germination physiology to sea-grass conservation. Others have used information about physiological tolerances and requirements to predict responses of marine plants [7] and terrestrial plant diversity [8] to climate change.

Detection and assessment of current conservation problems

Human influence on natural systems is increasing continuously. Thus, it will become increasingly important to understand what aspects of human influence cause ‘stress’ in animals in these natural systems. Following Romero [9], we define a ‘stressor’ as a noxious stimulus and the ‘stress response’ of an organism as a suite of physiological and behavioral mechanisms to cope with stress. The duration of a stressor is important for organisms. Acute stress, such as predator attacks, typically lasts only a short period of time, whereas chronic stress, such as long-term climate change and/or starvation, becomes long-lasting. We suggest that a good start to conceptualize the influence of stressors on organisms is achieved by expanding McEwen and Wingfield’s stress model [10]. They introduced three concepts: (i) ‘allostasis’ is the maintenance of homeostasis through change; (ii) ‘allostatic load’ results from activities and experiences of individuals during daily life, which animals can deal with up to a limit; and (iii) ‘allostatic overload’, which is a state in which organisms can no longer cope with external requirements. Only if a stimulus pushes the organism into allostatic overload will it need to change its physiology and behavior to survive. Under most circumstances, the organism copes adequately with environmental stimuli and continues along its life-history path [2,9,11]. An organism will then be ‘stressed’ only if an allostatic overload is reached. McEwen and Wingfield suggest allostatic overload results from energy requirements that are beyond the capacity of the organism to replace from environmental resources. Psychological stressors, human activities, social interactions and pathogens also might induce allostatic overload even if they do not necessarily increase overall energy demand. However, such stressors might act by changing the energy balance of an organism, for example, by reducing energy intake or by

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Available online 11 November 2005

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reducing digestive efficiency. Allostatic overload might be a useful concept for conservationists to quantify because it provides an integrated measure of the multitude of environment stressors afflicting wild animals.

Several techniques exist already that enable the remote monitoring of wild animals (Table 1). Researchers can use biotelemetry to detect behavioral and physiological changes in real time with minimal disruption to the animal [12]. These tools can now be applied to animals as small as insects and are resulting in the simultaneous monitoring of an increasing number of variables (e.g. heart rate, opercular rate, tail or wing or appendage beats). In addition, doubly labeled water, a method to quantify CO_2 production via isotope turnover, is effective for monitoring the energetics of free-ranging animals [13–15]. To assess reproductive characteristics including estrous cycles and pregnancy for imperiled wildlife [16] as well as stress levels [17,18], conservation physiologists increasingly use non-invasive fecal steroid metabolites [19,20].

Understanding the physiological causes of stress and the individual responses to it will enable us to develop effective countermeasures [11]. A classic example is the northern spotted owl *Strix occidentalis caurina* (Box 1). Conservation physiologists can assess the stress responses of animals resulting from seemingly benign human activities such as ecotourism, recreational fishing or vehicle traffic. Nimon *et al.* [21] used data loggers located in artificial eggs to measure heart rate in nesting gentoo penguins *Pygoscelis papua* and determined that human presence as well as behaviors such as movement (by humans) caused the heart rate to increase. In Emperor penguins *Aptenodytes forsteri*, human disturbance can result in an energetically costly increase in body temperature that accounts for up to 10% of the daily energy budget during molt [22]. In Magellanic penguins *Spheniscus magellanicus*, Walker *et al.* [23] found that chicks do not habituate as well as adults to tourist activity. Here, physiological (hormone) studies uncovered what would have probably been missed in more conventional

Table 1. Examples of physiological disciplines and their potential contributions to conservation physiology

Physiological discipline	Examples	Potential contributions to conservation physiology	Refs
Endocrinology	Blood sampling or non-invasive feces collections; quantification of glucocorticoid, reproductive steroid or growth hormone levels; pregnancy rates	Enables the assessment and quantification of anthropogenically induced chronic or acute stressors that can ultimately affect fitness or survival. Provides tools for assessing strategies for ameliorating or minimizing stress responses. Provides information about the reproductive biology of organisms that can be used for captive breeding or biological control. Helps promote understanding causes of low recruitment (poor juvenile survival versus low birth rates owing to poor condition of adults)	[2,3,15,18,68]
Environmental and ecological physiology	Biotelemetry; implanted data loggers to quantify body temperature, energy expenditure or activity	Enables understanding of the distribution and abundance of different organisms in different environments based on environmental tolerances. Elucidates the responses of organisms to environmental change and the development of predictive models	[12,21,22,25,75]
Comparative physiology and biochemistry	Tools available for surrogate species can be transferred to endangered species	Develops generalizations and relationships that can be used in predictive capacities	[43–45]
Evolutionary physiology	Theoretical models	Provides information about the factors that guide, direct and constrain physiological evolution. Links directly to the life-history and, thus, population biology and fate of organisms. Develops models to predict the long-term evolutionary consequences of selection for different phenotypes	[7,64]
Immunology and epidemiology	Tests for the functioning of systemic innate, cell-mediated or humoral immune responses	Provides an understanding of the effects of immune disorders and disease on organismal performance and survival. Aids in understanding pathogen behavior and consequences, which is particularly important for conducting population viability analysis of stressed or rare organisms	[4,39]
Physiological genomics	Gene arrays for expressed genes	Details the functioning of gene products in the context of the whole organism and its environment. Reveals information that can be used to understand how organisms will respond to environmental change and for characterization of molecular physiological diversity	[55]
Neurophysiology	Direct neuropeptide manipulations in wild animals; biotelemetry of neural activities; effects of underwater noise on marine mammals	Linkages to conservation biology not as clear as other physiological disciplines. Facilitates understanding of the neural basis of behaviors, which is important because a fundamental understanding of conservation-related animal behavior has been repeatedly identified as an essential prerequisite for biological conservation	[76,77]
Environmental toxicology	Determination of trace elements; experimental tests of negative health effects	Provides information about the physiological effects of different environmental contaminants on organisms. Enables the assessment of strategies (e.g. regulatory guidelines) for minimizing those effects	[53]

Box 1. Physiological assessment of environmental stressors

Perhaps one of the most useful tools in conservation physiology is the rapid assessment of environmental stress via the measurement of glucocorticoid 'stress' hormones (Figure I). These steroid hormones are ubiquitous in vertebrates and occur at low (baseline) levels in all individuals [2]. In many cases when individuals are experiencing increased environmental demands such as inclement weather [66] or predation [68], glucocorticoids increase in the circulation and, subsequently, in the feces. Conservation physiologists often experimentally induce mild stress (capture and handling) to assess the capacity of an individual to react to environmental stress [2].

However, not all environmental conditions provoke a detectable increase in glucocorticoid levels [69]. Conversely, increased glucocorticoids could indicate an adaptive response of healthy individuals to short-term environmental challenges. Thus, glucocorticoid data have to be interpreted carefully against background baseline data. To be the most useful to the conservation physiologist as a rapid assessment tool, elevated glucocorticoid levels should correlate with survival probabilities. An increasing number of studies indicate this to be the case, but sometimes only when a threshold level is surpassed [17,60,65]. In general, monitoring glucocorticoid hormones enables conservation managers to anticipate where problems will arise or to highlight specific conservation concerns.

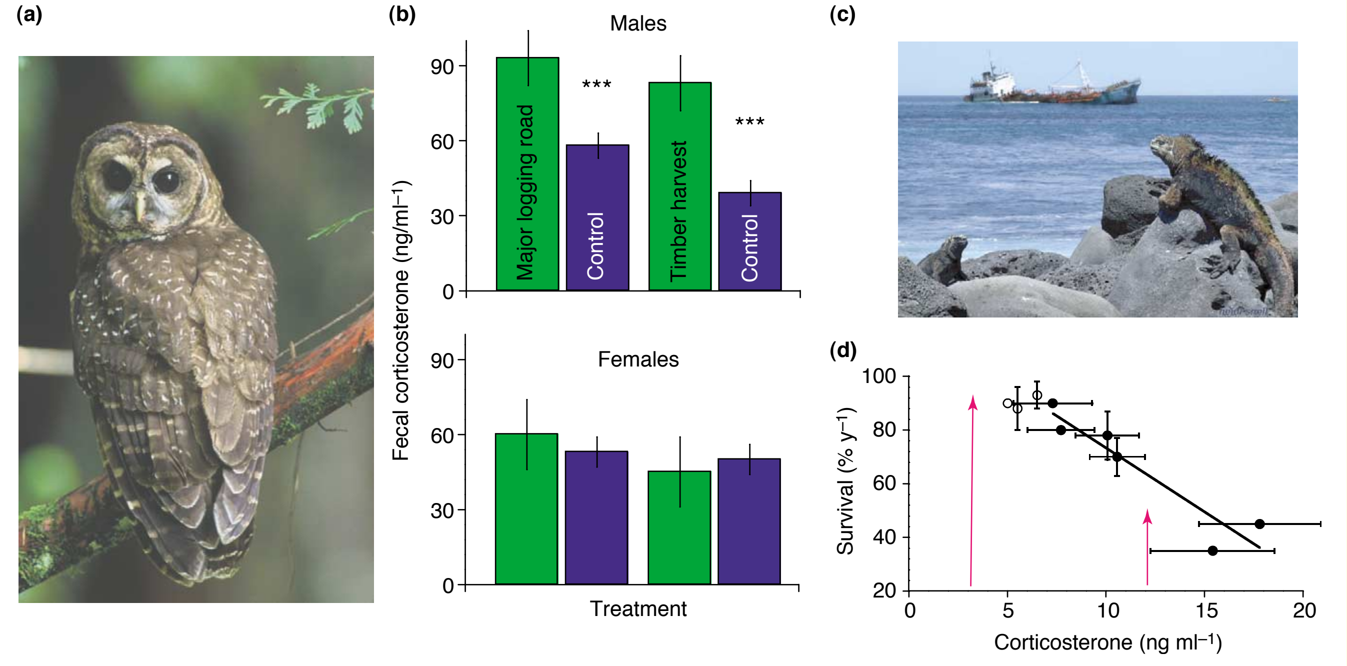

Figure I. Examples for the rapid assessment of stress. The northern spotted owl *Strix occidentalis caurina* **(a)** is threatened throughout its range by the loss and adverse modification of suitable habitat. Because the owls depend on old-growth and late-successional forests, loss of these forests as a result of timber harvesting threaten the future of the owls. Wasser *et al.* [19] suggested that logging road-traffic and timber harvest activities increase the fecal corticosterone levels of males, but not females. The sex difference in physiological response is intriguing and changes seasonally [70], and could provide an avenue for further investigations in the mechanisms of how road traffic affects males and females differently. Fecal corticosterone levels **(b)** suggest that male owls living within 0.41 km of logging roads (light green bars) or near timber harvest areas (dark green bars) are potentially stressed by human activities (blue bars indicate control levels) [19]. In the Galapagos Natural World Heritage site, marine iguanas *Amblyrhynchus cristatus* were fouled by an oil spill **(c)**. The corticosterone levels of even slightly oiled iguanas increased from $\sim$4 ng ml^{-1} to $\sim$13 ng ml^{-1} [red arrows, **(d)**]. When plotted against a previously determined relationship between survival and 15-min stress-induced corticosterone levels across various islands, the increase in corticosterone predicted a decrease in survival by $\sim$50% that was later confirmed quantitatively by mark-recapture studies [61]. (a) and (b) reproduced with permission from John and Karen Hollingsworth/USFWS and Heidi Snell, respectively; (b) and (d) redrawn with permission from [19] and [61], respectively.

field work. Creel *et al.* [18] showed that snowmobile activity can result in increased release of glucocorticoid stress hormones in elk *Cervus canadensis*, but that there were no detectable negative population effects such as local population declines. In some instances, physiological measures might also enable conservation managers to relax restrictions; for example, ecotourism was found to not lead to a rise in baseline corticosterone levels in tame Galapagos marine iguanas *Amblyrhynchus cristatus* [24].

However, the interpretation of physiological measurements is not always unambiguous: whereas Creel [25] and co-workers [26] suggested that radio collaring did not cause chronic stress in African wild dogs *Lycaon pictus*, others assert that various other manipulations (e.g. handling associated with radio collaring as well as vaccination) can result in deadly stress [27,28]. This disagreement is impossible to resolve retrospectively because individuals were not followed over time to quantify the potential influence of a singular stressful event. However, future experiments might aim at determining how single intensive periods of stress influence individual fitness. The importance of long-term data to interpret demographic impacts of animal manipulations was shown for Hawaiian monk seals *Monachus schauinslandi*. Careful handling techniques, including radio tagging and blood sampling of 549 seals, had no detectable deleterious effects [29].

Even if there are contested cases, the question is generally not whether animals are stressed, but what specific environmental stimulus stresses an animal the most. Using the concept of allostatic overload enables us to quantify the additive effects of various stressors that can elucidate specific conservation problems. For example, by-catch arising from commercial fishing can result in substantial physiological disturbance to fish [30], shellfish [31] and marine mammal species [32,33], leading to sublethal impacts that can result in subsequent death. In these cases, it is possible to link acute stressors to physiological changes that impact population declines and to single out the most important stressors that need to be avoided.

As efforts continue to focus on our understanding of the long-term consequences of climate change, there is a strong emphasis on understanding and predicting sublethal physiological responses to different warming and cooling scenarios such as cardio-respiratory or locomotory responses to thermal change [34,35]. The physiology of an animal determines the range of environmental conditions under which it can persist without fitness impairments. Knowledge of the relationship between animals and their environment is essential for our understanding of the consequences of habitat alteration and environmental perturbations including climate change. Knowledge of environment-animal relations enables the development of models to predict the effects of environmental change before its occurrence.

Alteration or destruction of habitat often results in changes to local environmental conditions that can have devastating effects on fauna. For example, a study by Homan *et al.* [36] determined that variation in habitat quality was related to the corticosterone stress response in spotted salamanders *Ambystoma maculatum* that resided in sites with different degrees of forest loss. Similar alterations in forest structure have been used to provide a mechanistic explanation of bird community structure following logging in French Guiana [37], suggesting that related physiological intolerances are causing the avian demise. Nestlings of an area-sensitive passerine, the Eurasian tree creeper *Certhia familiaris*, had elevated corticosterone in small, dense patches of forest relative to larger, old-growth patches, indicating the importance of habitat characteristics on physiology and fitness of this species, especially while young are in the nest [38,39]. Comparative environmental tolerance analyses of endemic and exotic species can be useful for evaluating crucial environmental conditions for survival and problems of habitat overlap [40–42].

The usefulness of conservation physiology is that it can reduce the complexity of conservation problems to highlighting a single set or small number of the most important stressors for organisms [43–45]. The problems with this approach, however, are that sufficient baseline data often do not exist and that not enough studies have yet unequivocally shown individual fitness (and population level) consequences of specific stressors. As the study of conservation physiology evolves, remote physiological assessments are likely to develop further to enable long-term monitoring in harsh field environments. The National Ecological Observatory Network NEON-initiative (http://www.neoninc.org/) already aims at including physiological parameters of free-roaming animals in a continent-wide monitoring effort. Thus, many more baseline data will soon become available and meta-analyses of the impact of stressors on population-level phenomena will be possible.

Using conservation physiology to alleviate conservation problems

Physiology and conservation are already strongly linked in zoo biology, veterinary sciences and animal husbandry [46]. Here, we highlight some new physiological approaches to the conservation of species that are critically endangered in the wild.

Endocrine techniques can indicate problems in captive-breeding programs and guide hormone therapy in critically endangered species. For example, populations of the Toki, the Japanese crested ibis, *Nipponia nippon* are now reduced to approximately 300 captive and free-living individuals in China. Based on studies in Japanese quail *Coturnix japonica*, Wingfield *et al.* [47] suggested the use of gonadotropins to induce gonadal maturation in non-reproductive individuals to bring them into reproductive condition before old, reproductively experienced individuals died out. Although these techniques are still being developed, the results look promising [48]. Similarly, physiological assessments of gonadal and endocrine state in endangered Hawaiian honey creepers *Trepanididae* spp. in the wild might provide a baseline for captive-breeding programs [2,49]. Knowledge of endocrine state will enable researchers to pair individuals of similar reproductive and endocrine state, thus making prolonged pair synchronization periods, which can take years in captivity, unnecessary. None of these captive techniques, however, should replace the vigorous protection of animals in the wild.

An often overlooked aspect in conservation biology is details of animal nutrition, both in captive-breeding programs and in the wild. Because Galapagos land iguanas *Conolophus* spp. were eradicated on some islands in the archipelago, the Galapagos National Park Service and the Charles Darwin Foundation (http://www.darwin-foundation.org/) decided in 1976 to start a reintroduction program. However, efforts to breed land iguanas in captivity were hampered initially by an overwhelming mortality of hatchlings suffering from intestinal blockages, bloating diarrhea and torsion. When nutritional physiologists were consulted, it became clear that the hatchlings were being fed inappropriate diets. Fiber content and protein were too low, such that hindgut fermentation was abnormal and individuals died, problems that were easily remedied once identified [50]. The population decline in another reptile, the desert tortoise *Gopherus agassizii* of the Southwestern USA, was thought to be caused by predation, human collection or disease. However, the primary cause of this conservation problem again appears to be nutritional stress, here caused by the need to excrete potassium with the help of (scarce) water and nitrogen (Box 2). To evaluate multiple competing hypotheses regarding the decline of marbled murrelet *Brachyramphus marmoratus* populations in California, Peery *et al.* [51] predicted how behavioral, physiological and demographic characteristics would respond to possible limiting factors. Using physiological indicators, the

Box 2. Conservation physiologists to the rescue of endangered wildlife

The role of nutritional physiologists

The desert tortoise *Gopherus agassizii* has shown widespread population declines that were attributed initially to increasing populations of native predators, habitat destruction, highway mortality and removal of adults for pets [71]. Subsequently, diseases were thought to be responsible. However, nutritional stress was determined eventually to be the most important cause for the slow demise of the tortoises [72]. Well-adapted physiologically and behaviorally to living in dry, desert environments, desert tortoises derive most of their water intake from the plants that they eat. However, desert plants often accumulate potassium as a means of enhancing water uptake from dry soils. High cation loads (ingested with plants) are a problem for tortoises because they do not have salt glands. Instead, they cope with the potassium load by producing uric acid that precipitates with cations such as ammonium, potassium and sodium. However, when winter rains are scarce, the plants available in spring are so loaded with potassium that tortoises lose water and nitrogen while excreting the excessive salt. In wet years, tortoises can select rain-loving legumes that have relatively little potassium and therefore recover. Thus, potassium load is less of a problem for tortoise populations in the south, where summer rains enable them to drink. The important message for conservation managers is that habitat management should aim at increasing the presence of plant species that are low in potassium (e.g. via cattle grazing restrictions). Counterintuitively, tortoise food resources need to be protected from livestock grazing the most in years with high winter rainfall [72] because low-potassium plants are most abundant under wet conditions and tortoises need to recover in wet years.

The role of aquatic physiologists

Adult Pacific salmonids *Oncorhynchus* spp. represent a fascinating example of the conservation progress that can be made by incorporating physiological research and knowledge into decision-making. Before beginning their upriver migration, adult salmon are targeted by commercial fisheries in the coastal region. In Canada, imperiled species (e.g. coho salmon *O. kisutch*) are protected from commercial harvest by regulations, but are still captured incidentally. During the late 1990s, the use of fish crates was mandated under the belief that holding by-catch in crates filled with water after capture would reduce mortality and enable more individuals to be released alive. Shortly thereafter, physiological assessments revealed that the crates failed to enhance recovery of coho salmon and might have exacerbated biochemical disturbance [73]. Working with commercial fishers, physiologists developed a novel recovery chamber and were able to release fish in good shape that were classified as dead upon capture [74], thus resulting in regulatory adoption of this strategy. They also proposed an alternative holding technique that involved forcing fish to swim at low speeds in pens alongside the boat. This facilitated clearance of metabolites and prevented expression of cortisol, thereby contributing to increased by-catch survival [74].

authors revealed that, in some years, food availability results in nutritional limitations on murrelets, thus affecting demography and life history.

Three main conservation strategies exist to support wildlife that is in immediate danger of (local) extinction: *in situ* conservation efforts, temporary captive holding and breeding, and/or translocation. Here, we concentrate on the latter two, the impact of which on individuals can and should be assessed with physiological methods. Animals soiled with crude oil are often held temporarily in captivity during rehabilitation. Much has been learned from the Exxon Valdez oil spill, for example, about the effects on cleaned sea otters *Enhydra lutris*, which showed about 43% survival in their first post-cleaning year, a rate that was much lower than comparable populations [52]. Ben-David *et al.* [53] determined that rehabilitation is a viable option for river otters *Lontra canadensis*, but that otters with low hemoglobin levels died more frequently after release. When Magellanic penguins were oiled in Argentina, some were brought into captivity for rehabilitation. However, this approach is questionable given that Fowler *et al.* [54] conclude that oiled penguins held captive for washing had elevated corticosterone levels and appeared to be stressed both by captivity and by the washing process. It is so far unclear what the long-term effects of captive treatment are in these specific instances.

Conservation programs that involve the translocation of animals can also benefit from, and be evaluated by, physiological information. For example, researchers used molecular physiology (expression of metabolic enzymes) to identify unstressed sites on coral reefs for use in restoration transplant efforts in the Red Sea [55]. The octocoral *Dendronephthya klunzingeri* from the unstressed sites had substantially better survival and growth rates than did those taken from sites identified as stressed. For red deer *Cervus elaphus* translocations, Waas *et al.* [56] showed that every human intervention strongly affected heart rate and lactate levels, the latter being an unwanted product of anaerobic glycolysis indicating oxygen debt. The authors recommended that translocation events should include frequent breaks in a dark, cool environment with ample water and be restricted to outside of the reproductive period. Hartup *et al.* [57] assessed the effects of human-guided migration of sandhill crane *Grus canadensis tabida* and revealed that fecal corticosterone levels were consistent with levels observed in other migrants, suggesting that this conservation strategy does not impart undue stress and is potentially a viable option for other imperiled species such as whooping cranes *Grus americana*. However, the lack of a corticosterone response does not always indicate a lack of stress (Box 1). In another translocation experiment, Cooke *et al.* [58] determined that mixing even geographically close largemouth bass *Micropterus salmoides* stocks from adjacent molecularly defined conservation management units in the Midwestern USA reduced swimming performance. Interstock hybrids also had altered metabolic rates that were possibly related to the non-adaptive performance. Therefore, the authors suggested that translocation should be restricted to within a watershed because it can affect the locally adapted resident populations.

Physiological methods can help conservation managers to alleviate problems by identifying key aspects or time periods of how and when organisms are stressed.

Box 3. Evaluating and predicting conservation problems

Threats to species are sometimes not apparent immediately, but biotelemetry, the remote monitoring of physiological traits [12], can often help to determine the particular mechanisms of species decline. It can also further highlight bottlenecks in energy supply or determine the timing and/or location of important life-history events.

Why do wide-ranging seabirds decline?

Black-browed albatrosses *Diomedea melanophris* occur all around the southern oceans between 25° and 60° S (Figure I). The Falkland Islands hold over 85% of the global population and are the most important breeding area worldwide for this species. Recent studies by Falklands Conservation (http://www.falklandsconservation.com/) revealed a dramatic decrease in numbers of breeding black-browed albatrosses, from 458 000 in 1995 to 382 000 in 2000, which could make them a globally ‘vulnerable’ species. Albatrosses might face a double challenge: they are under threat from long-line fisheries, which hook and drown the birds as they dive for the baited lines, and, at the same time, overfishing can deplete food stocks and additionally endanger birds. Physiological biotelemetry studies can assess where, and how severely, birds are at risk. Bevan *et al.* [62] attached satellite transmitters to albatrosses from South Georgia and implanted heart-rate and body-temperature loggers, the latter assessing the energy expenditure during foraging flights as well as food intake (via a decrease in deep body temperature by cold, ingested food). The combined physiological and location data can inform conservation managers where albatrosses most probably fish for food, but also how overfishing changes the energy budget and subsequent survival of wide-ranging birds.

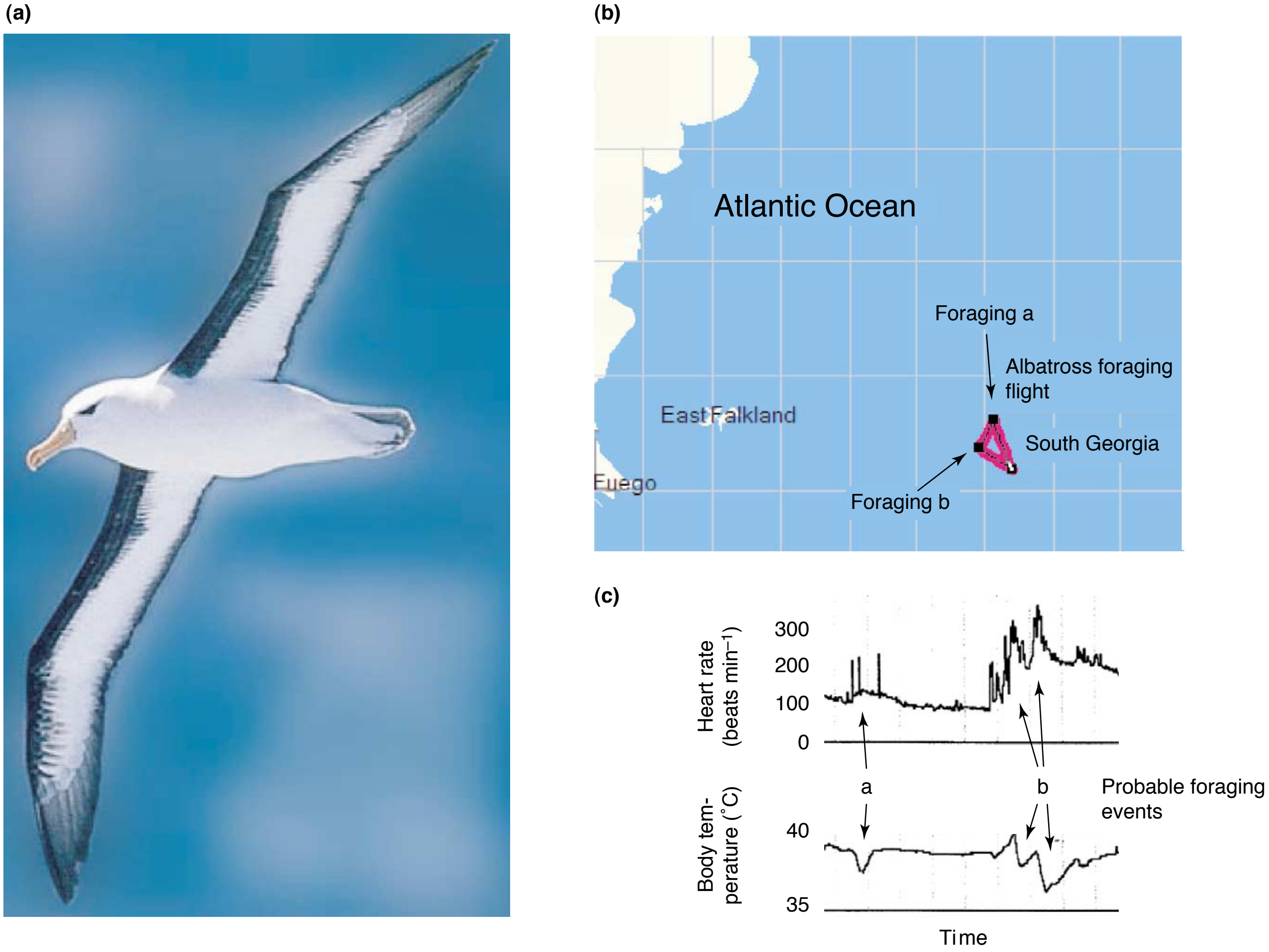

Figure I. Physiological telemetry in albatrosses. A population of black-browed albatrosses **(a)** breeds in South Georgia (38°W, 54°S) and makes regular foraging flights in the Southern Oceans **(b)**. The graph **(c)** shows heart-rate and body-temperature traces from the albatross’ route, indicating where each individual foraged (increased heart rate and lowered body temperature highlighted by arrows). Reproduced with permission from Falkland Conservation (a) and [62] (b,c).

However, this approach is not yet used sufficiently to enable a broad-based assessment of cost:benefit ratios of specific measures for conservation managers and zoos [59]. We suggest that ongoing conservation programs should be accompanied by physiological assessments until a general understanding of the various classes of conservation problems is reached using case studies. Subsequently, conservation strategies can be checked against a catalog of potential manipulations and stressors. Such an approach is beneficial because physiological assessments in themselves can stress animals under certain circumstances.

Using physiology to monitor and prevent future conservation problems

When the link between baseline physiological traits and fitness is known, conservation managers can use physiological traits to predict and anticipate future problems.

In Galapagos marine iguanas, stress-induced corticosterone levels predict population survival during El Niño famine periods [17]. When a seemingly minor oil spill occurred, increased corticosterone levels predicted (contrary to the common expectation at the time) that a major mortality wave would occur [60]. This was confirmed later and iguana mortality data were instrumental in a lawsuit that attempted to prevent a recurrence of spills [61]. Similarly, baseline energy expenditure and food-intake data for black-browed albatrosses *Diomedea melanophris* coupled with spatial foraging information enabled conservation physiologists to predict how overfishing in the South Atlantic would affect the populations of this magnificent seabird (Box 3; [62]).

In many cases, however, baseline information is nonexistent or insufficient to predict where and when problems will arise. Such is the case for the biological impact of anthropogenic noise on marine mammal populations, including marine and submarine traffic noise, scientific noise, military operations or industrial drilling. For this controversial issue, it was recommended that glucocorticoid and other serum-hormone concentrations should be assessed [63]. If baseline data were already available, it would be easy to quantify the impact of now almost ubiquitous noise on marine mammals. Without such a baseline, researchers need to find individuals in pristine areas to establish how noise potentially increases the allostatic load of individuals. To determine dose–response curves between noise and stress, it was recommended that heart-rate measurement devices and a tissue and/or blood sampling package should be developed to collect blood samples *in vivo* [63]. Such combined measurements of cortisol concentrations and energy expenditure (via heart rate) would enable the assessment of the allostatic load of individuals in their natural environment [10].

In general, the advantages of having physiological baseline data on organisms in their natural environment are high, but few such data exist, making a conservation-physiology approach more cumbersome (e.g. necessitating dose–response curves instead of simple post-impact measurements). What has not yet been achieved in many cases is the combination of physiological measurements with behavioral and population studies as well as modeling approaches to understand how future problems can best be avoided. Thus, ample need exists for quantitative models of physiological responses of organisms in altered environments [64].

Where should the field of conservation physiology be going?

Physiological information that can be derived from field research is essential to ensure the success of conservation programs [59]. We are confident that the many disciplines of physiology, ranging from developmental physiology to endocrinology (endocrine disruptors) to physiological genomics, have much to contribute to the conservation of biodiversity [43–45]. We suggest that successful education in conservation-physiology programs will combine curricula in environmental studies, politics, conservation science and physiology. Students should learn how to use the eco-physiological toolbox (Table 1) in conservation projects such as reserve design or conservation management planning. Examples already exist that use physiological assessments in combination with demographic data of animals for ecotourism planning [65] or that incorporate findings from physiological studies into decision making for the management of threatened natural resources (e.g. Pacific salmonids *Oncorhynchus* spp.; Box 2). Furthermore, we propose that several areas in conservation biology will benefit from including ecophysiological data on wild animals to a greater extent (e.g. reintroduction, translocation and captive-breeding programs). Trying to understand how animals cope with the ongoing urbanization of modern landscapes provides a significant challenge for physiological conservationists. Fortunately, the proposed National Ecological Observatory Network includes gradients from wild to urban areas, and thus will enable the mechanistic study of urbanization problems for conservation.

Conclusions

We suggest that researchers working on physiological assessments of conservation problems should recognize their efforts as a new scientific field, conservation physiology [3]. By doing so, it would be challenged to refine its goals and applications, and to come up with training strategies for the next generation of conservationists. Many challenges lie ahead. How can stress in wild organisms best be detected? What single factors contribute most to allostatic overload of individuals [66]? How can such undue stress on individuals best be avoided or alleviated, both for wild populations and for individuals that are either temporarily or permanently in captivity for breeding purposes? A conservation-physiology database needs to be established that enables conservation managers to quickly identify the most appropriate solution to conservation problems. Furthermore, the scientific community should work towards a broadly accepted set of predictive models in conservation practices that specifically include physiological parameters. Judging from the high interest of students and the general population in conservation issues, we believe that conservation physiology has a bright future and will join other, established conservation approaches (such as conservation genetics) in preserving the biodiversity of this planet through the peak of human population within the next 30 years [67].

Acknowledgements

We thank Cory Suski, David Philipp, Tony Farrell, David Patterson, Scott Hinch, Jeff Young, David Wahl, Jason Schreer, Glenn Wagner, Bruce Tufts, Art Devries, Patrick Weatherhead, David Wilcove, Claire Kremen, Michaela Hau and the Princeton Eco-Phys laboratory for productive discussions on the interface of conservation and physiology. Thanks to Jim Adelman, Laura Spinney, Kelly Lee, Ela Hau and six anonymous reviewers for constructive criticism of the manuscript. Financial support was provided by the Natural Sciences and Engineering Research Council of Canada, the Izaak Walton Killam Trust, the University of British Columbia, and the Illinois Natural History Survey to S.J.C., and Princeton University and NSF IRCEB to M.W.

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