Biological Conservation and Stress

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I. INTRODUCTION

In this contribution we review why stress has important implications for biological conservation and consider practical ways in which conservationists can identify and tackle problems caused by stress. We take an evolutionary approach to stress, its consequences, and the adaptations that permit animals to cope with stress. Using information from several scientific disciplines we outline the factors known to cause stress and the Darwinian fitness consequences of stress. Increasingly anthropogenic factors such as environmental pollution, tourism and leisure activities, hunting, noise, and global warming are thought to cause stress. We investigate when anthropogenic factors are likely to generate stress, what conditions favor detrimental fitness consequences, and which stress responses provide a reliable indicator of a potentially harmful situation.

There is extensive literature on both stress and biological conservation, but there has been little integration of the two disciplines (for an admirable exception, see Hoffmann and Parsons, 1991), and there has been no comprehensive review of the importance of stress to conservation. In part it may be because biological conservation studies and stress studies tend to focus on different parameters. Biological conservation generally concentrates on populations and species communities and rarely considers mechanisms operating at the level of the individual that may be ultimately responsible for population and community changes (e.g., Frankel and Soulé, 1981; Soulé, 1986; Primack, 1993). Research on stress is normally concerned with individual organisms and their developmental, behavioral, metabolic, endocrinological, and immunological responses to stress, but it rarely (for exceptions, see Fraser and Broom, 1990; Hoffmann and Parsons, 1991) considers the consequences of stress for the reproductive success of individuals and the persistence of populations. It is the purpose of this review to show that (1) stress is a valuable concept in biological conservation;

their life cycle even in free-ranging populations. In such species, specific neuroendocrine mechanisms are the prime cause of reproductive suppression, whereas the general adrenocortical response plays no role or only a minor one (Mays *et al.*, 1991; Schoech *et al.*, 1991; Wingfield and Lewis, 1993; Faulkes and Abbott, 1997; French, 1997; reviewed by Abbott *et al.*, 1997; Sapolsky, 1997). Because little is known about how such specific neuroendocrine mechanisms may be triggered by environmentally dependent changes in agonistic behavior, it is unclear to what extent the activation of such mechanisms may be used as an indicator of stressed states.

In contrast, in many other group-living species, most or all females and/or males attempt to reproduce. Socially subordinate individuals in such species may experience reproductive failure as a consequence of an increased production of glucocorticoids caused by harassment by dominant conspecifics (Wasser and Starling 1986; Sapolsky, 1987, 1997; Altmann *et al.*, 1988; Dunbar, 1989). Note that such harassment has sometimes been interpreted as an adaptive reproductive strategy of social superiors (e.g., Wasser and Starling, 1986). Thus, reproductive suppression may occur because stress triggers a significant adrenocortical response, but further information is required to assess whether the stress derives from environmental conservation-relevant sources, or whether it is the consequence of adaptive behavior of conspecifics.

e. The Adrenocortical Response. Among several components of the hormonal response system (Section II,A), the adrenocortical response is frequently cited as a key component of a generalized hormonal stress response that can be conveniently measured even under field conditions. This is because activation requires several minutes before a rise in plasma glucocorticoid concentration is detectable, and field conditions often require such time periods before a blood sample can be taken (Wingfield *et al.*, 1996). It is not, however, appropriate to consider it uncritically as an all-embracing panacea. Stress responses need not involve the adrenocortical axis (Section II,A), and glucocorticoid production may serve other functions in the context of reproductive activity, basal metabolism, or mobilization of reserves (Buttemer *et al.*, 1991; Wilson and Wingfield, 1992, 1994; Saltzman *et al.*, 1994). However, the adrenocortical response is a reliable indicator in many cases, and there is evidence that raised levels of glucocorticoids induce profound changes in immunological competence (see previous discussion) and are associated with an increase in heart rate and energy expenditure (see following discussion). Such changes result in detrimental fitness consequences in dasyurid marsupials (see previous discussion) and alpine marmots, *Marmota marmota* (Arnold and Dittami, 1997).

f. The Sympathetic-Adrenal Medullary Response. In contrast to the adrenocortical response, the sympathetic-adrenal medullary response (producincubation and nestling phases increased (1) time and energy expenditure of marsh harrier, *Circus aeruginosus*, parents on reproductive and nonreproductive activities, and (2) plasma urea concentrations in nestlings, suggesting a detrimental effect on lifetime reproductive success (Fernandez and Azkona, 1993). Madsen (1995) reported on the results of a "natural" experiment, in which farmers either disturbed or did not disturb grazing pink-footed geese, on their subsequent body condition and breeding success. Disturbed geese had a poorer body condition and were significantly less likely to breed successfully. The presence and behavior of tourists at nesting beaches of green turtles, *Chelonia mydas*, reduced the arrival of females by a third but did not influence the proportion of successful nesting, incomplete nesting, or no nesting attempts (Jackson and Lopez, 1994). Recreational disturbance of winter denning sites of American black bears, *Ursus americanus*, resulted in the abandonment of dens and cubs and a delay in entry to hibernation (Goodrich and Berger, 1994). Experimental harassment of mule deer by all-terrain vehicles induced reproductive pauses in the subsequent breeding season (Yarmoloy *et al.*, 1988).

Does wildlife habituate to disturbance? In many cases it does, as evidenced by a gradual decline in the behavioral response of disturbed wildlife to groups of tourists (e.g., Van Heezik and Seddon, 1990). However, as discussed in Section II,B, disturbance may continue to have detrimental fitness consequences even when animals are habituated. Habituation cannot be expected to occur under all circumstances, and is less likely to occur if the disturbance involves close approaches or unusual or unpredictable events (Hüppop and Hagen, 1990). For instance, bighorn sheep, red deer, and marmots, *Marmota marmota*, were less responsive to people on major roads or hiking trails than to people encountered off-trial or with a domestic dog as companion (Schultz and Bailey, 1978; MacArthur *et al.*, 1982; Mainini *et al.*, 1993). However, the experiments reported in these studies in some cases cannot exclude the possibility that individuals less sensitive to disturbance, for example, individuals prepared to take higher risks because they are of below-average quality, settle closer to major roads or hiking trails. Some studies demonstrate that animals did not habituate, even after years of exposure, or may even become sensitized by repeated disturbance events. For instance, paragliding in the Swiss Alps initiated flight responses in chamois, *Rupicapra rupicapra*, and capricorn, *Capra ibex*, and led to changes in habitat utilization by these species. Experimentally disturbed animals did not show any evidence of habituation (Schnidrig *et al.*, 1992; Ingold *et al.*, 1996), although differences in the routine of experimental and usual paragliders may have prevented habituation to occur. Mountain goats, *Oreamnos americus*, showed substantial individual differences in response tion. In part, this is because surgery is often an emergency procedure, as in the case when animals become entangled in objects, or when it is likely that the animal will die or suffer if nothing is done. However, some procedures require routine rather than emergency surgery. These include muscle biopsies for sampling genetic material or the implantation of radio transmitters and other devices that in the course of research projects collect data from the animal's body.

In some species, surgery and radio implantation may cause substantial postsurgery mortality. Trials with implanted American river otters, *Lutra canadensis*, illustrated the importance of diet and extended periods of post-surgery recovery time in appropriate holding pens (Woolf *et al.*, 1984; Hoover *et al.*, 1985). Even under improved conditions, 30% of otters died during the postsurgery holding period. Mortality within 12 months of radio implantation of African wild dogs in Kruger National Park was more than twice as high as mortality of unhandled African wild dogs (East, 1996). These results contrast with numerous studies that found no effects of surgery and implantation of radio transmitters on subsequent survival or behavior (white-footed mouse, *Peromyscus leucopus:* Smith, 1980; canids: Green *et al.*, 1985; yellow-bellied marmot, *Marmota flaviventris:* Van Vuren, 1989; armadillo, *Dasypus novemcinctus:* Herbst, 1991; ring-necked pheasant, *Phasianus colchicus:* Ewing *et al.*, 1994).

The effect of muscle biopsies on fitness in birds varies between species. In white-throated sparrows and Indigo buntings, *Passerina cyanea*, muscle biopsies did not affect body condition or survival of either overwintering or breeding individuals (Westneat, 1986; Westneat *et al.*, 1986). In contrast, muscle biopsies of white ibises, *Eudocimus albus*, led to complete nest desertion (Frederick, 1986). Frederick (1986) could show that this effect was not due to the procedures of capture or handling as such, as ibises that were captured, handled, and blood sampled, but not biopsied, were not affected.

6. *Tagging and Radio-Tagging*

For individual identification purposes, individuals are commonly tagged with plastic ear tags, neck or foot rings, freeze-branded, or hot-branded. The fitness consequences of such tags and improvements that may minimize such consequences have been reviewed repeatedly (see Putman, 1995). One key issue that is often neglected is that social relationships and social success may be permanently affected by tagging (because of the associated disturbance, human smell, etc.) or by the quality of the tags themselves. For instance, radio-tagging mule deer fawns may result in females rejecting their fawns, which in turn reduces the fawn's chance of survival (Goldberg and Haas, 1978). Individually distinct color-banding may permanently affect