



Evaluating methods to quantify anthropogenic stressors on wild animals[☆]

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Abstract

Humans have a variety of direct and indirect impacts on wildlife and a number of methods have been proposed to identify and quantify anthropogenic stressors that negatively impact wildlife. The ideal method would ultimately help predict the presence, absence, or population viability of animals living with a particular stressor. We critically review seven methods that have been used, or are potentially useful, to identify anthropogenic stressors on animals. We rank them from fitness indicators to disturbance indicators: breeding success, mate choice, fluctuating asymmetry, flight initiation distance, immunocompetence, glucocorticoids, and cardiac response. We describe each method's ease of use, precision in quantifying the stressor, accuracy in predicting the presence, absence, or population viability of a species experiencing a given stressor, and the repeatability of the results across populations and species. From this analysis, we conclude that there is no single optimal method to quantify anthropogenic stressors; method selection will depend on precise goals and fiscal constraints.

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1. Introduction

Humans have a variety of direct and indirect effects on animals, and wildlife managers must develop ways to identify and quantify these effects in order to manage populations. A number of

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techniques have been developed to measure anthropogenic stressors; all have the ultimate goal of determining if a population can coexist with a particular human activity. For example, considerable effort has focused on developing Geographic Information Systems (GIS) that map both human impacts (e.g., the extent of an oil spill, the presence of a road, trail or a certain level of recreational use) and the presence or absence of wildlife (e.g., White, 1997; Wright and Begg, 1997; Kerkhoff et al., 2000). While useful in understanding the spatial pattern of potential impacts, GIS methods do not allow us to develop a detailed awareness of how non-humans perceive various human activities. This degree of specificity is essential if we are to identify and manage human impacts on wildlife. The ideal method would permit inferences about the precise stressor, and ultimately would be useful in predicting the presence, absence, or population viability of animals living with that impact or stressor.

Many methods are used to analyze the effects humans have on wildlife. We focus this review primarily (but not exclusively) on studies of birds (where a large portion of conservation research is focused; Marzluff and Sallabanks, 1998), and on seven tools that are either commonly used today (breeding success, fluctuating asymmetry—FA, flight initiation distance—FID, glucocorticoids, and cardiac response), or have greater potential as knowledge about them increases (mate choice and immunocompetence). We focus on behavioral ecological methods because ultimately a species' behavioral response to humans will influence its ability to coexist with humans. We evaluate each tool's potential usefulness based on the following factors: ease of use (including time needed for measurements and the invasiveness of the method), precision of quantifying impact, accuracy in predicting a species' presence, absence, or population viability as a function of the measured stressor, and repeatability across populations and species. We selected these factors because they address important questions that managers often ask when considering a method, and because it is possible to ultimately link them with reproductive success and thus fitness. In many cases, work with captive animals will allow future researchers to properly identify the relationship between putative human stressors and a species' response. We begin with the most ultimate (*sensu* Tinbergen, 1963) measure—breeding success—and continue through to the most proximate method—cardiac response.

2. Breeding success

Breeding success is a common measure of human impact because if individuals do not breed, the population cannot persist. Breeding success can be measured in a variety of ways. Direct measures of breeding success in birds include clutch size, hatching success, and fledging success; in mammals, litter size, and the number of young that are weaned are common measures of breeding success. However indirect measures, such as the number of nests or adults in an area, may also be used. Furthermore, other tools discussed in this paper are also often used when looking at the affects human disturbance can have on breeding success such as FID and cardiac response.

2.1. Ease of use

The ease of measuring breeding success is variable. In many cases nests can be marked externally and observed from afar, and it is relatively straightforward to evaluate individual reproductive success without overtly disturbing subjects. However, some studies are more invasive and require banding or otherwise marking individuals, while others incorporate more detailed monitoring, which includes weighing nestlings and monitoring their growth.

The more invasive the study becomes, the less ‘easy’ it becomes, and the more likely one is to have the study itself impact the organism in question.

Indirect correlates of nesting success are also used to measure breeding success. For example, documenting the frequency with which birds are flushed off their nest can be useful because when parents are flushed off nests, the eggs (or nestlings) are left exposed to the elements, and predation (Anderson and Keith, 1980). Additionally, cardiac response has been used as a correlate of breeding success for individuals that are negatively influenced by anthropogenic noise. For example, helicopters have been shown to cause individual Adélie penguins (*Pygoscelis adeliae*; both chicks and adults) to increase their heart rates and to leave the colony; in a few cases nest desertion by adults occurred (Culik et al., 1990). When indirect measurements are employed, it is necessary to not only look at nest abandonment, which is often temporary (Lord et al., 2001), but also to determine what final effect the abandonment actually has on the nest contents.

2.2. Precision in quantifying impact

When measuring breeding success, it is important to identify the facet of human disturbance actually causing the changes in reproductive success. Comparisons between sites are difficult because they should be well matched along all axes of habitat quality except for the type of human disturbance. However, in cases when young abandonment is directly associated with a particular human disturbance, this method can be accurate and useful.

2.3. Accuracy in predicting presence, absence, or population viability

Breeding success can be a very accurate predictor of population viability, especially when quantifying reproductive success directly because if a local population has no breeding success, the population is either declining or it is being maintained solely by immigration. For example, in Adélie penguins, chick survival and hatching success was lower in areas with frequent human activity (Giese, 1996). Other, more indirect, measures may not be as accurate. For example, counts of nests or adults do not always predict the number of offspring fledged, many nests may fail, or many adults may not be breeding successfully. Additionally, the distribution of nests or territories (Skagen et al., 2001; Ortega and Capen, 2002) may be important if nests are no longer built in once-preferred areas because of human disturbance, and individuals are forced to breed in less productive areas. This too (i.e., documenting where animals nest) is an indirect measure because it does not count the actual numbers of successful fledglings that are required to estimate population growth trajectories.

Behavioral ecological theory predicts variable nest defense as a function of breeding cycle (Montogomerie and Weatherhead, 1988). Thus, it is important to consider the stage of the breeding cycle during which the study is done and the time that humans interact with breeders. Short-term studies may fail to detect the reproductive success of a population and could over-, or under-estimate the overall reproductive success. For example, Vos et al. (1985) studied the relationship between flight initiation distance and breeding in Great Blue Herons (*Ardea herodias*) and found that the birds responded to humans very differently depending on the stage of the breeding season. Herons flushed from their nests quickly early in the breeding season, while towards the end of the breeding season the researchers rarely saw a bird leave its nest site (Vos et al., 1985). This type of response variation is predicted by behavioral models of nest defense (Montogomerie and Weatherhead, 1988), because re-nesting opportunities decline and the probability of offspring survival is greater as the season progresses.

2.4. Repeatability across populations and species

Measuring breeding success is repeatable and is useful for any population or species where measurements can be made accurately. However, there is variation in the response of birds to human disturbance (for review see [Carney and Sydeman, 1999](#)). Therefore, care must be given to test the breeding success of the population in question, rather than assume that there will or will not be an effect based on previous studies. As more studies are completed, it may be possible to generalize that some species will be more vulnerable to human impact than others. Future research should aim to identify robust generalizations about human disturbance and breeding success (e.g., [Owens and Bennett, 2000](#)); ultimately we should aim to identify those life history or natural history characteristics that predict response to human disturbance ([Blumstein et al., 2005](#)).

3. Mate choice

Disturbance by humans can potentially alter patterns of mate choice and such changes may have serious evolutionary consequences. Mechanisms of mate choice are not often considered in investigations of human impact, despite their potential impact on population dynamics ([Blumstein, 1998](#)). Animals routinely make presumably adaptive mate choice decisions ([Bateson, 1983](#); [Andersson, 1994](#)). One well-known example of this phenomenon is illustrated by [Seehausen et al.'s \(1997\)](#) study of the effects of eutrophication on mate choice in cichlid fish. Turbidity due to eutrophication has affected the ability of haplochromine cichlids in Lake Victoria to discriminate among colors, mitigating sexual selection, which is based on coloration ([Seehausen et al., 1997](#)). Species diversity has decreased in areas of high turbidity (in part through hybridization); thus human activities have had a profound effect on the evolution of haplochromine cichlids ([Seehausen et al., 1997](#)). More generally, human impacts can modify the benefits or costs associated with a particular mechanism of mate choice, or they can influence the expression of a condition-dependent trait. Females of many species base mate choice decisions on the expression of condition-dependent traits like tail length, color, or display rates ([Andersson, 1994](#)). If anthropogenic disturbance affects the ability of individual males to obtain sufficient energy to grow a long tail, allocate nutrients to coloration, or display at a vigorous rate, and if females elect to not mate with these “deficient” males, then human impacts have affected the probability of breeding ([Blumstein, 1998](#)). Failure to mate is not unheard of in nature ([Boag and Grant, 1981](#)), and with fewer males breeding, some females may go unmated or there may be a loss of heterozygosity ([Blumstein, 1998](#)). Either outcome has evolutionary and population dynamic consequences and are thus of conservation concern.

3.1. Ease of use

Investigations of mate choice mechanisms can be more complex than other methods used in conservation research and studies in captivity may uniquely offer sufficient control to properly identify mechanisms. Behavioral ecologists recognize several strategies animals employ to choose their mates ([Janetos, 1980](#); [Wittenberger, 1983](#); [Real, 1990](#)). Contemporary theory suggests that multiple traits may be used by females assessing males ([Künzler and Bakker, 2001](#)), and traits may include the typically studied static morphological traits such as tail length ([Andersson, 1982](#)), as well as more dynamic behavioral traits ([Rosenthal et al., 1996](#)). However, by focusing on condition-dependent traits ([Andersson, 1994](#); [Blumstein, 1998](#)), which may be

indicators females use of high-quality males, it may be possible to quantify human impacts on a sexually-selected system. Of course, other methods to assess impacts may work by affecting mate choice decisions. For example, females have been shown to prefer males who are more symmetrical for a certain trait (Møller, 1992; Thornhill, 1992); in some cases mating success appears to be lower for individuals with high fluctuating asymmetry (Markow and Ricker, 1991; Harvey and Walsh, 1993; Arcese, 1994). This relationship, however, is not inevitably reported (Markow and Ricker, 1991). Additionally, because mate choice decisions themselves may be based on variation in the assessor's quality (e.g., Hingle et al., 2001), some variation in mate choice may relate to female, not male variation. Thus, high-quality females may prefer high-quality males and vice versa.

3.2. *Precision in quantifying impact*

In some situations, particularly in cases of one major and specific disturbance, it may be possible to link the changes in mate selection to the disturbance. However in most situations, a disturbance may incorporate many factors, such as human presence, loud noises, and other animals, and it may be difficult to tease apart which particular factor is causing the changes observed in mate selection. Captivity offers the experimental control that may be necessary to identify key factors, and zoos and wildlife parks may be optimal locations in which to study mate choice experimentally.

3.3. *Accuracy in predicting presence, absence, or population viability*

Modification of the mechanisms animals use to select their mates may have implications for species survival through its effects on an individual's reproductive success, and thus its effects on population growth rate and the effective population size (Anthony and Blumstein, 2000). Additionally, as has been shown with the cichlids, the break down of mate choice systems may result in hybridization (Seehausen et al., 1997).

3.4. *Repeatability across populations and species*

If mechanisms of mate choice reflect adaptive decisions made by individuals, then different populations may employ different mechanisms. Thus, there is no reason to expect mate choice mechanisms to be repeatable across a range of populations. However, it should be possible to make generalizations about how the expression of condition-dependent traits are affected by human impacts and the effect of these traits may be generalizable across populations or similar taxa.

4. **Fluctuating asymmetry**

Vertebrates are expected to develop bilaterally symmetrical traits symmetrically. Fluctuating asymmetry (FA) is one of three types of asymmetry (directional asymmetry, anti-symmetry, and FA), which results when individuals do not develop as expected. FA results in a "normal (or binomial) distribution of the signed differences between the sides and an equal mean development on each side" (Van Valen, 1962, p. 126). Any deviation from bilateral symmetry can result in FA (Palmer and Strobeck, 1986), and FA is a common (if not the most common) measure of developmental instability (Van Valen, 1962; Clarke, 1995a; Markow, 1995).

More specifically, FA has often been used to explain disturbances in development resulting from stress (Leary and Allendorf, 1989; Parsons, 1990, 1992; Graham et al., 1993; Bjorksten et al., 2000). Asymmetrical individuals may be less attractive and therefore be less likely to mate (see above), and finding evidence of developmental instability in human-impacted areas implies that animals are sensitive to these impacts.

4.1. Ease of use

Measurements of FA are relatively simple, non-invasive, and inexpensive (Leary and Allendorf, 1989; Lens et al., 2002a,b). Additionally, reasonable sample sizes can be obtained fairly easily because recaptures are not necessary (Lens et al., 2002b). A unique advantage of FA is that for some questions, museum specimens collected from an area before an impact can be used as baseline levels to compare to specimens collected after impact (for examples see Zakharov and Yablokov, 1990; Wright and Zamudio, 2002). However, care must be taken when using museum specimens for collections may not accurately reflect wild populations (e.g., Swaddle et al., 1994), and symmetry of specimens could be distorted during preparation—especially in bird and mammal study skins.

Although measurements in the field may be easily obtained, studies of FA require much forethought to prevent errors in the experimental design. For example, measurements on only one trait are often not enough to conclude that an individual's development has been affected (Leary and Allendorf, 1989; Palmer, 1994); thus it is preferable to examine several traits (Palmer, 1994). Measurements must be taken with precision because the differences between sides are often quite small (Palmer, 1994; Lens et al., 2002b), and measurement error can bias estimates of the between-side variance (Palmer and Stoback, 1986; Palmer, 1994; Merilä and Björklund, 1995; Björklund and Merilä, 1997; Van Dongen, 2000). In general, FA studies require reasonably large sample sizes (Clarke, 1995a; Van Dongen, 1999) and careful analysis (see Palmer and Stoback, 1986; Palmer, 1994).

4.2. Precision in quantifying impact

Attributing variation in FA to a particular anthropogenic stressor may be more precise in captivity where individuals can be housed under controlled conditions (see Bjorksten et al., 2000). Under field conditions, many factors may influence developmental stability. However, field studies of FA may be valuable where it is possible to compare isolated populations that are subjected to different key environmental factors.

4.3. Accuracy in predicting presence, absence, or population viability

FA can only be an accurate predictor of presence, absence, or population viability if there is a strong relationship between FA and fitness characteristics such as health, survival, or reproductive success. Some researchers propose (or have found) that highly stressed or low-quality individuals have high levels of FA, and that FA can be used as an indicator of fitness (Quattro and Vrijenhoek, 1989; Thornhill and Sauer, 1992; Møller and Swaddle, 1997; Møller and Thornhill, 1998; Møller, 1999). If this correlation is in fact valid, FA may be valuable in studies of human impact (Sarre et al., 1994), and some studies have focused on the relationship between FA and environmental stress caused by human disturbance (Valentine et al., 1973; Bengtsson et al., 1985; Zakharov and Yablokov, 1990; Pankakoski et al., 1992; Clarke, 1993).

This issue is however highly controversial; many researchers do not believe there is a strong relationship between fitness and FA (Clarke, 1995b, 1998; Markow, 1995; Leung and Forbes, 1997; Dufour and Weatherhead, 1998; Palmer, 2000), while Møller (1999) revealed an intermediate effect size. It has been suggested that any relationship found between FA and fitness should be “interpreted with caution” (Leung and Forbes, 1997, p. 405) and that selective reporting has overemphasized the power of this relationship (Palmer, 2000; but see Møller, 1999).

Despite this controversy some studies have shown that FA can be used as a predictor of a species' population viability. For example, Lens et al. (2002b) studied three populations of Taita Thrushes (*Turdus helleri*) each inhabiting a more or less degraded forest. Lens et al. (2002b) found that compared to the population in the least degraded habitat, the population in the most degraded habitat showed lower levels of symmetry and survival, whereas the population in the moderately degraded habitat only showed lower levels of symmetry. Hence, levels of asymmetry were apparent before survival decreased, therefore FA may be useful as an early warning system (Graham et al., 1993; Clarke, 1994, 1995a). Lastly, studies of FA may more accurately identify stressors when there are relatively high levels of stress than low levels of stress (e.g., Lens et al., 2002a).

4.4. Repeatability across populations and species

One major concern in FA studies is the low repeatability of individual FA measurements (Van Dongen, 1999) and the lack of replicated studies (Palmer, 2000). Many studies that found a relationship between FA and fitness were made at the population level (Møller, 1997), but populations can be affected by many factors (Bjorksten et al., 2000), and it is not clear if there is a relationship at the individual level (Clarke, 1998). Thus, it is difficult to determine which individuals are most fit. However, Møller (1999) reviewed a number of individually-based studies. It is also difficult to quantitatively compare data from published studies, frequently because of limited analytical power (see Palmer, 1994). Finally, FA may be affected by body size and age (Palmer, 1996), and thus may be not only species-specific, but also trait, and stress-specific making it very difficult to generalize about relationships between stress and asymmetry (Bjorksten et al., 2000).

5. Flight initiation distance

Animals commonly flee from approaching humans and this deceptively simple observation has generated two complementary lines of research: one focusing on theoretical behavioral ecological questions, and the other on more applied wildlife management questions. The exact distance at which an animal begins to flee has been variously called ‘flight-initiation distance’ (e.g., Ydenberg and Dill, 1986; Bonenfant and Kramer, 1996), ‘flush distance’ (e.g., Holmes et al., 1993; Richardson and Miller, 1997), and ‘escape flight distance’ (e.g., Madsen and Fox, 1995; see Taylor and Knight, 2003 for a recent review of terminology). Of central concern is that FID is also used by wildlife managers to quantify human disturbance (e.g., Buehler et al., 1991; Carney and Sydeman, 1999) and to define ‘set-back distances’ (e.g., Holmes et al., 1993; Rodgers and Smith, 1995; Giese, 1998) or ‘buffer zones’, areas beyond which people can be said to minimally disturb or impact wildlife (e.g., Holmes et al., 1993; Rodgers and Smith, 1997; Carney and Sydeman, 1999; Rodgers and Schwikert, 2002; Fernández-Juricic et al., 2005). This concept often is—or should be—used in designing captive facilities that do not compromise animal

wellbeing by forcing animals to remain in close proximity to human visitors (Morgan and Tromborg, 2007). While managers acknowledge the variability in FID (e.g., Carney and Sydeman, 1999), they nevertheless use estimates of a species' FID to attempt to minimize human impact.

5.1. *Ease of use*

Measuring FID is one of the easiest methods we evaluate. Individual animals are experimentally approached either on foot or using a potentially disturbing vehicle until they move away (e.g., off-road vehicle—Walther, 1969; Anderson et al., 1996; Rodgers and Smith, 1997; boats—Buehler et al., 1991; Rodgers and Smith, 1997; Rodgers and Schwikert, 2002; and other personal watercraft—Rodgers and Schwikert, 2002). It is particularly important to note the distance the experimental approach was begun (Blumstein, 2003) because animals are expected to vary FID as a function of perceived risk, and the 'starting-distance' is a measure of perceived risk. Additionally, it is desirable to note the distance the subject first orients towards the observer because this 'alert distance' illustrates when a disturbance actually begins.

5.2. *Precision in quantifying impact*

Behavioral ecologists have realized that, as for many other antipredator behaviors, individuals should vary FID dynamically so as to minimize the costs of disturbance while maximizing the chance of survival (Ydenberg and Dill, 1986; Bonenfant and Kramer, 1996; Frid and Dill, 2002). Studies have demonstrated that FID can be influenced by many variables (e.g., flock size—Burger and Gochfeld, 1991; angle of approach—Burger and Gochfeld, 1990, 1991; time of year—Richardson and Miller, 1997; time of day—Delaney et al., 1999; reproductive state—Bauwens and Thoen, 1981; distance to refuge—Dill and Houtman, 1989; whether or not a population is hunted—Louis and Le Berre, 2000; type of disturbance—Rodgers and Smith, 1997; starting distance—Blumstein, 2003; and the number of intruders—Geist et al., 2005). When quantifying human impacts, FID is best used by comparing 'disturbed' and 'undisturbed' populations, where differences should be attributable to differential habituation (Ikuta and Blumstein, 2003; Runyan and Blumstein, 2004).

5.3. *Accuracy in predicting presence, absence, or population viability*

There are at least two mechanisms by which flightiness could influence a population's viability. First, if nesting birds are flushed off their nests, recruitment could be negatively impacted (Carney and Sydeman, 1999) and a population could decline until it becomes locally extinct. Second, if human disturbance makes a particular area economically costly (e.g., Gill and Sutherland, 2000; Gill et al., 2001) via the energetic costs of constant flight, for example, species may avoid a disturbed area. To date, we are aware of no studies that have specifically correlated variation in FID with a species' presence–absence in a particular area (but see Fernández-Juricic, 2000, 2002; Fernández-Juricic et al., 2001).

5.4. *Repeatability across populations and species*

Behavioral biologists recognize that antipredator behavior has heritable components (Riechert and Hedrick, 1990), and that there are species-specific types of antipredator behavior

(Edmunds, 1974; Morse, 1980; Lima, 1993). While FID does have a species-specific component (Blumstein et al., 2003), it is not obvious how a given species will respond to increased human activity. Some populations or species seemingly habituate to increased disturbance (Ikuta and Blumstein, 2003) while others are sensitized to human activities (Blumstein, unpublished data; Müllner et al., 2004). Ecological differences between populations may account for differences in FID but, if measured, these may be statistically controlled for (e.g., Ikuta and Blumstein, 2003). Moreover, even when habituation occurs, it may often be partial (Frid and Dill, 2002), which means that species-specific responses to disturbance (Blumstein et al., 2003) may make community-level responses to disturbance predictable (e.g., Fernández-Juricic, 2002).

While many factors can influence FID (e.g., Frid and Dill, 2002), and a given FID estimate may be location specific, there is repeatable variation in a species' relative flightiness (Blumstein et al., 2003). Thus, FID can be used to estimate the relative flightiness of species. Future studies will need to better develop the relationship between relative flightiness and a species' presence–absence.

6. Immunocompetence

The Hamilton–Zuk hypothesis of parasite-mediated sexual selection (Hamilton and Zuk, 1982) has been followed by the immunocompetence handicap hypothesis (Folstad and Karter, 1992), which proposes that steroid hormones, which aid in the development of secondary sexual characteristics, are produced at an expense of immune function. Both hypotheses have generated a plethora of studies testing the interactions between male quality, hormones, and immune function. In addition, the field of immunocompetence is growing at an exponential rate with new studies that focus on male quality, female quality, as well as the quality of their offspring. Because immunocompetence is influenced by stress (e.g., Harbuz and Lightman, 1992; Biondi and Zannino, 1997; Råberg et al., 1998), and some immune responses are apparently energetically costly for the animal (e.g., in House sparrows, *Passer domesticus*; Martin et al., 2003), studies of immunocompetence are well suited for conservation research aimed at quantifying human impacts.

6.1. Ease of use

Correlates of immunocompetence are often measured in one of three ways: (i) counting parasites on individuals, (ii) instigating an immune challenge (humoral or cell-mediated), or (iii) monitoring levels of blood cells (such as leukocytes, or the ratio of heterophil to lymphocytes) or proteins (such as plasma proteins or serum proteins). All methods require capturing and handling of individuals. To test an organisms' response to an immune system challenge, individuals must be injected with the immune challenge (often a vaccine or attenuated pathogen). Following the challenge there are two ways to quantify immune response. The skin at the injection site may be examined for a visible swelling (like skin tests used to test for human tuberculosis antibodies), and/or a blood sample may be taken and directly examined for the presence of antibodies. The former is less expensive and requires less training and equipment (Smits et al., 1999). Another common approach is to look at the relationship between the parents' level of immunocompetence and the 'quality' of their offspring, because offspring quality can be affected by their parents' ability to resist parasites or diseases. These studies require monitoring of offspring survival. Results from immunocompetence testing can be highly variable because the methods require precision and care (for example see Smits et al., 1999) and there can be seasonal fluctuations in

immune function (Lochmiller et al., 1994; Nelson and Demas, 1996). In addition, combinations of tests are often necessary to identify a true measure of immunocompetence (for review see Norris and Evans, 2000).

6.2. Precision in quantifying impact

Immunocompetence can change in response to changes in the environment (such as temperature or food availability; Lifjeld et al., 2002), which lead to changes in behavior. Individuals forced to aggregate in large groups, for example, may have depressed immune systems (Tella et al., 2001; but see Møller et al., 2001). It can be difficult to determine the precise correlate of a reduced immune response, or to detect increased levels of diseases or parasites. An organisms' immune response can be affected by degraded food supplies (Hoi-Leitner et al., 2001; Lifjeld et al., 2002), reproductive effort (Sheldon and Verhulst, 1996), testosterone levels (Zuk, 1996), competition (Tella et al., 2001), levels of parasites and diseases (Møller and Saino, 1994; Ots and Hõrak, 1996), or climatic change that affects pathogen distribution (Patz and Reisen, 2001). These types of changes often result from human impacts. For example, male ovenbirds (*Seiurus aurocapillus*) have higher energy demands in contiguous forest than in forest fragments, resulting in lower quality individuals, whereas individuals in the forest fragments appear to have a higher immunological condition at the end of the breeding season (Mazerolle and Hobson, 2002). To precisely determine the stressor initiating the current state of immunocompetence it is necessary to either study the same population before and after an impact (rarely possible), or to have two similar sites where differences can be determined (such as the above study comparing individuals living in contiguous and fragmented forest habitats; Mazerolle and Hobson, 2002).

In addition, captive studies have helped reveal the relationship between impact and immune response. For example, Fairbrother et al. (1994) investigated the effects of selenium, arsenic, and boron on aquatic birds and found that toxicity leads to reduced immune function (for a review of toxicity in aquatic birds see Hoffman, 2002). Furthermore, long-term exposure to sound (a fire alarm bell) has been shown to cause stress and immunosuppression in broiler chickens (Lazarevic et al., 2000). Although, these studies were done in captivity, similar studies could be conducted on free-living individuals.

Lastly, not only do environmental factors have an effect (as mentioned above; Lifjeld et al., 2002), but age (Ots and Hõrak, 1998; Lazarevic et al., 2000), sex (Ots and Hõrak, 1998), and duration of treatment also play a role in immunocompetence (Lazarevic et al., 2000). Thus, all of these factors must be taken into consideration when undertaking a study on immunocompetence.

6.3. Accuracy in predicting presence, absence, or population viability

It is typically assumed that conspecifics with the fewest parasites will be selected as mates (parasite-mediated sexual selection), yet in many cases high-quality males (ones selected by females) have the largest parasite loads (for review see Getty, 2002; but see Møller et al., 1999). As for reproduction, females with higher parasite loads (Merila and Andersson, 1999), or immunized individuals (Ilmonen et al., 2000; Hasselquist et al., 2001), have been shown to have lower reproductive success. In addition, male or female parents have been shown to have a lower immune response or increased parasitism with increased parental activities or brood size (Richner et al., 1995; Deerenberg et al., 1997; Nordling et al., 1998; Moreno et al., 1999; Boonstra et al., 2001; Saino et al., 2002). Brood size also may have an effect on the immune function of offspring, because offspring raised in enlarged broods have been shown to have lower

immune responses than offspring raised in reduced broods (Saino et al., 1997; Hōrak et al., 1999). Therefore, it is important to investigate the immunocompetence levels of parents and their offspring during the time of parental care. In addition, more studies are needed to clarify the relationship between immunocompetence and fitness because there is some controversy over the evidence of a causal relationship (Norris and Evans, 2000; Møller and Saino, 2004).

6.4. Repeatability across populations and species

The field of immunocompetence (and wildlife pathology in general) is still young. While it offers promising tools to quantify anthropogenic stressors, knowledge of repeatability is lacking and more studies are needed to develop a better understanding of the consistency of these methods. Tella et al. (2002) and Smits et al. (1999; also see 2001) found that cell-mediated immune response (measured by the phytohaemagglutinin assay—a common measure of immunocompetence in birds) was highly repeatable within species. Tella et al. (2002) also found chicks to have a stronger immune response than adults, and that while nestling period was correlated with chick response rates, adult response rates were related only to body size, period of development, and longevity. Developmental stage can have an effect on immune response (also see Smits and Williams, 1999) and different species may respond differently to immune challenges. With time we will have a better understanding of the trends and patterns found in immunocompetence testing.

7. Glucocorticoids

Stress is a measure of an animal's behavioral and physiological response to physical and social changes in its environment (Broom and Johnson, 1993; Sapolsky, 1990, 1992). In vertebrates, stress can be directly measured by looking at changes in concentrations of glucocorticoid hormones (Harvey et al., 1984) after controlling for other important factors that may influence glucocorticoid levels (time of year, reproductive status, or because individuals must adaptively mobilize energy reserves—Hofer and East, 1998; Romero and Wikelski, 2002). Glucocorticoids are naturally secreted to allow individuals to mobilize energy reserves in order to adaptively cope with adverse conditions (Romero et al., 1998). A short-term stress response can suppress reproductive or territorial behavior (see Wingfield, 1984, 1988) and increase energy reserves through an increase in gluconeogenesis (Sapolsky, 1990). This rapid mobilization of energy helps the individual become alert and respond to the stressor (for example, through escape). Chronic environmental stressors, however, may lead to non-adaptive levels of glucocorticoid secretion which can cause deleterious effects for the animal (for reviews see Buchanan, 2000; Sapolsky et al., 2000) which may include reproductive inhibition (Wingfield, 1984, 1988), immune system suppression (Munck et al., 1984; Apanius, 1998), neuronal death (Sapolsky et al., 1990; Sapolsky, 1992; McEwan and Sapolsky, 1995; Bremner, 1999; Kimonides et al., 1999), and impaired cognitive function (McEwan and Sapolsky, 1995; Bremner, 1999; de Kloet et al., 1999). Chronic levels of stress, therefore, can lead to reproductive failure and premature death (for a more detailed review of the effects of glucocorticoids on vertebrates in relation to conservation research see Wingfield et al., 1997). Chronic stress can be caused by the inability of an animal to habituate to human disturbance. Measuring glucocorticoid levels, however, has only recently been considered or used to study anthropogenic stressors on wild animals (Wasser et al., 1997; Fowler, 1999; Palme et al., 2000; Foley et al., 2001; Millsbaugh et al., 2001; Turner, 2001; Creel et al., 2002; Romero and Wikelski, 2002; Müllner et al., 2004). Glucocorticoids can be measured

in three ways: in the blood plasma, in feces, and in urine. Here we will focus on plasma and feces (urine is typically collected only from captive animals), each of which has its own limitations.

7.1. *Ease of use*

Plasma and fecal samples can be obtained and processed quickly, relative to other measures of quantifying impacts. For most birds, as little as 10 μl of plasma are needed to quantify glucocorticoids, thus, only a small blood sample (ca. 25–50 μl) is required. Difficulty in obtaining the blood sample is directly related to the difficulty of capturing and immobilizing the subject. Feces, on the other hand, can be obtained non-invasively, however validations are necessary for each species and the specific antibody used for quantification must be chosen with care (Goymann et al., 1999; Wasser et al., 2000). Because of the other factors that naturally influence glucocorticoid levels (sex, age, reproductive status), it is important to collect feces from individually-identified subjects. In some cases it may be important to first catch and mark subjects to facilitate this.

7.2. *Precision in quantifying impact*

Measurements of both plasma and fecal glucocorticoids have been used to investigate the consequences of human disturbance. The main difference in these two methods is that plasma samples can be taken at the time of a particular human impact, such as directly after the onset of a human activity (e.g., a loud noise). Thus it is possible to do a within-subject comparison between samples taken pre- and post-impact or to compare those taken from individuals subject to no disturbance. These within-subject comparisons are particularly useful because of expected individual differences in baseline glucocorticoid levels.

Additionally, plasma samples are often used to determine an individual's stress response due to capture and restraint via 3–6 sequential bleedings within 30 or 60 min of capture (Wingfield et al., 1992; Smith et al., 1994; Dufty and Belthoff, 1997; Breuner et al., 1999). This 'capture–stress protocol' provides information both about the peak glucocorticoid response and the slope of the relationship between the initial levels and peak levels (over time). Fecal samples may provide information about basal glucocorticoid levels of the individual. However, if feces are collected before and after the onset of an anthropogenic stressor, and if the time that it takes for corticosteroids to be excreted in feces is known, it should be possible to use fecal samples to detect the effect of a particular stressor. Basal glucocorticoid levels may be useful when comparing individuals under different levels of disturbance or when comparing the hormone levels of the same individuals at different times of impact (Wasser et al., 1997; Palme et al., 2000; Millsaugh et al., 2001; Creel et al., 2002). While plasma samples can also be used in this way (Fowler, 1999; Romero and Wikelski, 2002; Turner, 2001; Müllner et al., 2004), taking blood samples is more invasive.

7.3. *Accuracy in predicting presence, absence, or population viability*

Chronic stress has been shown to cause deleterious effects (see above), thus chronically high glucocorticoid levels could directly lead to the absence of a focal species. Elevated glucocorticoid levels resulting from a human disturbance during the reproductive season may generally be associated with reproductive failure. However, at this time, the relationship has only been shown in birds, and studies must go beyond simply comparing glucocorticoid levels, to looking directly at

breeding success as a function of glucocorticoid levels (Müllner et al., 2004). Additionally, Romero and Wikelski (2001) found that corticosterone levels predicted marine iguana (*Amblyrhynchus cristatus*) survival during El Niño in the Galápagos. Ultimately, it is likely that glucocorticoid levels can be used to predict survival in other wild populations as well.

7.4. Repeatability across populations and species

Previous studies in a variety of species have found that measurements of glucocorticoid levels are fairly constant and repeatable within a species, but show considerable changes seasonally (Romero, 2002). However not all species respond the same way to anthropogenic stressors. For example, Fowler (1999) found that Magellanic penguins (*Spheniscus magellanicus*) became so habituated to human ecotourists that their glucocorticoid levels were lower in tourist sites. Romero and Wikelski (2002) found however that Galápagos marine iguanas showed no difference in basal glucocorticoid between tourist and non-tourist sites even though they showed a difference in the stress-induced glucocorticoid response (iguanas at the tourist site showed a lower glucocorticoid response). In contrast, juveniles of the folivorous forest bird in the Amazon, the hoatzin (*Opisthocomus hoazin*), apparently becomes hypersensitive to ecotourist visits, whereas juvenile birds in non-tourist areas showed lower stress responses (Müllner et al., 2004). Additionally, little penguins (*Eudyptula minor*) in Australia also showed a lower stress response in non-tourist compared to tourist sites (Turner, 2001). Thus, at this time there does not appear to be a pattern in species response to human impact and each species must be investigated independently.

8. Cardiac Response

Cardiac measurements have been used for over 20 years to help quantify human impact in many vertebrates including ungulates (MacArthur et al., 1979, 1982; Moen et al., 1982; Anderson et al., 1996), seals (Perry et al., 2002), and birds (Culik et al., 1990; Nimon et al., 1995; Weimerskirch et al., 2002). These measurements can be especially useful because animals can show an increase in heart rate due to human impacts without showing overt changes in behavior (Culik et al., 1990; Wilson et al., 1991). For example, Culik et al. (1990) found that incubating Adélie penguins responded to approaching humans by significantly increasing their heart rate, even though they continued to incubate and appeared to be undisturbed. Thus, heart rate is a measure of the stress response and may predict potential chronic stress, elevated glucocorticoid levels and the correlated negative consequences for health and reproduction. Additionally, heart rate can be a predictor of metabolic rate, and thus it can be a surrogate measure of energy expenditure (Pauls, 1980; Bevan et al., 1992; Nolet et al., 1992; Butler, 1993).

8.1. Ease of use

A variety of methods are available to measure cardiac response, each appropriate for different organisms under different conditions. The most invasive method is surgical implantation of a cardiac data logger. Data loggers record heart rate over time and, once removed, heart rate at any given moment can be compared to a record of environmental disturbance or social activity (Woakes et al., 1995). Any surgical procedure can be risky for individuals because they must be captured and anesthetized during the procedure. However when successful, individuals have been shown to continue in their daily routine with no significant costs (Guillemette et al., 2002). A slightly less invasive method affixes a cardiac transmitter on the back of individuals.

These devices may have electrodes placed under the skin (Weimerskirch et al., 2002) and in addition they may involve attaching a harness to the animal (MacArthur et al., 1979, 1982). Although less invasive and easier to attach, external loggers may hinder activities or provide additional costs to individuals (Ropert-Coudert et al., 2000). For birds, artificial eggs with microphones have been placed in nests of incubating individuals and the heart rate is recorded acoustically (Nimon et al., 1996; Giese et al., 1999). Of course the latter only records heart rate while the individual is at its nest site. Overall, measures of heart rate can be used to dynamically study the response of individuals to external stimuli and, by doing so, clearly identify aspects of human disturbance that animals find particularly ‘disturbing’.

If one wants to use heart rate as an indicator of energy expenditure, careful calibration over a variety of heart rates is necessary while an individual is in a metabolic chamber. This requires another type of manipulation and the experiment itself has been shown to increase individual cardiac responses (Weimerskirch et al., 2002). Moreover, the relationship between oxygen consumption and heart rate is not always found (see Webb et al., 1998), and it may be necessary to study many individuals to obtain accurate results (Bevan et al., 1994). In addition, body mass and sex must be taken into account while identifying the relationship between heart rate and oxygen consumption (see Green et al., 2001).

8.2. Precision in quantifying impact

Monitoring heart rate is a sensitive and precise way to measure human impact. Incorporating measures of cardiac response with behavioral observations can identify the specific events that affect animals. For example, Anderson et al. (1996) was able to show how moose (*Alces alces*) heart rate was influenced by military maneuvers by looking at heart rate before, during, and after disturbance. This cardiac response was correlated with moose flight response and was elicited by both human and mechanical stimuli (Anderson et al., 1996). Additionally, moose took longer to recover after a human disturbance than they did after mechanical disturbance (Anderson et al., 1996). Using heart rate transmitters and behavioral observations Culik et al. (1990) demonstrated the heart rate for incubating Adélie penguins under different conditions including at rest, standing, with human disturbance, and with helicopter disturbance. Cardiac measurements can be a powerful tool to detect how individuals respond to specific stressors and are uniquely able to document how long it takes them to recover from a particular disturbance.

8.3. Accuracy in predicting presence, absence, or population viability

Cardiac responses may foreshadow chronic stress responses and this sensitivity makes it uniquely suited to identifying stressors precisely. Combining knowledge of cardiac responses to human disturbance with additional knowledge of the relationship between heart rate and metabolic rate, a detailed understanding of energy expenditure can be developed. Energy expenditure is likely to be associated with reproductive effort (Bryant, 1988; Spencer and Bryant, 2002) and survival (Daan et al., 1996; Speakman, 1997; Speakman et al., 2002). Thus, it may influence the population viability of some species when disturbed by humans.

8.4. Repeatability across populations and species

Heart rate (and the response to stimulation) varies with body size, species, and can vary with sex. Additionally, as mentioned before, different populations and individuals can have different

responses to human disturbance. For example, Weimerskirch et al. (2002) found that after handling, the heart rate of male wandering albatrosses (*Diomedea exulans*) returned to basal levels significantly faster than did the heart rate of females. Therefore, factors such as sex must be considered when measuring cardiac response.

9. Discussion

By far, the greatest challenge for those trying to quantify human disturbance on wildlife is that these measures should ultimately be linked to individual fitness. It is through an explicit link to individuals that we can develop the individually-based models that will be able to predict the

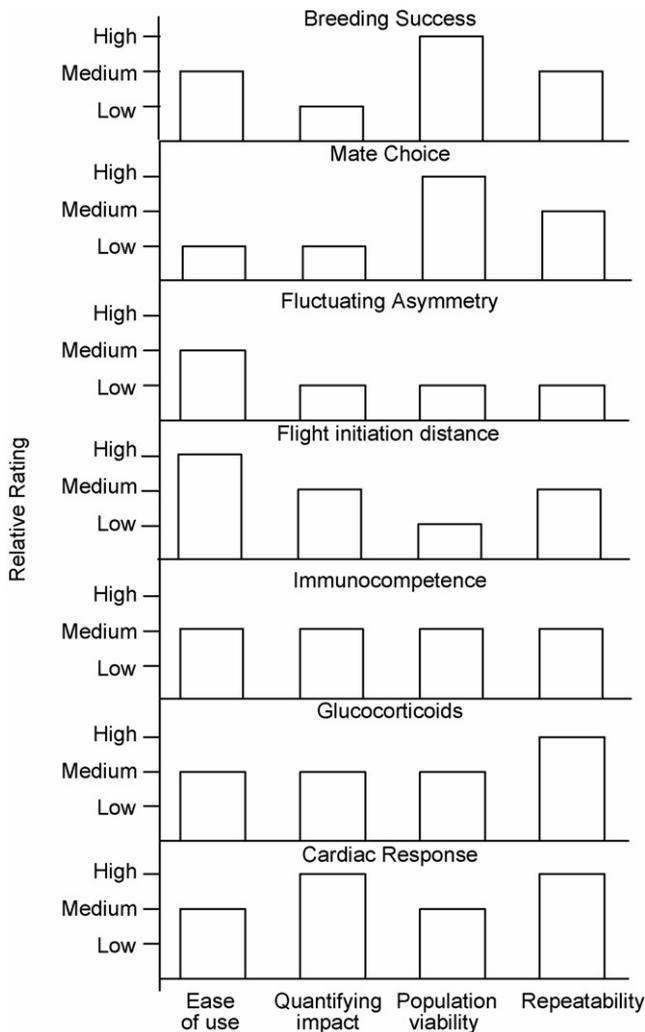


Fig. 1. A graphical comparison of the methods to identify anthropogenic stressors on wildlife. Each measurement (breeding success, mate choice, fluctuating asymmetry, flight initiation distance, immunocompetence, and glucocorticoids) is assigned a relative rating of high, medium, or low for each factor analyzed (ease of use, quantifying impact, population viability, and repeatability).

response to anthropogenic change (Norris, 2004). Another fruitful line of research is cross-validating the various measures. We typically have no data on the relationships between different measures, and this research may suggest that some methods are better than others with respect to identifying stressors. With these important cautions, we have highlighted each method's strengths and weaknesses by classifying each criterion for a given method as low, medium or high, and summarize these graphically (Fig. 1). We acknowledge that this is a somewhat arbitrary ranking but it does provide a focus for method selection. Managers may use this figure to help select a method appropriate for a particular question. To compare methods, we averaged the performance indicators and ranked the mean response. Measures of cardiac response ranks the highest, followed by glucocorticoids, which is followed by both breeding success and immunocompetence, then by FID, mate choice, and FA. FID ranked the highest for ease of use, and the lowest, along with FA, for accurately predicting presence–absence, although we acknowledge that critical studies of the relationship between FID and presence remain to be conducted. FA additionally ranked low for repeatability and precision in quantifying the impact. Taken together we do not believe that FA is a good method to quantify impacts although measurements of FA may supplement other methods. Measurements of mate choice and breeding success were also ranked low for quantifying impact, however these methods were the highest ranked for predicting presence–absence. Mate choice was ranked the lowest for ease of use, however few studies have used this approach and more studies are needed to determine exactly how difficult this measurement is in practice. Cardiac response was ranked the highest for precisely quantifying the stressor and for repeatability, although glucocorticoids were also ranked high for repeatability. We again emphasize that future studies should explore the ability of these methods to accurately predict the distribution and abundance of species subject to human impacts.

In conclusion, managers should carefully evaluate the benefits and costs of each method before choosing one. Using several methods might ultimately provide better predictive value and, by doing so, we will ultimately be in a better position to evaluate the predictive ability of these different methods. Future research should focus specifically on linking indirect measures of anthropogenic stressors to the population viability of focal species.

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