Appendix I to the Working Paper on Human Disturbance to Wildlife in the Broader Antarctic Region: A Review of Findings

Review of recent research into the effects of human disturbance on wildlife in the Antarctic and sub-Antarctic region

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TABLE OF CONTENTS

A. INTRODUCTION	3
B. SUMMARY OF DISTURBANCE RESEARCH IN THE ANTARCTIC AND SUB-ANTARCTIC	
1. Main findings	
2. Trends in Antarctic and sub-Antarctic disturbance research	6
C. FUTURE DIRECTIONS IN DISTURBANCE RESEARCH	7
Explanatory variables a. Visitor group size b. The relationship between minimum approach distance and starting distance	8
c. Frequency of visitors d. Visitor distribution e. Visitor access points and wildlife refuge areas	8 9
f. Level of disturbance	9 9
h. Species i. Stage of breeding j. Visitor behaviour k. General	10 10
2. Response variablesa. Behaviour	12 12
b. Physiology i. Glucocorticoid levels ii. Heart rate iii. Health and immunocompetence	12 12
c. General D. REFERENCES	13
TABLE 1	
TABLE 2TABLE 3	38 40
APPENDIX I	41

A. INTRODUCTION

Human presence in the Antarctic (south of 60 degrees latitude) and the sub-Antarctic (for the purposes of this paper, south of 40 degrees latitude) has increased rapidly over the last six decades. Scientists and support staff have occupied the Antarctic continent at stations continuously since 1944 and at the South Orkney Islands since 1903. Tourism on the continent began with an over-flight by a tourist aircraft in 1956 and a tour ship visit in 1958 (Splettstoesser et al. 2004). There are now 32 stations in the Antarctic (Splettstoesser et al. 2004) and six on the sub-Antarctic islands that have no permanent inhabitants (de Villiers et al. 2006a). Tourist activity is largely related to cruise-ship and flight operations at the Antarctic Peninsula, the Ross Sea and sub-Antarctic islands (Hall and McArthur 1993). In 2004 it was projected that by 2006/07 the Antarctic would be visited by 22,000 tourists (Splettstoesser et al. 2004) - the actual figure for this season was over 37,000, with 29,530 landed passengers (IAATO 2007a). Visitor numbers at those sub-Antarctic islands without permanent inhabitants tend to be comparatively low, with South Georgia receiving the highest number (around 4000 per annum). Several sub-Antarctic island groups - the Prince Edward, Snares, Antipodes and Bounty Islands – do not allow any onshore tourism (de Villiers et al. 2006a). There is ready public access to several mainland seal and seabird breeding sites in southern Argentina, Chile and New Zealand, as well as sites on the Falkland Islands. Many of these sites have some degree of formal protection.

Onshore human activities in the Antarctic and sub-Antarctic, including habitat destruction or modification, the introduction or spread of alien organisms (including diseases), and pollution, can have numerous negative effects on native wildlife. One threat to wildlife that has received increasing attention from scientists and managers is that of human disturbance. Tourist, research and logistical activities all have the potential to cause disturbance to wildlife, particularly where these activities take place near breeding sites. Animals may respond negatively to pedestrian approaches, drive- or fly-bys or approaches by transport such as boats and aircraft, handling, and external or internal devices fitted for research purposes. Responses are affected by the type, intensity, duration, timing and rate of the disturbance, and are likely to be species- and site-specific. Major categories of negative effects include direct injury or death, disruption of activities or increase in stress levels; and loss or modification of habitat (Green and Higginbottom 2000). The biggest sector of ecotourists comprises bird-watchers who are, on average, well-educated, wealthy and environmentally conscious. Yet a review of 27 studies on the effects of wildlife observation and photography on birds reported negative effects in 19 studies (Sekercioglu 2002).

In the Antarctic and sub-Antarctic region, wildlife may be especially vulnerable to disturbance effects. Many of the seal and seabird species targeted by tourism in the region tend to be colonial, thus large sections of a population may be affected simultaneously. The resilience of animals to disturbance may be quite low, since species must survive in a harsh environment with a limited breeding season, and tend to be long-lived and slow-breeding (there is late onset of sexual maturity and some species only breed once a year or once every two years), with reliance on coordinated care of offspring by both parents. Wildlife in the region is at a disadvantage in being able to deal with human disturbance, since species are not evolutionarily adapted to deal with land-based predators. Escape can be energetically expensive – most species are relatively large, and penguins are flightless.

This paper reviews research (published or in press only) over the last two decades into the effects of various types of human disturbance on wildlife in the Antarctic and sub-Antarctic region. The results of a few studies published prior to 1988 are also referred to below, but not included in analyses. The review concentrates on research which has implications for disturbance related to tourism activities. It identifies trends and possible future directions in disturbance research approaches.

B. SUMMARY OF DISTURBANCE RESEARCH IN THE ANTARCTIC AND SUB-ANTARCTIC

1. Main findings

The main findings of the papers reviewed are summarised in Table 1.

At some locations and for certain species, the disturbance associated with general human activities (a combination of tourism, research and / or the logistical activities associated with these) has little apparent effect on wildlife population trends, in comparison with the effect of fluctuations in environmental conditions (e.g. Fraser and Patterson 1997, Cobley and Shears 1999, Micol and Jouventin 2001, Carlini et al. 2007). However, at some sites and for some species, human activities have been implicated in population declines (e.g. Wilkinson and Bester 1988, Muller-Schwarze 1984, Jouventin and Weimerskirch 1990, Harris 1991, Woehler et al. 1991, 1994, Micol and Jouventin 2001), although such declines have occasionally been partially reversed after restrictions were placed on activities (e.g. Thomson 1977, Woehler et al. 2003) or after human disturbance ceased (e.g. Young 1990). The mechanism for population declines may be decreased breeding success (e.g. Woehler et al. 1994, Giese 1996) and for birds, this may in turn be related to decreased fledging mass (e.g. McClung et al. 2004, Ellenberg et al. 2007). However, decreased breeding success or correlates thereof are not always associated with human activities (e.g. Cobley and Shears 1999, Ratz and Thompson 1999, Engelhard et al. 2001) and natural environmental factors may influence breeding success more than certain types of human disturbance (e.g. Holmes et al. 2005a). Some species may tolerate a degree of human disturbance (e.g. Young 1990, Harris 1991) or even benefit from human activities, which may artificially inflate certain predator populations (e.g. Hemmings 1990) to the detriment of prey populations. Human disturbance may also cause changes in the distribution of breeding sites (e.g. Pfeiffer and Peter 2004), by discouraging first-time breeders to settle near sources of disturbance or by causing prospective breeders to move into sub-optimal breeding habitat (e.g. Robertson 1997). Consequently, nesting density at sites may be affected (e.g. Fowler 1999). Disturbance may also cause deviations from paths by birds in transit (e.g. Burger and Gochfeld 2007), thus incurring energetic costs for parents and delaying the feeding of their offspring.

Pedestrian approaches alter the behaviour of the approached animals. Altered behaviour may result in energetic and / or time costs (e.g. Burger and Gochfeld 2007), and there is some evidence that certain behavioural responses (rates of vigilant acts) correspond to physiological changes that may impact fitness (heart rate) (Holmes et al. 2005b). The identification of key wildlife response behaviours can assist with the self-regulation of visitor behaviour (Holmes 2007). Human intrusion into bird colonies may create predation opportunities for species such as gulls (e.g. Kury and Gochfeld 1975), but it appears that predators do not always take advantage of such opportunities (e.g. Crosbie 1999), and factors other than level of disturbance - such as colony size and the presence of alternative prey - may also influence

predation rates (e.g. Weidinger 1998). Pedestrian approaches can cause physiological changes in the absence of noticeable overt behavioural responses (e.g. Giese 1998). Covert responses include the elevation of heart rates (e.g. Giese 1998, Holmes et al. 2005b) and increased expression of stress hormones (e.g. Fowler 1999, Ellenberg et al. 2007). However, in some cases, levels of human disturbance do not result in detectable physiological differences (e.g. Engelhard et al. 2002a, b). Even if there are behavioural and physiological responses, these may only be short term (e.g. Engelhard et al. 2002a, de Villiers et al. 2006b) and their biological significance may be questionable. Animals may exhibit behavioural habituation (e.g. Yorio and Boersma 1992, Boren et al. 2002) and physiological habituation (e.g. Walker et. al. 2006) to certain kinds of human disturbance, although the facility for physiological habituation may be age-dependent (e.g. Walker et al. 2005). Habituation may only take place if disturbance is regular and predictable (e.g. van Polanen Petel et al. 2007). Human intrusions (e.g. Simeone and Schlatter 1998) or construction activities (e.g. Micol and Jouventin 2001) may also result in the destruction of nest sites.

Aspects of pedestrian approaches that are likely to influence the strength of response by wildlife include approach distance (e.g. Pfeiffer and Peter 2004, de Villiers et al. 2005, de Villiers et al. 2006b), visitor group size (e.g. Holmes et al. in press, van Polanen Petel et al. in press), predictability of the disturbance (e.g. van Polanen Petel et al. 2007) and visitor behaviour (e.g. Yorio and Boersma 1992, Nimon and Stonehouse 1995), including speed of approach (e.g. Yorio and Boersma 1992) and angle of approach (e.g. Martin et al. 2004, Burger and Gochfeld 2007). Susceptibility to human disturbance may be species-specific (e.g. Holmes 2007). Especially sensitive species include Gentoo Penguins (Jouventin et al. 1984, Holmes 2007) and Southern Giant Petrels (Jouventin et al. 1984, Woehler et al. 2003, Pfeiffer and Peter 2004), but species-specific sensitivity may also vary according to site (consider Gentoo Penguins at Macquarie Island - Holmes 2007, and at Port Lockroy - Muller-Schwarze 1984). Other factors that may influence sensitivity to disturbance include stage of breeding (e.g. Kury and Gochfeld 1975, Holmes et al. in press), breeding experience (e.g. de Villiers et al. 2005), time of day (e.g. Burger and Gochfeld 2007) and colony size (e.g. Giese 1996). Responses may be influenced by distance to conspecifics (e.g. Martin et al. 2004, van Polanen Petel et al. in press), the presence of shelter (e.g. Yorio and Boersma 1992) or proximity of a refuge (e.g. van Polanen Petel et al. in press), the location of offspring relative to parent and disturbance source (e.g. van Polanen Petel et al. in press), age and sex (Boren et al. 2002, Walker et al. 2005), and the length of the fasting period (Hood et al. 1998). There is a great deal of individual variation in responses to disturbance (e.g. Ellenberg et al. 2007) and some of this variation may be explained by personality differences.

To reduce the disturbance associated with pedestrian approaches to wildlife, mechanisms have been suggested for the spatial regulation of visitors, including the setting of minimum approach distance guidelines (e.g. Wilson et al. 1991, Giese 1998, Holmes et al. 2005b), restricting visits to sections of a colony associated with particular wildlife activities, such as seal haul-outs rather than breeding sites (e.g. Boren et al. 2002), limiting visits to only colonies or sections of colonies that have had time to habituate (Yorio and Boersma 1992, Fowler 1999), spreading visitors out over a large area thereby minimizing disturbance to individual animals (e.g. van Polanen Petel et al. 2007), exclusion zones around breeding sites of sensitive species (e.g. Holmes 2007), avoiding paths used by wildlife in transit between breeding sites and the sea (e.g. Burger and Gochfeld 2007), restriction of tourists to particular access paths (e.g. Pfeiffer and Peter 2004, de Villiers et al. 2006b), the provision of safe buffer zones (e.g. Martin et al. 2004) and the erection of barriers

(e.g. Kury and Gochfeld 1975) or hides (e.g. Ratz and Thompson 1999) (although the latter may not be effective in the long term, e.g. Robertson 1997). Suggested mechanisms for the temporal regulation of visitors include limiting visits at certain times of the breeding season (e.g. Boren et al. 2002, Holmes et al. in press), and restrictions on the rate of visitation (e.g. Kury and Gochfeld 1975, Burger and Gochfeld 2007) and the time of day of visits (e.g. Burger and Gochfeld 2007). Disturbance may also be controlled by limiting visitor group size (e.g. Burger and Gochfeld 2007), capping the number of visitors, or limiting the types of activities that are allowed at a site (e.g. Thomson 1977). Visitor education is important, and could include instruction regarding appropriate visitor behaviour (e.g. Ellenberg et al. 2007) as well as instruction regarding key animal responses to disturbance (e.g. Holmes 2007). The presence of wardens at breeding sites may be effective in regulating visitor behaviour (e.g. Otley 2005). Some sites may benefit from formal protection (e.g. Simeone and Schlatter 1998, Woehler et al. 2003).

Research can also cause declines in wildlife populations (e.g. Wilson et al. 1990) and in some instances may have as serious (e.g. Giese 1996) or more serious (e.g. Fowler 1999) consequences than tourism. Handling of animals and the fitting of external devices can have severe consequences, such as the lengthening of foraging trips and resultant nest abandonment (e.g. Wilson et al. 1989), although this is not always the case (e.g. Yorio and Boersma 1994, Hull and Wilson 1996). Certain species may be sensitive to repeated handling, but others may be quite robust (e.g. Vleck et al. 2000, Engelhard et al. 2002a, b).

In Antarctica, airborne tourism involves overflights without landings, and flights with landings (Swithinbank 1993). None of the sub-Antarctic islands without resident human occupants have aircraft landing strips, but as in Antarctica (Harris 2005), there are recommendations in place for aircraft operations (de Villiers et al. 2006a). The impacts of aircraft operations on wildlife range from insignificant (e.g. Burton and van den Hoff 2002) or minor (Giese and Riddle 1999) behavioural changes, to increases in heart rate and temporary nest desertions resulting in some active nest mortality (Wilson et al. 1991), multiple nest desertions (e.g. Sladen and Leresche 1970) and mass panic and the resulting death of thousands of birds (Rounsevell and Binns 1991). Published research has only focussed on the effect of aircraft operations on penguins and seals. The effects of aircraft operations on Antarctic birds have been reviewed (Harris 2005). However, few studies have quantified the effects of vehicle and boat disturbance on wildlife in the region. IAATO provides guidelines for vessel operations (IAATO 2007b), but few sub-Antarctic islands without resident human occupants have such guidelines in place. Most of the latter islands that allow motorized vehicles restrict operations of these vehicles to certain areas (de Villiers et al. 2006b). Some species may respond more to land than sea approaches (Boren et al. 2002). There may be habituation to certain types of boat disturbance, but boat approaches to breeding seabird colonies may also cause colony desertion at certain times (Schiavini and Yorio 1995). The noise associated with all forms of transport is likely to be audible to animals under the sea surface (van Polanen Petel et al. 2006), and underwater explosions can cause mortality (Brown and Adams1983). The severity of impacts is related to the species concerned, the timing of transport-related operations relative to the breeding season of the species, the type of transport, and the distance from wildlife concentrations at which transport operates.

2. Trends in Antarctic and sub-Antarctic disturbance research

There has been a marked decrease in the proportion of studies making use of long-term databases to examine disturbance-related population trends or comparisons of breeding success or correlates thereof. The focus in the last decade has instead been on short-term studies (usually conducted over one or two breeding seasons, and sometimes over a few days in one season only) (Table 2). Few studies in either decade have been purely observational; there is usually either a comparison over time (i.e. temporal trends) or across space (i.e. comparing results obtained at sites with different levels of human disturbance), or a comparison against a control (for example, comparing heart rate increases in response to natural predators with those in response to approach by a human). In both decades, the emphasis has been on comparisons across space or against a control, and there has been a decrease in the monitoring of temporal trends in the last decade (Table 2).

The focus in the first decade was almost exclusively on the impact of human disturbance on penguins (Table 2), with 50% of studies considering the impact on Adélie Penguins. In the second decade, the species base of studies was broadened to include more species of seals (six of 12 seal disturbance studies have focussed on Southern Elephant Seals), more penguin and other seabird species (Table 2), and only 15% of the studies considered Adélie Penguins.

More than half of studies in the last decade, compared to just under half in the previous decade, have focussed on the effects of pedestrian approaches. Responses of wildlife to approach by a human / humans on foot are increasingly considered against the predation-risk hypothesis, which proposes that wildlife may view anthropogenic stimuli as a predation threat (Frid and Dill 2002). The proportion of studies considering aircraft disturbance has decreased but for the first time, the effects of vehicles and boats operating near-shore have been investigated (Table 2).

The emphasis on measuring behavioural response variables is stronger than ever, and behaviour is often considered in combination with heart rate as a physiological correlate of fitness. Increasingly, however, other physiological measures are being incorporated into studies. Pre-eminent among these is the concentration of the stress hormone, corticosterone, although a few studies have considered other blood chemistry parameters that may relate to health and / or immunocompetence (Table 2). In the most recent decade, few studies have commented on the possible impacts of human disturbance on distribution patterns of wildlife.

In studies of the impacts of pedestrians at wildlife sites, the emphasis has remained on comparisons of the effects of the history of disturbance (Table 3). Results of these studies have implications for the spatial management of visitors, and might suggest some form of zonation or visitor exclusion, unless the results indicate habituation. In the last decade, the effect of approach distance has been considered in nearly half of these studies. In comparison, little attention has been given to the efficacy of other forms of spatial mitigation, e.g. the provision of viewing hides or platforms for visitors, and / or refuge areas for wildlife. In both decades, few studies have tested the efficacy of temporal regulation of visitors. Surprisingly few disturbance studies have quantified the effects of visitor group size and visitor behaviour on wildlife responses, and none have considered the effectiveness of tour guides or wardens on controlling visitor behaviour (Table 3).

C. FUTURE DIRECTIONS IN DISTURBANCE RESEARCH

From the range of results found in the disturbance research studies summarised here, it is apparent that there is a great deal of variation in the way that disturbance associated with human activities affects wildlife in the Antarctic and sub-Antarctic region. Wildlife responses are affected by numerous extrinsic and intrinsic factors, many of which are incompletely understood. There is no "one size fits all" solution to managing human disturbance in the region. For example, the setting of a single minimum approach distance for pedestrian approaches that applies to all species at all sites is likely to be inappropriate for at least some species and some sites. Studies that are specific with regard to species, site and type of disturbance will be best suited to produce results that are of use in the management of human activities near wildlife aggregations.

Baseline data associated with long-term studies will be valuable in determining the effect of human disturbance relative to natural environmental fluctuations on population numbers, breeding success and species distributions. Long-term studies are also the only way that cumulative effects of human disturbance on wildlife can be measured (see also Holmes et al. in press). Short term studies can be useful for determining the proximate mechanisms that lead to long-term trends (Holmes et al. in press), and for testing management options (such as recommended minimum approach distances) and for pinpointing behavioural "tell-tales" that indicate an unacceptable level of disturbance. Together, results from short- and long-term studies can be used to produce regional or site-specific management guidelines.

Disturbance research studies over the last two decades suggest that future research might give attention to the following:

1. Explanatory variables

a. Visitor group size

Only three published studies (Burger and Gochfeld 2007, Holmes et al. in press, van Polanen Petel et al. in press) have quantitatively considered the effect of visitor group size on wildlife, although many studies have investigated the effect of approach distance on wildlife. Yet it has been demonstrated that if the number of visitors to an area fluctuates spatially and temporally, then fixed set-back distances or buffer zones are unlikely to be effective (Beale and Monaghan 2004a). A solution may be to keep larger groups further away, or set minimum approach distances according to the largest visitor group size for a site, or to cap party size (Beale and Monaghan 2004a).

b. The relationship between minimum approach distance and starting distance Most studies that recommend minimum approach distances do this on the basis of the distance at which the study animal changes behaviour, or flees. No studies in the region have considered the effect of the starting distance between observer and animal on the minimum approach distance, yet for 64 of 68 species of Australian birds, there was a significant positive relationship between these two distances (Blumstein 2003). When quantifying the effect of approach distances, therefore, starting distance should be used as a covariate (Blumstein 2003).

c. Frequency of visits

Only two published studies have considered the effect of frequency of visits on wildlife responses to human disturbance in the region (Walker et al. 2006, van Polanen Petel et al. in press), although there has also been an unpublished study on the effects of repeated approaches on Wandering Albatrosses (M. Wheeler, unpublished data). Animals may become sensitised to or may habituate to repeated visits. It is recognised that the absence of noticeable behavioural responses does not

necessarily indicate habituation (e.g. Beale and Monaghan 2004a), and increasingly physiological evidence of habituation is being sought. However, even if animals at a site show all evidence of habituation, it should be borne in mind that disturbance may merely have caused nervous individuals to abandon the affected site, freeing space for more tolerant individuals.

d. Visitor distribution

Wildlife may benefit from spreading out visitors over a large area, thereby reducing the disturbance to any one individual, or from concentrating visitors into one area, leaving other areas visitor-free. It has been suggested that the optimal management strategy depends on the number of visitors and the distance to which wildlife is approached. At sites where disturbance levels are low, it may be best to limit visitor access to a small area, whereas at sites with higher disturbance levels, the best strategy may be to spread visitors out evenly over a larger area (Beale 2007). These alternate strategies could be investigated for sites in the Antarctic and sub-Antarctic.

e. Visitor access points and wildlife refuge areas

Protective barriers, viewing platforms, hides and access paths effectively limit approach angles and / or distances and provide areas of refuge, potentially allowing animals to behave as they would in an undisturbed environment (e.g. Ikuta and Blumstein 2003). Even the demarcation of the minimum approach distance, without the erection of a physical barrier, may have the desired effect (Otley 2005). At Boulders Beach, South Africa, where visitors access the edge of an African Penguin *Spheniscus demersus* breeding beach via walkways leading to viewing platforms, nesting penguins show no sign of the nervousness displayed at other sites (de Villiers et al. unpublished data). Evidence for the effectiveness of hides in reducing disturbance is equivocal (Robertson 1997, Ratz and Thompson 1999).

f. Level of disturbance

Many studies have compared disturbance effects at sites with different levels or types of disturbance. In such cases, it is important to address all relevant variables that differ between study sites (e.g. nesting habitat, or colony size), not just the history of disturbance. This may best be done by some form of multivariate modelling. Failure to control for such factors confuses interpretation of apparent differences due to human disturbance.

It should also be borne in mind that the severity of disturbance effects may be exacerbated by secondary effects such as the presence or density of predators near a breeding site, or nesting density. It is particularly important to take the latter into account because at a population scale, declines in survival or fecundity will result from density-dependence rather than directly through disturbance (Gill 2007).

When the effects of human disturbance at particular sites are evaluated, it is important to adequately describe the type and level of disturbance at those sites so that the conclusions of the studies can be properly evaluated. Similarly, it is useful to make mention of how long a particular site has been colonised by the study species. This may be relevant to the question of habituation.

g. Effects of various forms of transport

The effect of forms of transport other than aircraft has received little attention in disturbance research in the region. Most terrestrial approaches to wildlife in the region are on foot, but over-snow vehicles are in use and research into the potential impacts of such transport has been undertaken at one site (van Polanen Petel et al.

2006, 2007). Wildlife may respond to transport-related activities, even if such activities take place out of sight. In the Antarctic, ship-based visitors are usually transported to wildlife breeding sites by boat. Near-shore boat activity and human activity at landing sites may affect penguins and seals in transit to and from nest sites, and boat activity may disturb feeding activities of near-shore feeding species (Yorio et al. 2001).

h. Species

Globally, about half of the published literature on the negative effects of human disturbance on wildlife involves fairly conspicuous avian species (Green and Higginbottom 2000). In sub-Antarctic and Antarctic research, penguins - large and charismatic species with spectacular aggregations that attract many visitors - were the focus for many years. Other seabird species are increasingly being studied, and the question of species-specific sensitivity to human disturbance bears further investigation (e.g. Ellenberg et al. 2006, Holmes et al. 2007). Attention could also be given to impacts on burrowing birds. In the past decade there have been a number of studies on the impacts of disturbance on seals. On the whole, the seal species studied appear to be robust in terms of terrestrial disturbance. At certain sites, however, some species may be quite responsive to aircraft activity (e.g. sub-Antarctic Fur Seals at Marion Island, M. Wheeler, unpublished data), but few studies have quantified the responses of seal species to such activities. Published research into the effects of aircraft operations on wildlife has been restricted to penguins and seals (although impacts on Southern Fulmars have been investigated - M. Giese, unpublished data).

Much of the global published literature on disturbance effects on avian species, with recommendations for minimum approach distances, relates to flighted birds (Green and Higginbottom 2000). It should be borne in mind that the mechanisms governing "fight or flight" decisions (Canon 1915) are likely to be quite different for flightless species.

i. Stage of breeding

Animals are likely to be more sensitive to disturbance at certain stages of breeding, since parental defence of offspring is likely to increase as the breeding season progresses (e.g. Côté 2000). Few studies in the region have considered the effects of disturbance during the pre-laying period. Animals may be particularly sensitive to disturbance at physiologically stressful times, yet almost no studies have considered the effects of prolonged periods of fasting during certain life stages. Only one study has measured responses of moulting birds to disturbance (Holmes et al. in press).

j. Visitor behaviour

Visitor regulation in the Antarctic and sub-Antarctic is generally by means of voluntary guidelines. These include guidelines set by the International Association of Antarctic Tour Operators (Splettstoesser and Folks 1994, IAATO 2007) and various other site-specific guidelines (IAATO 2003, SCAR 2004, IAATO 2005, references within de Villiers et al. 2006a). This "soft" approach to visitor management, which emphasizes management of the visitor experience, rather than a "hard" approach of physical, regulatory and economic management, has been judged to be successful in the Antarctic, where visitor numbers are quite low. However, if the number of visitors to the region continues to increase, the "soft" approach may become inappropriate (Mason 2005). For the Antarctic, it has been stated that "individual concerns for the environmental fragility of the continent will override any need for formal regulations and their enforcement" (Splettstoesser and Folks 1994). However visitor compliance with guidelines is already imperfect. Inadvertent and deliberate infringements of

guidelines occur, suggesting that guidelines may prove inadequate to prevent negative impacts on wildlife (Davis 1995). The same has been shown for voluntary guidelines for whale-watching in the northeastern United States (Wiley et al. 2008). IAATO's minimum recommended ratio of guides to tourists is 1: 20-25 (Splettstoesser and Folks 1994), yet the effectiveness of such ratios has not been tested in an Antarctic or sub-Antarctic setting. There has been little quantification of the relationship between visitor behaviour and the responses of approached wildlife in disturbance research in the region (but see Holmes et al. 2005b, Burger and Gochfeld 2007). No studies have quantified the effectiveness of guides or wardens in influencing visitor behaviour. Several studies have alluded to the effects of aspects of visitor behaviour on wildlife but few studies have identified "tell-tale" behaviours that indicate a stress response on the part of approached animals (suggested in Giese 1998, described for three penguin species in Holmes 2007) – information that could be valuably employed in the management of the visitor experience.

Without the buy-in of politicians, managers and members of the public, conservation efforts in the region are unlikely to succeed. Access to wildlife areas is a major means of increasing the public value of those areas and hence the pressure to conserve them (Gill 2007). The ecotourist can be cultivated as an educated and sophisticated ally in conservation efforts (Giannecchini 1993), but ecotourism will necessitate a trade-off between negative effects on wildlife and positive effects on visitors' perceptions. Visitors appear to want an "up close" experience for the enhanced environmental awareness and mood benefits that this brings (Schänzel and McIntosh 2000). However, few disturbance studies have interviewed visitors regarding their degree of satisfaction with their experiences at wildlife sites, or their adherence to and opinions of wildlife viewing regulations. A recent survey at King George Island provided useful insights into the opinions of station personnel regarding disturbance-related guidelines, and the potential for conflict between visits, conservation, science and logistics (Pfeiffer et al. 2007).

k. General

The most serious threats to seabirds are direct mortality of adults due to fishing activities, as well as marine pollutants and climate change (Thompson and Hamer 2000). The effects of human disturbance should be viewed within this context. However, even if disturbance is a relatively minor threat to wildlife, it may be an aggravating circumstance. The relative roles of decreasing food availability and human disturbance at breeding sites on the decline in Adélie and Chinstrap Penguins at King George Island, South Shetlands, was a topic of debate in the 1990s (Culik and Wilson 1991, Culik and Wilson 1995, Nimon et al. 1995). Disturbance may have little effect on wildlife when environmental conditions are favourable, but the additional stress that it represents may become significant when conditions are unfavourable.

A potential avenue for investigation is the effect of disturbance by one species of wildlife on another, e.g. the effect of fur seals on the distribution of Wandering Albatrosses (Croxall et al. 1990). It has been suggested that another is the effect of human activity on land-based predators of seabirds (Holmes et al. in press).

The proximate mechanisms resulting in habituation are still incompletely understood and further investigation will be useful for informing management decisions.

2. Response variables

a. Behaviour

Changes in behaviour are often used as measures of the susceptibility of wildlife to human disturbance, but the interpretation of behavioural responses in terms of long-term effects on an animal's fitness is ambiguous (Gill et al. 2001). The common interpretation is that individuals that react more intensely to disturbance are more susceptible to it and the implication is that the fitness of strongly reacting animals may be compromised. However, such individuals might be able to react intensely to perceived threats because they are in good condition (e.g. Beale and Monaghan 2004b). The relationship between intensity of behavioural response and fitness proxies such as health and immunocompetence is being addressed in one sub-Antarctic study (M. de Villiers et al. unpublished data). A recent approach to linking behavioural responses to population consequences is to use individual-based models consisting of fitness-maximising individuals (Stillman et al. 2007).

b. Physiology

It has recently been pointed out that in order for conservation strategies to be successful, it is important to understand the physiological responses of organisms to environmental change (Wikelski and Cooke 2006). Physiological techniques can provide data on the causes underlying conservation problems such as declines in populations (Carey 2005, Wikelski and Cooke 2006).

i. Glucocorticoid levels

A number of recent disturbance studies have used corticosterone levels as a measure of disturbance-related stress. It is often assumed that blood samples taken within minutes of capture of an animal will provide a measure of basal (unstressed) corticosterone, however it should be remembered that the onset of the hormonal stress response is rapid and may begin upon detection of the researcher by the study animal, rather than upon capture. The time of day at which animals are sampled is not always taken into account in disturbance studies, nor is the length of time elapsed since the study animal's last meal, yet in some species glucocorticoid release is subject to episodic, circadian and meal-stimulated patterns (Baxter and Tyrrell 1987). Stress hormone response to adrenocorticotropic hormone (ACTH) challenge is a useful measure of chronic stress, but does require repeated sampling (e.g. de Villiers et al. 1997) and thus a level of researcher disturbance that may be considered undesirable or unethical. It has been suggested that although a decreased corticosterone response may indicate habituation to disturbance, it may also affect an animal's long-term ability to access stored energy in times of need (Walker et al. 2006).

ii. Heart rate

The interpretation of heart rate responses that are measured with quite invasive devices (such as ECG units) can be problematic, since it may be difficult to separate the effect of the fitting of the device from the effect of the disturbance being measured, e.g. a pedestrian approach (but see Giese et al. 1999). Increasingly, artificial eggs are being used as a less invasive measure of heart rate. The disadvantage of this technique is that the heart rates of nervous birds that abandon their nests upon egg deployment are never measured (also mentioned as a shortcoming in Ellenberg et al. 2006), and neither are increases in heart rate that occur when an approached bird stands up on its nets. For colonial breeders, it is usually only birds in peripheral nest sites that are included in heart rate experiments. Since such birds are likely to have relatively high natural stress levels as a result of

high rates of predation (references in Vinuela et al. 1995, Côté 2000), such results may not be applicable to the rest of the colony. In evaluating heart rate responses to human disturbance, it is essential to have an idea of natural heart rate fluctuations in the absence of human activity.

iii. Health and immunocompetence

Blood chemistry parameters can provide useful information regarding the health status and immunocompetence of animals. Measures of parental health and immunocompetence may allow the identification of good breeders in a population (Moreno 2003). Also, health status and immunocompetence may be related to levels of chronic stress resulting from human disturbance. In Antarctic and sub-Antarctic disturbance research, this relationship has only been studied for Southern Elephant Seals (Engelhard et al. 2002b) and Wandering Albatrosses (M. de Villiers, unpublished data).

c. General

Although human disturbance may elicit behavioural and physiological changes, it is useful to compare the magnitude of these changes with their natural range, in order to assess their potential fitness consequences. Because the range of some indicators may be large, it will be useful to employ multiple indicators of disturbance and to select those with low intraspecific variation (Blumstein et al. 2005).

Disturbance studies often refer to the large amount of individual variation in the response variables measured. Further exploration of this variability may prove useful. Seabirds typically also show a large amount of individual variation in lifetime breeding success, with a small part of the population making a disproportionately large contribution to future generations. Measures of parental health and immunocompetence may allow the identification of good breeders (Moreno 2003). Lastly, there is a large body of literature dealing with animal personalities or different styles of coping with environmental challenges or stressors (Koolhaas et al. 1999, Carere et al. 2003, Dingemanse et al. 2004, Sgoifo et al. 2005, Storey et al. 2006)

that may help to explain individual variation. This is an aspect which is being

considered for the first time in Antarctic and sub-Antarctic research (U. Ellenberg, unpublished data).

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13

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TABLE 1. Summary of disturbance research over the last two decades (1988 – 2007/08) in the Antarctic and sub-Antarctic region.

DISTURBANCE TYPE	SPECIES	LOCATION	RESULT	REFERENCE
aircraft	Penguins, Procellariforms: King Penguin, Gentoo Penguin, Wandering Albatross	Sub-Antarctic (Marion Island)	A C-130 Hercules made three passes at 100-300 m altitude, with airdrops at 150 m. King Penguin adults and crèching chicks stampeded, but there were no injuries or deaths and the birds quickly recovered and moved back into the colony. Wandering Albatrosses (brooding and guarding) showed minor responses to the aircraft 50 m away. Non-breeding Gentoo Penguins fled, but those guarding chicks did not.	Cooper et al. 1994
aircraft	Penguins, Seals: Leopard Seal, Ross Seal, Crab-eater Seal, Adélie Penguin, Emperor Penguin	Antarctic (East Antarctica pack ice)	6300 km of straight line transects were flown over pack ice by a Sikorsky S76 twin engine helicopter at a height of 130 m. A horizontal distance of 100 - 200 m caused non-breeding seals to move on average 5 m (maximum 20 m). A horizontal distance of more than 200 m caused an average movement of 1-3 m (maximum 20 m). Non-breeding penguins moved further - up to 25 m - on average 15 m at a horizontal distance of 100-200 m, but there was hardly any movement at 800 m.	Southwell 2005
aircraft	Penguins: Emperor Penguin	Antarctic (Amanda bay, Prince Elizabeth Land)	Up to 80% of crèching chicks moved (10 m or less) during the overflight of the Sikorsky S76 twin engine helicopter at 1000 m. Rates of flipper-flapping, vigilance and comfort acts increased and then abated directly after the overflight.	Giese and Riddle 1999
aircraft	Penguins: King Penguin	Sub-Antarctic (Macquarie Island)	An overflight at 250 m and an airdrop by a C-130 Hercules aircraft was presumed responsible for the mass stampede and subsequent asphyxiation and death of 7000 adults and crèching chicks.	Rounsevell and Binns 1991
aircraft	Seals: Southern Elephant Seal	Sub-Antarctic (Macquarie Island)	Sikorsky S76 helicopter operations near moulting male seals (helicopter landing 20 m away) had minimal effects – the only difference in behaviour of seals over two days of operations, in presence and	Burton and van der Hoff 2002

			absence of the helicopter, was increased head-lifting.	
aircraft, boat, vehicle	Seals: Weddel Seal	Antarctic (near Davis Station, East Antarctica)	All the sources of noise tested, if generated at sufficient levels, are potentially audible to seals. Most noise levels recorded were above the assumed detection threshold of seals. But even at the closest distances, anthropogenic noise levels were less than those of the loudest seal vocalisations. Noise generated by pedestrians walking on ice, four-wheel all terrain vehicles and tracked all-terrain vehicles are likely to be inaudible or barely audible. Noise by Twin Otter aircraft, helicopter (Aerospatiale A S350B single engine) and Zodiac are likely to be barely- to clearly-audible. Seals did not alter individual call types in response to low-level tracked vehicle noise, but did decrease calling rate.	Van Polanen Petel et al. 2006
aircraft, pedestrian	Penguins: Adélie Penguin	Antarctic (Esparanza Station, Peninsula)	Adult penguins had an average resting heart rate of 86 bpm, a maximum heart rate in response to natural disturbance of 118 bpm, and an average rate in response to human approach of 127 bpm. Sea King helicopter operations near a breeding site caused an increase in adult heart rate to an average rate of 145 bpm. Chick heart rate in response to an approaching helicopter was 260 bpm, and to a helicopter flying over at 50 m was 273 bpm. Incubating adults sat tight when the helicopter was at 20 m, but when chicks were crèching, adults and chicks ran at 300 m. Penguins didn't get used to repeated flights at more than 400 m. Panic runs occurred when the helicopter was still 1500 m away, later in the season.	Culik et al. 1990

aircraft, pedestrian	Penguins: Adélie Penguin	Antarctic (site not mentioned)	Heart rates of nesting birds rose from 76 to 135 bpm when approached on foot from 50 to 4 m. Birds with large chicks fled more easily when approached than those with eggs or small chicks (critical distances 6.1, 0.3 and 1.3 m respectively). At 20 m, penguins in transit deviated up to 70 m from paths to avoid humans. Twin Otter: The first reaction occurred when the aircraft was 1 km away, and penguins began moving away at 500 m. Normal behaviour resumed when aircraft retreated to 600 m. Hercules: The first reaction occurred at 1.1 km and all penguins were moving at 500 m. Many were still moving when the aircraft retreated far off, and normal activity resumed at 2.8 km. Super Puma helicopter: Penguins first reacted at 600 m and all were moving at 400 m, but most stopped moving when the helicopter was 1.5 km away again. Brooding adults stayed on nests when the helicopter was 25 m away, but heart rates increased from an average of 83.4 to a maximum of 286 bpm. Three days of helicopter activity delayed penguins' return to nests after foraging trips and caused a 15% decrease in bird numbers in the colonies and active nest mortality of 8%.	Wilson et al. 1991
aircraft, research	Penguins: Emperor Penguin	Antarctic: Drescher Inlet Ruser Larsen ice shelf	Human induced stresses can result in increases in body temperature equivalent to 10% of daily energetic costs of moulting penguins - costs are higher for chicks than adults. Stress due to MBB BO105 helicopter flights are equivalent to those related to a weighing procedure (bagging and restraining penguins).	Regel and Putz 1997

boat	Cormorants: Rock Shag Phalacrocorax magellanicus	Sub-Antarctic (Beagle Channel, Argentine side)	Incubating and brooding Rock Shags were generally tolerant to humans but before egg-laying and after fledging, a boat approach to 100 m caused birds to start abandoning, leading to chain reaction that led to abandonment of entire colony.	Schiavini and Yorio 1995
boat, pedestrian	Seals: New Zealand Fur Seal	Sub-Antarctic: Abel Tasman National Park, Kaikoura and Whakamoa, New Zealand	The most important factor determining seal responses to experimental approaches was previous exposure to tourist activity. Seals at sites with high levels of tourism responded less dramatically and at closer distances than at a non-tourist site (but there was considerable individual variability in degree of habituation). Seals responded more intensely when approached on land than by kayak or boat. Adult females approached by pedestrians or small boats fled into sea, but adult males stayed in the colony to fight and pups fled to hide among rocks.	Boren et al. 2002
general	Penguins: Adélie Penguin	Antarctic (Cape Hallet)	Penguin numbers declined markedly between 1959 (62900 pairs) and 1968 (37000 pairs), increased from 1981 (66000 pairs) to 1984, and thereafter fluctuated around the pre-decline level. Not all abandoned subcolonies were re-colonized after the disturbance ended, due to a permanent change in habitat. The largest effects on penguin numbers were due to research and intensive banding.	Wilson et al. 1990

general	Penguins: Adélie Penguin	Antarctic (Esperanza/Hope Bay, Peninsula)	Population trends in areas with low levels of disturbance were compared to those in areas with high levels of disturbance. Number of breeding pairs decreased in both types of areas; number of chicks fledged increased by 6.7% in a low disturbance area and decreased by 4% in a high disturbance area this was attributed to the fact that breeding group size was smaller in high disturbance areas, and to the edge effect. There was no difference in the number of chicks fledged per marked nest in the two areas. Populations in both areas decreased over the 10-year period - by 37.4% in low disturbance areas and by 38.6% in high disturbance areas (note a decrease of 69% in another population on King George Island between 1995 and 2004, where disturbance was minimal).	Carlini et al. 2007
general	Penguins: Adélie Penguin	Antarctic (Windmill Islands, Wilkes Land)	There was a population increase of 209% over the entire area and period. At every site except Shirley Island, numbers increased. On Shirley Island, numbers increased between 1961/62 and 1968/69 but remained stable after that, coincident with the opening of Casey Station. There were greater declines in the part of the colony closer to the station, and more new colonies formed in the part of the colony further from the station.	Woehler et al. 1991
general	Penguins: Adélie Penguin Pygoscelis adeliae	Antarctic (near Casey Station, Wilkes Land, East Antarctica)	There was a 320% increase in the number of breeding pairs of penguins at Whitney Point (few visitors), similar to increases elsewhere over the same time period. At Shirley Island (many visitors), there was a decrease in numbers of 27.7%. Mean breeding success was 0.75 At Shirley, compared to 0.91at Whitney. New colonies at Whitney and Shirley Island had lower breeding success than older colonies - this could be due to the age of breeders, breeding experience, and duration of the pair bond.	Woehler et al. 1994
general	Penguins: Adélie Penguin, Cape Petrel,	Antarctic (Pointe Géologie, Adélie Land)	There were increases in Adélie Penguin numbers at all sites (including those on an island with a station	Micol and Jouventin 2001

	Snow Petrel, Southern Giant Petrel		and summer helicopter activity), except on an island where building activities led to the forced removal of penguin pairs and destruction of nest sites – there, breeding success decreased by 14%. 34% of Cape Petrel breeding sites were lost due to the building of airstrip but overall the population increased (but note that only 16% of displaced birds were found to return to the original site to breed after construction). There was a 9% decrease in Snow Petrel numbers, largely due to loss of 21% of breeding sites due to airstrip building. When the station was extended, Southern Giant Petrel breeding pairs moved to two nearby islands, one of which was successfully and one unsuccessfully colonised. Numbers decreased by 87% on the archipelago (more than in AAT) due to high levels of human disturbance (a helicopter landing zone situated 40 m from a breeding site).	
general	Penguins: Gentoo Penguin	Antarctic (Goudier Island, Port Lockroy, Peninsula)	Breeding parameters were compared on an island with no tourism and another with tourism and research. There was no difference between islands in the proportion of birds that laid eggs, or hatching success or the proportion of single-chick broods. There was a higher incidence of single-egg clutches on the tourist island, but this was not due to disturbance but rather to nest site characteristics. There was no difference in chick mass or survival up to 20 days of age in one control and one tourist colony.	Cobley and Shears1999
general	Penguins: Gentoo Penguin	Sub-Antarctic (Macquarie Island)	The behavioural responses (consistent with threat perception) of incubating penguins at a colony near the station, and colonies off-station, were compared. Responses were higher at off-station than on-station colonies, probably because of habituation and predator exclusion near the station. Off-station, there was no relationship between pedestrian activity and breeding success. Breeding success was positively related to colony size and negatively related to the	Holmes et al. 2005a

general	Seals: Southern	Sub-Antarctic	activity of other penguins, the number of nearby Southern Elephant Seals, and the location of colonies within short grassland. Pup weaning mass was positively associated with	Engelhard et al.
gonora	Elephant Seal	(Macquarie Island)	first-year survivorship. Pup mass was compared in a remote area and in an area of high human presence. Remote area pups were significantly heavier. But remote area mothers were significantly longer and, relative to the size of the mother, there was no difference in pup mass between areas. There was no explanation for why longer mothers should prefer the more remote area.	2001
general	Seals: Southern Elephant Seal	Sub-Antarctic (Macquarie Island)	Behaviour of lactating seals in areas of high and low human disturbance was compared. There was a threefold increase in alertness in response to human approach in the high disturbance area, but alertness quickly returned to pre-disturbance levels after departure. There were no significant differences in behaviour in the absence of humans in the two areas.	Engelhard et al. 2002a
pedestrian	Penguins, Skuas: Gentoo Penguin,Sub- antarctic Skua, hybrid Sub-antarctic/South Polar Skua	Antarctic (Cuverville Island, Peninsula)	There were no differences in rates of predatory activity when visitors were and were not present. This held true for the period from laying to crèching.	Crosbie 1999
pedestrian	Penguins: Adélie Penguin	Antarctic (Palmer Station, Peninsula)	All Adélie Penguin populations were at a high in 1975 but decreased after that. A major decrease in 1987 corresponded with disruption of food webs due to climate change. Over the same period, populations in seldom-disturbed areas declined by 43%, compared to a 19% decline by those exposed to increasing amounts of ecotourism. This was despite the fact that a colony where tourism occurred had the largest number of Brown Skuas, unfavourable nest site topography and the fewest large penguin colonies.	Fraser and Patterson 1997

pedestrian	Penguins: Adélie Penguin	Antarctic (Rookery Lake, Vestfold Hills)	Incubating penguins that were approached to 30 m experienced no noticeable change in behaviour or heart rate. Approaches to 15 m resulted in significantly elevated heart rates but no change in behaviour. Approaches to 5 m changed behaviour (68% of birds stood), elevated heart rate and significantly interrupted incubation behaviour. Average heart rates were 82.4±11.7 (resting), 96.4±4.7 (approached to 15 m) and 126.3±5.8 bpm (approached to 5 m; a greater increases than that caused by natural disturbances).	Giese 1996
pedestrian	Penguins: Chinstrap Penguin	Antarctic (Deception Island, South Shetlands)	The behaviour of one-year old penguins was monitored. The effect of the angle of pedestrian approach was significant when penguins were far from subcolonies, but not when they were near - penguins fled faster and at greater distances when approached directly than when approached obliquely. Penguins closer to subcolonies allowed closer approaches and didn't flee so far or so fast. They avoided fleeing into the colony rather than trying to maximise distance from approacher. Young penguins must make a trade-off between avoiding the approacher and avoiding aggression from adults if they flee into the colony.	Martin et al. 2004
pedestrian	Penguins: Emperor Penguin	Antarctic (Snow Hill, eastern side of Peninsula)	The behaviour of adult penguins in transit from breeding colony to sea was monitored, Behavioural responses to the presence of tourists were recorded. In transit, the distance at which penguins noticed people (mean 35.6 m), changed direction (22.8 m), and changed behaviour (walking rather than energy-efficient tobogganing), and the number and duration of pauses, all increased with increasing numbers of tourists. Penguin group size was significantly smaller for penguins passing people than for penguins travelling parallel to people. Of penguins approaching people, 91% changed direction. Delays of up to 47 minutes were recorded for penguins passing people.	Burger and Gochfeld 2007

			Penguins were less responsive later in the day. At the breeding colony, people were required to keep 5-10 m from penguins but penguins often approached closer, and effect of people seemed minimal.	
pedestrian	Penguins: Gentoo Penguin	Antarctic (Cuverville Island, Antarctica)	The mean basal heart rate of incubating penguins was 83.8 bpm. Human appearance at 15-20 m and gradual approach to 3 m did not cause heart rate changes, but sudden movements at this distance resulted in brief increases in heart rate of up to 50% for 10-second periods. Mean heart rate during slow approaches (pausing at 5 m intervals) was 84.3 bpm, whereas rapid approach to 1 m led to a 45-110% increase in heart rate.	Nimon et al. 1995
pedestrian	Penguins: King Penguin, Gentoo Penguin, Magellanic Penguin	Sub-Antarctic (Volunteer Point, Falkland Islands)	Most visitors were "novice generalist" tourists as opposed to "expert specialists." There were few contraventions of visitor guidelines. 100% of tourists spent an average of 63 minutes at King Penguin colonies and 50% of visitors spent on average 19 minutes at Gentoo Penguin colonies. The maximum rate of visitation was 17.6 visitor hours per day at King Penguins and 4.7 visitor hours per day at Gentoo Penguins. Patterns of visitation were predictable and may have allowed habituation. Less than 20% of penguins of all three species that commuted during daylight hours, did so during times of day when most visitors were present. There was no difference in Gentoo Penguin breeding success at a tourist site and two seldom-visited sites. King Penguins seemed less responsive than a few years previously, after a barrier ring of white rocks was erected to indicate the minimum approach distance.	Otley 2005

pedestrian	Penguins: King Penguin, Gentoo Penguin, Royal Penguin	Sub-Antarctic (Macquarie Island)	The responses of three species of penguins to pedestrian approaches during the guard stage were compared. Gentoo Penguins were more sensitive than King or Royal Penguins, with altered behaviour for five minutes after approach. Useful response behaviours for visitors are rapid head turns (all species), reaching and striking at conspecifics (King and Royal Penguins), and bill pointing (Gentoo Penguins). One King Penguin abandoned its chick when approached.	Holmes 2007
pedestrian	Penguins: King Penguin, Gentoo Penguin, Royal Penguin	Sub-Antarctic (Macquarie Island)	(Note that only results not already published elsewhere are summarized here.) Guarding Gentoo Penguins reacted more to pedestrian approaches by a group of five people than to single person approaches, indicating that they associated a higher level of risk with larger visitor groups. Royal Penguins were most responsive to pedestrian approaches during incubation and moult. Harmful effects of disturbance could be reduced by increasing minimum approach distances during these stages.	Holmes et al. in press
pedestrian	Penguins: Magellanic Penguin	Sub-Antarctic (Punta Tombo, Argentina)	Penguins with chicks at three colonies were compared: a tourist colony, an isolated study colony and an isolated colony. The least intense behavioural response was elicited from tourist-visited birds. Basal corticosterone levels were highest in the isolated colony, and "disturbed" corticosterone levels (15-min after disturbance) were highest in the isolated and study colonies. But nesting density was lower in the tourist colony.	Fowler 1999

pedestrian	Penguins: Magellanic Penguin	Sub-Antarctic (Punta Tombo, Argentina)	The responses of chicks in a tourist area and an undisturbed area were compared. There was no difference in mass and body condition or basal corticosterone levels at hatching, midway through growth or near fledging. But higher corticosterone stress responses were recorded for chicks at hatching (but not at fledging) in the tourist area. All older chicks had a robust stress response. Fledglings in the undisturbed area fled when approached to no closer than 9 m, whereas fledglings in the tourist area fled when approached to within 0.5 m. Tourist chicks show behavioural habituation but did not have a decreased stress response to restraint and capture.	Walker et al. 2005
pedestrian	Penguins: Magellanic Penguin	Sub-Antarctic (Punta Tombo, Argentina)	Penguins in a tourist area and an undisturbed area were approached on foot. Incubating penguins in the tourist area displayed fewer head turns during a 15-minute nest visit. Basal corticosterone levels of penguins in this area were the same as those in the undisturbed area, but in penguins in the tourist area had lower ACTH-induced corticosterone levels. Previously undisturbed penguins showed behavioural and physiological habituation to repeated 15-min/day visits after five days.	Walker et al. 2006
pedestrian	Penguins: Magellanic Penguin	Sub-Antarctic (Punta Tombo, Argentina)	Behaviour of breeding penguins at four sites was compared: tourist area, entrance access road, restricted area with no visitors, and scientific study area. Penguins reacted at the greatest distances in the areas with the least disturbance. More stood on their nests in these areas, and only birds in this area deserted. Breeding success and fledging weights were similar in the tourist and non-tourist areas. General observations were that there was much individual variation in behavioural response to approach, that birds not breeding or in transit fled more easily than birds on nests, that walking fast and sudden movements elicited greater reactions, and that penguins in open areas reacted more than those	Yorio and Boersma 1992

			in bush.	
pedestrian	Penguins: Magellanic Penguin, Humboldt Penguin	Sub-Antarctic (Puñihuil Islands (two islands), southern Chile)	The number of collapsed penguin burrows at islands visited by tourists was counted. 28% of burrows on island 1 (often-visited, goats present) were collapsed, and 10% on island 2 (seldom-visited, no goats seen) were collapsed, i.e. 18% more burrows were collapsed at the often-visited site (with goats), compared with a less often visited site.	Simeone and Schlatter 1998
pedestrian	Penguins: Royal Penguin	Sub-Antarctic (Macquarie Island)	The heart rates of incubating penguins were measured. There was a 1.23-fold increase in resting heart rate, and a six-fold increase in vigilance, in response to pedestrian approach to 5 m. These increases were significantly greater than responses to skua overflights and agonistic encounters with conspecifics. No desertions were observed in response to human approaches, but penguins were responsive to even subtle movements. There was a significant positive correlation between rate of vigilant acts and heart rate.	Holmes et al. 2005b
pedestrian	Penguins: Yellow-eyed Penguin	Sub-Antarctic (Dunedin, New Zealand)	Breeding success and behaviour were compared at colonies with and without tourist disturbance. The number of breeding pairs increased at the same rate in both colonies. There was considerable inter-annual variation in fledging success, and both areas had similar very low breeding success in 1995/96. At the tourist colony, the number of nests in view of hides increased faster than out of view of hides. There was no significant difference in feeding patterns during the guard stage in the two colonies.	Ratz and Thompson 1999
pedestrian	Penguins: Yellow-eyed Penguin	Sub-Antarctic (Otago Peninsula, South Island, New Zealand)	Breeding parameters were compared at five breeding areas, with different levels of visitor frequency. Probability of chick survival was positively associated with mass at fledging. Fledging mass of chicks at sites with high disturbance levels was significantly different (0.76 kg less) that that of chicks at sites with low disturbance levels.	McClung et al. 2004

pedestrian	Penguins: Yellow-eyed Penguin	Sub-Antarctic (Otago, South Island, New Zealand)	Comparisons were made between a tourist and a monitoring site. At the tourist site, breeding success and fledging weights were lower. Basal corticosterone levels of adults were similar at the two sites but stress-induced corticosterone levels (15 minutes after capture) were higher at the tourist site. At both sites, high parental basal corticosterone levels correlated with low fledging weight. Aggressive penguins had higher basal corticosterone levels than calm penguins. This species has very low basal corticosterone levels compared to other penguin species.	Ellenberg et al. 2007
pedestrian	Procellariforms: Northern Giant Petrel	Sub-Antarctic (Marion Island)	The mean resting rate of incubating petrels was 80.1 bpm. Heart rates increased upon detection of a person 40 m away, and continued to increase during approach to 5 m. The maximum increase in response to natural disturbance was 97%, and to human disturbance 204%. Northern Giant Petrels can be as responsive as Southern Giant Petrels to disturbance.	de Villiers et al. 2006b
pedestrian	Procellariforms: Northern Royal Albatross	Sub-Antarctic (Taiaroa Head, New Zealand)	Albatrosses at an observatory on the mainland were monitored. Over time, the density of nests near the observatory decreased but increased further away. However, 44% and 61% of eggs laid out of sight and in site of the observatory produced fledged chicks. Fewer first time breeders nested in view of the observatory after 1975. Courtship behaviour and nest site selection was increasingly conducted out of sight of the observatory. The average distance that chicks in view of the observatory moved from their nests was 47 m, compared to 12 m for chicks out of view. Since the 1970s, the climate has become warmer and drier, causing problems with nest construction, the drying of egg membranes making it harder for chicks to hatch, and the establishment of blowflies which attack hatchlings.	Robertson 1997

pedestrian	Procellariforms: Wandering Albatross	Sub-Antarctic (Ile de la Possession, Crozet Islands)	Birds in a seldom-visited area were approached to 1 m. Heart rates of incubating birds nearly doubled as soon as a human was detected, and continued to increase as the approacher neared the nest. Heart rates were three times higher at less than 20 m from nest. Increases of 3-4 times resulted from handling. In comparison, heart rates increased by up to 20% due to interactions with conspecifics and natural predators.	Weimerskirch et al. 2002
pedestrian	Procellariforms: Wandering Albatross	Sub-Antarctic (Marion Island)	Historically, the number of albatrosses breeding in the vicinity of the station more than halved within the first two decades of human occupation. Behavioural responses of incubating and brooding adults were recorded. Twice as many birds stood and vocalised in response to a pedestrian at 5 m from the nest, compared to 15 m from the nest. Study colony birds had higher vocal response scores than non-study birds. There was a tendency for overall intensity of behavioural response to decrease with increasing distance from the station, and study colony birds had higher vocal response scores than non-study colony birds. A better breeding record was associated with lower vocal and overall response scores.	de Villiers et al. 2005
pedestrian	Seals: Weddel Seal	Antarctica (Long Fjord, Vestfold Hills and Penny Bay, Windmill Islands - East Antarctica)	Lactating females and their pups were more vigilant, and responded sooner, when approached by a group of people than by a single person on foot. When approached by one person, seals closer to water allowed closer approaches. For group approaches, seals closer to conspecifics could be approached more closely than those far from conspecifics (distance from water was not important).	Van Polanen Petel et al. in press

pedestrian	Seals: Weddell Seal	Antarctica (Penny Bay, Windmill Islands, East Antarctica)	The responses of lactating seals and their pups to regular visits (pedestrian approaches) over a short time period were compared to the response to irregular visits over a long time period. In response to regular visits, habituation took place over ten approaches within two hours. Irregular visits (daily visits over 3 weeks) did not result in any sign of habituation by adult females or pups, which instead appeared to become sensitised with repeated exposure.	Van Polanen Petel et al. 2007 (Applied An Behav Sci)
pedestrian, general	Procellariforms, Skuas: Southern Giant Petrel, Brown Skua, South Polar Skua, other species	Antarctic (Penguin Island, South Shetland Islands)	Fly-off distances for breeding skuas varied from 0 to 50 m. Brown Skua levels of aggression were not different in frequently and rarely visited areas, but South Polar Skuas were less aggressive in frequently visited areas. Non-breeding Southern Giant Petrels flew off at 50 m in often visited areas but in seldom-visited areas, most sat to 15 m. There was no difference in basal heart rates of incubating petrels in the two areas. When approached to less than 40 m, heart rate increases were greater than they were in response to natural disturbances. Heart rate increase upon approach to 20 m was 63% higher than resting heart rate. An observed shift in distribution of breeding petrels may be the result of avoidance of disturbed areas. Station disturbance caused decreased breeding success on Fildes Peninsula, and the shifting of nest sites elsewhere.	Pfeiffer and Peter 2004
pedestrian, research	Penguins, Skuas: Adélie Penguin and Antarctic Skua	Antarctic (Ross Island)	Penguin and skua demographics in a part of the colony near the station were compared with a part of the colony far from the station. For skuas, there was little difference in breeding density, territory pattern, breeding success or age structure between the two areas. Skuas were remarkably tolerant of human intrusion and nest checks in the colony. There was a decline in breeding groups of penguins close to the station, although the total number of penguins in the colony increased markedly.	Young 1990

pedestrian, research	Penguins: Adélie Penguin	Antarctic (Rookery Lake, Vestfold Hills)	Three sites were compared: undisturbed by humans, disturbance due to nest checking by researchers, and disturbance due to recreational visits. In small colonies (but not large ones), hatching success and chick survival were highest at undisturbed colonies and lowest at recreational colonies. Hatching success was 35% and 47% lower in the research and recreation colonies than in the undisturbed colony. Chick survival was 72% and 80% lower in the research and recreation colonies than in the undisturbed colony. There was no significant difference in breeding success in the research and recreation colonies. Skua predation was the most likely cause of egg loss due to disturbance - there were high numbers of skuas at the study sites.	Giese 1998
research	Penguins: Adélie Penguin	Antarctic (Prydz Bay area, East Antarctica)	Resting heart rates of incubating penguins measured with artificial eggs and external ECG units did not differ, providing there was 20 hours of acclimation after fitting the latter. 63% of birds approached to 5 m stood up on nests.	Giese et al. 1999
research	Penguins: Adélie Penguin	Antarctic (Torgersen Island near Palmer Station, Peninsula)	Handling at intervals of several days throughout the breeding season did not produce evidence of a chronic stress effect. There was a large amount of individual variation in corticosterone response. There was no effect of stage of breeding on corticosterone levels, but heterophil:lymphocyte ratio was significantly lower during the chick stage than during courting or incubation. In birds that had fasted more than 50 days, corticosterone levels increased.	Vleck et al. 2000
research	Penguins: Adélie Penguin	Antarctic: Esperanza Bay	The effect of research procedures (clipping tails and attaching devices) on breeding birds was measured. Tail-clipped birds had significantly longer foraging trips, which led to nest desertion in some cases. The larger the devices, the worse the effect and the longer the foraging trips.	Wilson et al. 1989

research	Penguins: Magellanic Penguin	Sub-Antarctic: Punta Tombo, Argentina	The effect of research disturbance (adult penguins banded and daily nest checks) during the breeding season was evaluated against a control (nest checks every 4 days). There was no significant difference in egg losses between experimental and control nests.	Yorio and Boersma 1994
research	Penguins: Royal Penguin, Rockhopper Penguin	Sub-Antarctic (Macquarie Island)	Breeding success was compared in a research area (nest checks, handling of eggs and chicks, and banding) and a control area. There were no differences in the number of active nests in the two areas, across the breeding season.	Hull and Wilson 1996
research	Procellariforms: Cape Petrel	Antarctic (Nelson Island, South Shetland Islands)	Colonies with high and low researcher disturbance were compared. Breeding success (29%) was the lowest ever recorded for this species, and was even lower (31%) in the low disturbance colony. 76% of nest failures were attributed to skua predation. Breeding success was twice as high in the pooled low disturbance colonies as in the high disturbance colonies. But disturbance level alone did not account for inter-colony variation in predation rate, which tended to increase with colony size, the presence of nearby breeding skuas and local availability of penguins as alternative prey. Nest cover influenced predation rates. Parental experience (reflected by egg shape) also had an effect, as did nesting density.	Weidinger 1998
research	Procellariforms: Southern Giant Petrel	Antarctic (three island sites, Australian territory, East Antarctica)	This species is highly sensitive to disturbance at breeding sites. Research disturbance (an intense ringing programme) was the main cause of rapid decreases (94%, 75% and 80%) at three of four monitored sites. After restrictions were placed on access to colonies and the types of research, there was a significant recovery in petrel numbers.	Woehler et al. 2003
research	Seals: Southern Elephant Seal	Sub-Antarctic (Marion Island)	No differences were detected in rates of decline (number of cows and weaned pups) in areas of high and low human activity.	Wilkinson and Bester 1988

research,	Seals: Southern	Sub-Antarctic	No chronic (although acute) effects of the degree of handling of pups were detected. During late lactation, mothers appeared to tolerate moderate degrees of handling, but repeated immobilisations of lactating females may have reduced adrenocortical responsiveness. There were no differences in corticosterone levels or responses of seals in areas of high and low human disturbance.	Engelhard et al.
general	Elephant Seal	(Macquarie Island)		2002b
research,	Seals: Southern	Sub-Antarctic	The blood chemistry (urea, creatinine, total protein, cholesterol etc.) of lactating mothers and their pups did not indicate an effect of handling. There was also no difference in the blood chemistry of mother-pup pairs in areas of high and low human disturbance.	Engelhard et al.
general	Elephant Seal	(Macquarie Island)		2002
vehicle	Seals: Weddell Seal	Antarctica (Penny Bay, Windmill Islands, East Antarctica)	Two types of over-snow vehicle (tracked all-terrain vehicle and a four-wheeled all-terrain vehicle) operating at the same distance from lactating seals, had similar effects on seal behaviour. The probability of looking at, and the duration of looking at, the vehicle were dependent on the distance of the vehicle from seal, the position of the mother relative to her pup, and the distance of the mother from water. No seals fled.	Van Polanen Petel et al. 2007

TABLE 2. Trends in disturbance research over two decades. Where human disturbance was of multiple origins (e.g. station, research and tourist activities) and the effects of these were not clearly separated in a study, the type of disturbance was classified as "general." Where studies considered the effects of approaches on foot to wildlife, or where this was the major type of disturbance, this was classified as "pedestrian." The sum of the number of studies per study characteristic does not necessarily equal the total number of studies in a time period, because not all studies fell into the sub-categories provided and some studies qualified for more than one sub-category.

STUDY CHARACTERISTIC		1988-1997 (n = 19)	1998-2007/08 (n = 39)	Total (n = 58)	
Term of study	Long term (changes over time)		8	4	12
	Short term (3 or fewer seasons)		12	36	47
Type of study	Observational		3	0	2
	Comparative: control		7	23	30
	Comparative: spatial		8	18	26
	Comparative: temporal		7	3	10
Target species	Seals		1	11	12
	Penguins		16	23	39
	Procellariforms		1	6	7
	Skuas		1	2	3
	Cormorants		1	0	1
Type of	Pedestrian		8	23	31
disturbance	Boat		1	2	2
	Aircraft		5	4	9
	Vehicle		0	2	2
	Research (handling)		6	6	12
	General		3	8	11
Response	Behavioural correlate of fitness		8	25	32
variable	Physiological correlate of fitness	Heart rate	3	6	9
		Corticosterone	0	6	6
		Blood chemistry	0	1	1
		Stomach temperature	1	0	1
	Population trend	•	6	4	10
	Breeding success	Direct measurement	9	7	16
	ŭ	Weaner/fledgling mass	1	6	7

38

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Mortality / nest site	e destruction	1	1	2
Distribution		4	2	6

TABLE 3. Summary of disturbance aspects considered in the analysis of studies of wildlife responses to pedestrian approaches. The percentage of studies in a sub-category is in parentheses. The sum of the number of studies per mitigation measure does not necessarily equal the total number of studies in a time period, because not all studies fell into the sub-categories provided and some studies qualified for more than one sub-category.

MITIGATION	INDEPENDENT VARIABLE	1988-1997 (n = 8)	1998-2007/08 (n = 34)	Total (n = 31)
Spatial	History of disturbance	4	12	16
	Approach distance	3	11	14
	Use of a hide	1	1	2
	Provision of a wildlife refuge	1	2	3
Temporal	Stage of breeding	1	2	3
	Time of day	0	1	1
	Rate of visitation	0	2	2
Other	Visitor group size	0	3	3
	Visitor behaviour	2	3	5

APPENDIX I. List of common and species names.

Common name

Adélie Penguin African Penguin

Antarctic / Brown / Southern / sub-Antarctic Skua

Cape Petrel
Chinstrap Penguin
Crab-eater Seal
Emperor Penguin
Gentoo Penguin
Humboldt Penguin
King Penguin
Leopard Seal

Leopard Seal
Magellanic Penguin
New Zealand Fur Seal
Northern Giant Petrel
Northern Royal Albatross
Rockhopper Penguin
Rock Cormorant
Royal Penguin
Snow Petrel

South Polar Skua Southern Elephant Seal

Southern Fulmar Southern Giant Petrel Sub-Antarctic Fur Seal Wandering Albatross

Weddel Seal

Yellow-eyed Penguin

Species

Pygoscelis adeliae Spheniscus demersus

Catharacta antarctica (subspecies?)

Daption capense
Pygoscelis antarctica
Lobodon carcinophaga
Aptenodytes forsteri
Pygoscelis papua
Spheniscus humboldti
Aptenodytes patagonicus
Hydrurga leptonyx

Spheniscus magellanicus
Arctocephalus forsteri
Macronectes halli
Diomedea sanfordi
Eudyptes chrysocome

Phalacrocorax magellanicus Eudyptes schlegeli

Pagodroma nivea Catharacta maccormicki Mirounga leonina

Fulmarus glacialoides Macronectes giganteus Arctocephalus tropicalis Diomedea exulans Leptonychotes weddellii Megadyptes antipodes