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A meta-analysis of human disturbance impacts on Antarctic wildlife

Bernard W. T. Coetzee* and Steven L. Chown

School of Biological Sciences, Monash University, Melbourne, Victoria 3800, Australia

ABSTRACT

Evidence-based assessments are increasingly recognized as the best-practice approach to determine appropriate conservation interventions, but such assessments of the impact of human disturbance on wildlife are rare. Human disturbance comprises anthropogenic activities that are typically non-lethal, but may cause short- and/or longer-term stress and fitness responses in wildlife. Expanding human activity in the Antarctic region is of particular concern because it increases the scope and potential for increased human disturbance to wildlife in a region that is often thought of as relatively untouched by anthropogenic influences. Here, we use a meta-analytical approach to synthesise research on human disturbance to wildlife over the last three decades in the Antarctic and sub-Antarctic region. We combine data from 62 studies across 21 species on the behavioural, physiological and population responses of wildlife to pedestrian, vehicle and research disturbances. The overall effect size indicated a small, albeit statistically significant negative effect of disturbance (−0.39; 95% CI: −0.60 to −0.18). Negative effects were found for both physiological and population responses, but no evidence was found for a significant impact on wildlife behavioural responses. Negative effects were found across pedestrian, vehicle and research disturbances. Significant and high among-study heterogeneity was found in both disturbance and response sub-groups. Among species, it remains unclear to what extent different forms of disturbance translate into negative population responses. Most current guidelines to limit wildlife disturbance impacts in Antarctica recommend that approaches be tailored to animal behavioural cues, but our work demonstrates that behavioural changes do not necessarily reflect more cryptic, and more deleterious impacts, such as changes in physiology. In consequence, we recommend that pedestrian approach guidelines in the Antarctic region be revisited. Due to the high heterogeneity in effects, management guidelines for different sites and species will need to be developed on a case-by-case basis, ideally in conjunction with carefully designed experiments. Guidelines to reduce the impact of research activities *per se* require development to reduce the potential impacts of conducting research. We identify research questions that, if answered, will further improve the evidence base for guidelines to manage human disturbance in Antarctica.

Key words: Antarctic conservation, Antarctic policy, conservation evidence, human disturbance impacts, systematic review.

CONTENTS

* Address for correspondence (Tel: +61 3 990 20910; E-mail: bwtcoetzee@gmail.com).

I. INTRODUCTION

Evidence-based conservation interventions have seen much recent growth in scope and number. Impetus to employ such approaches has come from the realisation that poorly supported practices result in suboptimal conservation outcomes (Sutherland *et al.,* 2004). By contrast, an evidence-based strategy, usually adopting a formal systematic review, promotes objective and defensible actions (Sutherland *et al.,* 2004; Pullin & Knight, 2005; Stewart, Pullin & Coles, 2007; Cook, Possingham & Fuller, 2013). Importantly, it also enables practitioners to modify interventions to achieve the greatest benefit as new evidence becomes available.

Although human disturbance impacts on wildlife are a growing conservation concern globally (Carney & Sydeman, 1999; Frid & Dill, 2002; Beale & Monaghan, 2004*b*; Blumstein *et al.,* 2005; Barron, Brawn & Weatherhead, 2010), systematic reviews (in the sense of Cook *et al.,* 2013) of these impacts are uncommon (Stankowich, 2008; Barron *et al.,* 2010). Rarely defined in the literature, human disturbance to wildlife is usually construed as anthropogenic activities that are typically non-lethal, but might cause either short- or longer-term stress or fitness responses. A suite of human activities, including construction, transport, natural resource extraction and tourism are sources of wildlife disturbance (Carney & Sydeman, 1999; Beale & Monaghan, 2004*b*; Blumstein *et al.,* 2005; Bejder *et al.,* 2006). Wildlife might also react to humans as ‘predation-free predators’, with a range of associated costs (Beale & Monaghan, 2004*a*). Both real predation and non-lethal human disturbance can create similar trade-offs for wildlife, between avoiding perceived risk from indirect predation effects and investing in other activities that benefit fitness, such as parental care, feeding, mating or breeding (Frid & Dill, 2002; Blumstein *et al.,* 2005). As a consequence, human disturbance can alter species behaviour (Carney & Sydeman, 1999; Holmes *et al.,* 2006; Burger & Gochfeld, 2007; Holmes, 2007) and physiology (Gabrielsen & Smith, 1995; Wikelski & Cooke, 2006). Such changes might ultimately result in declines in fitness, abundance and persistence (Ruhlen *et al.,* 2003; Stankowich, 2008; Barron *et al.,* 2010; Saraux *et al.,* 2011).

Human disturbance to wildlife is of particular concern in the broader Antarctic region. On the continent and its surrounding islands, human activities in the form of science and tourism are often co-located with areas supporting large numbers of breeding seabirds or seals (Tin *et al.,* 2009; Hughes *et al.,* 2011; Shaw *et al.,* 2014). In the case of tourism, activities focus on such colonies in particular, as is clear from analyses of site visits (Naveen *et al.,* 2001; Lynch *et al.,* 2009) and guidelines for visits to various sites (Poncet & Poncet, 2007; Poncet & Crosbie, 2012). Science activities often require direct interventions such as tagging or device fitting (Saraux *et al.,* 2011), which can cause disturbance (Barron *et al.,* 2010), but associated logistic support can also cause substantial disturbance (Cooper, Avenant & Lafite, 1994; Hughes *et al.,* 2008; Peter *et al.,* 2013). Such activities are on the increase as the numbers of tourists to the region rises and new scientific stations are constructed (Chown *et al.,* 2012*b*), which increase human disturbance potential.

The potential impacts of human activities on Antarctic wildlife have long been recognized. Article 3 of Annex II to the Protocol on Environmental Protection to the Antarctic Treaty states that ‘harmful interference [to fauna and flora] shall be prohibited’ (ATS, 1991). In consequence, several guidelines have been developed to reduce human disturbance. These include guidelines for the operations of aircraft (ATCP, 2004; Harris, 2005; de Villiers, 2008), guidelines for tourists (IAATO, 2014), and general guidelines for pedestrians (AAD, 2014; ANZ, 2014). These guidelines recognize the potential sensitivity of various species to disturbance given the nature of the region and differences among sites and species (ATCP, 2004; Harris, 2005; de Villiers, 2008; AAD, 2014; ANZ, 2014; IAATO, 2014). Nonetheless, as is frequently the case for conservation interventions elsewhere (Sutherland *et al.,* 2004), the origins of the recommendations to limit wildlife disturbance are frequently not clear or are based on just a few studies (Harris, 2005; ATS, 2014).

In an unpublished narrative review, which formed the basis for a discussion of disturbance effects at the Antarctic Treaty (ATCM XXXI WP12, 2008), de Villiers (2008) pointed out that general interpretations of disturbance effects are complicated, at least in part, by the diversity of studies in the field. These include several human disturbance types, focal taxa, the documented responses of biodiversity and regions under investigation. For example, behavioural stress responses might or might not increase with human disturbance depending on the species investigated (Fowler, 1999; Engelhard *et al.,* 2002*a*; Holmes *et al.,* 2006; Burger & Gochfeld, 2007; Holmes, 2007). Similarly, changes in stress physiology (Regel & Putz, 1997; Weimerskirch *et al.,* 2002), such as increases in heart rate under disturbance (Pfeiffer & Peter, 2004), can be negligible when species are habituated (Viblanc *et al.,* 2012). Human disturbance has also been broadly implicated in population declines (Wilson *et al.,* 1991; Woehler *et al.,* 1991, 1994; Micol & Jouventin, 2001; Harris, 2009; Saraux *et al.,* 2011), declines in breeding success (Giese, 1996; McClung *et al.,* 2004; Ellenberg *et al.,* 2007; Saraux *et al.,* 2011) and the desertion of preferred breeding sites (Robertson, 1997). By contrast, in different regions, for a suite of species, population declines driven by human disturbance cannot solely be attributed to disturbance, but might rather also be the consequence of other environmental drivers (Cobley & Shears, 1999; Micol & Jouventin, 2001; Carlini *et al.,* 2007). Clearly, the impacts of human disturbance are variable in Antarctica, and in consequence, the generality, direction and strength of the responses of wildlife to human disturbance remain unclear (de Villiers, 2008). In consequence, current guidelines to minimize human disturbance in Antarctica might either be poorly supported by available evidence, or might be inappropriate.

Here, we use a systematic review framework in conjunction with a meta-analysis to examine the evidence for human disturbance impacts in Antarctica, including the sub-Antarctic. Our overarching question is: does human disturbance alter bird and mammal behaviour, physiology and/or population responses in the greater Antarctic region? Unlike a narrative review (e.g. de Villiers, 2008), a meta-analytical approach enables the statistical combination of a variety of responses and disturbances into a single framework, and more importantly, can reveal the direction and also increase the precision of estimates across disturbance types and wildlife responses (Koricheva, Gurevitch & Mengersen, 2013).

II. METHODS

(1) Overview

We followed the systematic review approach as set out by Pullin & Stewart (2006) and conducted a meta-analysis using best-practice approaches (Koricheva *et al.,* 2013). Pullin & Stewart (2006) recommend that the review question be formulated in consultation with relevant stakeholders. Our approach resulted directly from a request by Antarctic Treaty Parties to investigate guidelines underpinning wildlife approach distances in the Antarctic to minimize anthropogenic disturbance (ATCM XXX, 2007). This request resulted in a narrative review (de Villiers, 2008), a presentation of this information to the Treaty Parties (ATCM XXXI WP12, 2008) and requests for further information by Antarctic Treaty Parties on this conservation question (ATCM XXXI, 2008; ATCM XXXVII WP 5, 2014; ATCM XXXVII WP 13, 2014). Requests were made through the Scientific Committee on Antarctic Research (SCAR, 2014).

(2) Search strategy

We searched the published literature using key word searches in the *Google Scholar* and *Web of Science* databases (search conducted in October 2013). To formulate the initial search string we used details from a recent narrative review on human disturbance in Antarctica (de Villiers, 2008) to identify the disturbance types and wildlife responses predominantly identified in the literature. We used both structured key word searches, and opportunistic searches with the whole or sections of the initial search string with Boolean search terms: (human OR anthropogenic OR tourist OR ecotourist* OR research*) AND (disturbance OR stress OR activity* OR impact) AND (Antarctic* OR sub-Antarctic*) AND (heart rate OR physiology OR hormone* OR blood OR behaviour OR behavior OR abundance OR population). In addition, we assessed all references included in the review of de Villiers (2008), a global meta-analysis of transmitter effects on avian behaviour and ecology (Barron *et al.,* 2010), a global meta-analysis of hormonal stress responses in birds (Lendvai *et al.,* 2013), and a narrative review of disturbance effects on waterbirds (Carney & Sydeman, 1999). Reference lists from candidate materials were also searched for additional, relevant works. Studies were judged to be of appropriate quality and incorporated into the meta-analysis if they met the inclusion criteria (details below), but we made no further *a priori* qualitative assessment of study quality. Assessments of study quality are typically performed during systematic review (Pullin & Stewart, 2006; Cook *et al.,* 2013), but are not usually undertaken during meta-analysis because studies are deemed appropriate if they meet the meta-analysis inclusion criteria (Koricheva *et al.,* 2013).

After the removal of duplicates, the total initial list of 1370 materials consisted of peer-reviewed papers, reports, book chapters and dissertations. Because our search strategy identified many materials that were not relevant to our study, we excluded a further 1233 materials based on their relevance, to include a total of 137 candidate materials for a detailed assessment. From these candidate materials, we further only included studies conducted south of 40° latitude, so our analyses include the sub-Antarctic region, in keeping with the SCAR area of interest (SCAR, 2014). We retained studies of bird and mammal responses to human disturbance, and excluded those on disturbance caused by the impact of invasive alien species, camping, habitat destruction, pollution or trampling. The impacts of many of the latter disturbance types have been reviewed in narrative form elsewhere (e.g. Frenot *et al.,* 2005; Tin *et al.,* 2009, 2014).

Fig. 1. Conceptual unified framework adopted in this study on the types of disturbance and wildlife response measurements in the papers reviewed. Heterogeneity in the effects of disturbance on wildlife may be introduced by both the kind of measurement (treatment moderator) and/or methodological and ecological moderator variables. Both ecological and methodological moderators may influence species habituation potential. Picture credits: top (S.L.C.), bottom (B.W.T.C.).

We further selected studies that compared wildlife responses to disturbance quantitatively, under some form of what the authors considered human disturbance ('treatment'), and under conditions that the authors considered free from such disturbance ('control'), in terrestrial regions (details in Section II.3). In total, 62 studies met the criteria (see online Appendix S1) reporting 543 pairwise responses across 17 bird and four mammal species (species names in Appendix S2). We excluded 75 studies that underwent detailed assessment with reasons for the rejections provided in Appendix S3.

(3) Data capture

(*a*) *Data extraction*

Studies typically reported data on a disturbance type caused by anthropogenic activities, and data on a response type of wildlife to such disturbances (Fig. 1; Table 1). We could therefore capture data across a range of human disturbance types, and responses of wildlife to such disturbance (Fig. 1; Table 1). Studies were typically replicated experimental manipulations, where researchers subjected animals to some form of disturbance and compared results to the identical species free from such disturbance (see example papers in Table 1). For example, Giese (1996) compared hatching success of Adélie penguins (*Pygoscelis adeliae*) in undisturbed colonies to those exposed to simulated tourist visits and nest checking. Studies also included opportunistic observations of animals subjected to disturbance. For example, Hughes *et al.* (2008) documented short-term behavioural responses of king penguins (*Aptenodytes patagonicus*) to helicopter over-flights associated with logistic activities in comparison to behaviour before such disturbance. Some studies also made comparisons of wildlife responses to disturbance in discrete spatial regions that were judged by the authors to be subject to regular human disturbance, to other discrete spatial regions without such disturbance. For example, Holmes, Giese & Kriwoken (2005) compared heart rate changes in individuals of royal penguins (*Eudyptes schlegeli*) in colonies that were regularly visited by tourists (disturbed treatment), to the heart rates of individuals

Table 1. Disturbance types and response types reported in the literature, which determined our sub-group designations

Disturbance category	Disturbance definition	Response category of wildlife	Response/s types	Response example/s	Example papers
Pedestrian	Experimentally induced disturbance by human approach	Behavioural	Vigilance	Behavioural responses after experimental approaches	Holmes (2007)
Pedestrian		Physiological	Heart rate	Heart rate increase before and after experimental approach	Ellenberg *et al.* (2009)
Pedestrian		Population	Abundance	Hatchling success of species to simulated tourist visits	Giese (1996)
Vehicle	Wildlife responses to helicopters, snowmobiles or boats, compared to animals free from such disturbance	Behavioural	Vigilance	Behavioural change after controlled approaches by vehicles	Boren, Gemmell & Barton (2002)
Vehicle		Physiological	Heart rate	Heart rate increase during helicopter over-flights	Culik *et al.* (1990)
Vehicle		Population	Abundance	Decrease in seal abundance during helicopter over-flights	Wheeler (2009)
Research	Fitting devices to animals, banding animals, conducting surveys, handling during research or comparisons of populations undergoing such treatment	Behavioural	Vigilance, foraging time	Changes in vigilance behaviour or decreases in foraging time caused by fitting devices	de Villiers *et al.* (2005) and Beaulieu *et al.* (2010)
Research		Physiological	Changes in heart rate, temperature, stress hormones or blood chemistry	Changes in heart rate, stress hormones or blood chemistry	Engelhard *et al.* (2002*a*) and Viblanc *et al.* (2012)
Research		Population	Abundance and morphometric changes	Changes in species population attributed to research activity	Saraux *et al.* (2011)
Spatially aggregated	Spatial comparisons between regions that were typically under longer-term and high disturbance regimes from a range of human activities, and compared to regions that the authors considered free from such disturbance	Behavioural	Vigilance	Vigilance changes in individuals compared between undisturbed and disturbed regions	Walker *et al.* (2005) and Engelhard *et al.* (2001)
Spatially aggregated		Physiological	Heart rate, stress hormones, blood chemistry	Heart rate or stress hormone comparisons between undisturbed and disturbed regions	Walker *et al.* (2005) and Walker, Boersma & Wingfield (2006)
Spatially aggregated		Population	Abundance and morphometric changes	Abundance or morphometric changes in populations between undisturbed and disturbed regions	McClung *et al.* (2004) and Villanueva, Walker & Bertellotti (2012)

See Table 2 for effect sizes across sub-groups and sample sizes.

from another colony that rarely received tourist visits (undisturbed control).

Studies were only included if an appropriate effect size could be calculated from the data reported, and in which the direction of the response could be ascertained. To do so required one of the following statistics to be reported in the study: mean and variance, *F*-statistic, *t*-statistic, *Z*-statistic, chi-squared, graphics of such statistics, or raw data. WebPlotDigitizer v2.4 (Rohatgi, 2012) was used to capture data from figures. To avoid pseudoreplication, we preferred to capture primary data (means and variation) rather than their derivative statistics (*F*-statistic, *t*-statistic, *Z*-statistic, etc.). Data reported with standard errors and confidence intervals were converted to standard deviation using imputation methods (Higgins & Green, 2011).

(*b*) *Sub-group designation*

Evidence for different disturbance types was categorized into: 'pedestrian disturbance', 'vehicle disturbance', 'research disturbance' and 'spatially aggregated disturbance' (see example papers in Table 1). (*i*) Pedestrian disturbance was restricted to studies where researchers approached animals to simulate pedestrian activity, whether or not the authors intended to simulate disturbance from either research or tourist sources. (*ii*) Vehicle disturbance consisted of wildlife responses to helicopters, snowmobiles or boats, compared to animals free from such disturbance. No data were found that met the inclusion criteria on disturbances caused by fixed-wing aircraft. (*iii*) Research disturbance was restricted to intense disturbance typically associated with ecological research. This includes fitting devices to animals, banding animals, conducting surveys, and handling of animals during research. Because the longer-term impacts of research itself on species populations may be pronounced in the Antarctic region (Saraux *et al.,* 2011), we also included seven comparisons of populations that are subjected to such intense research disturbance (treatment) or not (control), in this sub-group. For example, Saraux *et al.* (2011) compared survival and reproduction (abundance responses) of populations of king penguins (*Aptenodytes patagonicus*) that were either banded for research purposes (treatment), or not banded (control). (*iv*) Spatially aggregated disturbances are comparisons between physical regions that are typically subject to long-term and high disturbance regimes from a range of human activities (treatment), with regions that the authors consider free from such disturbance (control). For instance, Walker, Boersma & Wingfield (2005) compared baseline and stress-induced corticosterone hormone changes in Magellanic penguin (*Spheniscus magellanicus*) from tourist-visited (treatment) or unvisited colonies (control). These comparisons were typically between areas either close to or far removed from scientific research stations, but we included areas that are frequently visited by tourists in this category, as wildlife there may also be subject to human disturbance (Culik & Wilson, 1995; Fowler, 1999; McClung *et al.,* 2004). Although noise pollution can cause disturbance to wildlife (e.g. Barber, Crooks & Fristrup, 2010), no suitable studies in Antarctica were found that satisfied our criteria.

Evidence for wildlife responses across the four different disturbance types detailed above were categorized into three main sub-groups; 'behavioural', 'physiological', and 'population' responses (see example papers in Table 1). (*i*) Behavioural responses included changes related to an animal's perception of threat (vigilance, aggression, and fleeing or altered conspecific interactions) or feeding behaviours (changes in foraging behaviour or foraging times). (*ii*) Physiological responses included changes in heart rate, hormonal changes in blood or faeces, temperature changes, blood chemistry or faecal hormone changes. (*iii*) Population responses included direct changes in abundance of species, or proxies for abundance such as fledging/hatching success and rates of egg loss. Because lower body mass, body condition or body length are often correlated with population decline (Peig & Green, 2009, 2010), we included morphometric measurements for both juveniles and adults as a population response.

(4) Data analysis

(*a*) *Main meta-analysis*

We calculated the Hedges g^* metric for each pairwise comparison, that is, the weighted average of the mean standardized difference (based on pooled variance measures; Koricheva *et al.,* 2013). We converted data reported as test statistics to the Cohens d effect size (Wilson, 2013), and converted these to Hedges g^* using the 'es.compute' package (Del Re, 2014) in R (R Core Team, 2014). We selected a single effect size measure that could incorporate variance, and to standardize across response variables. All subsequent analysis was conducted in the 'metafor' package (Viechtbauer, 2010) in R (R Core Team, 2014).

Because studies focussed on different species (e.g. Engelhard *et al.,* 2002*a*; Ellenberg, Mattern & Seddon, 2009), or followed different sampling designs (e.g. Culik, Adelung & Woakes, 1990; Holmes, 2007), and typically reported different numbers of comparisons per study (e.g. Engelhard *et al.,* 2002*b*; de Villiers, Cooper & Ryan, 2005), we calculated one effect size for each sub-group per paper, which is a standard approach in meta-analysis among studies (Koricheva *et al.,* 2013). Some studies reported across more than one sub-group and so 78 comparisons were obtained in total from the original 62 studies (see online Appendix S1). We then applied the random-effects model across studies (Koricheva *et al.,* 2013) with a maximum-likelihood variance estimator (Viechtbauer, 2010). The model coefficients and their corresponding standard errors for each study were thus used to calculate the overall effect size, as well as effect sizes for all of the sub-groups detailed above.

(*b*) *Heterogeneity statistics*

We used two metrics to characterize heterogeneity between studies: the Q-statistic and the I^2 value. The Q-statistic tests for total heterogeneity in effect size, where a significant value indicates that the estimated effect size is more heterogeneous than expected by chance (Koricheva *et al.,* 2013). The I^2 value is the total percentage of heterogeneity that can be attributed to between-study variance (Koricheva *et al.,* 2013). We also plotted effect sizes and confidence intervals from pair-wise comparisons in behavioural, physiological and population sub-groups to visualise better among-study heterogeneity.

(*c*) *Bias analysis*

We conducted a funnel plot and cumulative meta-analysis to assess the influence of bias in our study. A funnel plot graphs sample sizes against standard errors. Studies with the largest sample sizes are assumed to have a lower standard error, and so will be near the average effect size, while studies with smaller sample sizes will be spread on both sides of the average effect size. Deviations from this assumed relationship can indicate bias, although the source of such bias may be obscure (Koricheva *et al.,* 2013). Positive asymmetry in a funnel plot is taken to mean publication bias, as those studies with positive effects are submitted and/or accepted for publication with a greater frequency then those with negative effects (Koricheva *et al.,* 2013). A cumulative meta-analysis ranks all studies by precision, by starting with the studies with the largest standard error, after which the comparison with the next largest standard error is added and the effect size is recalculated, and so enables inspection of the development of the observed effect size with the addition of more precise data (Koricheva *et al.,* 2013). Bias in meta-analysis may be introduced by phylogenetic non-independence of species, because more closely related species may have more similar effect sizes (Koricheva *et al.,* 2013). The influence of phylogenetic non-independence is pronounced when conducting fixed-effects meta-analysis, but comparatively little additional variation in meta-analytic outcomes is explained when fitting a random-effects model incorporating a phylogeny (Chamberlain *et al.,* 2012). Since we fitted a random-effects meta-analysis, we did not correct for phylogenetic non-independence.

(*d*) *Effect size direction*

Deciding on the direction of the sign of an effect size is essentially arbitrary (Koricheva *et al.,* 2013). We considered the comparison of the two groups in our meta-analysis as the control mean (no disturbance, M_1), minus the experimental treatment (disturbance, or a spatial region under disturbance, M_2), so that a negative sign in the effect size reflects a negative effect of disturbance on wildlife. However, abundance responses are opposite to this expectation, because a lower abundance of animals under disturbance will be positive when calculating effect size ($M_1 - M_2$). Here we consider a decline in species abundance from disturbance a negative effect. Therefore, to enable consistent interpretation, the expected direction for abundance responses was inverted in all cases so that a negative sign reflected a negative effect of disturbance. For behavioural and physiological responses we maintained the effect direction as determined by the original authors.

(*e*) *Moderator variables*

Moderator variables (covariates) may help to describe variation in effect sizes found in a meta-analysis (Fig. 1). Moderator variables can be ecological variables (related to the taxon or the spatial location of studies), methodological variables (how the meta-analysis was conducted or the nature of the data) or treatment-related variables (i.e. in our case, moderators of disturbance itself; Koricheva *et al.,* 2013). We used a meta-regression analysis to determine the association of moderators with effect size variation. A meta-regression analysis is similar to regression analysis in that variation in effect size is predicted according to the values of one or more moderator, or explanatory, variables (Koricheva *et al.,* 2013). To describe variation in effect sizes from ecological sources (such as environmental gradients or species-specific effects), we analysed the influence of latitude, longitude, species and taxon (birds/mammals) as captured from the source studies. To describe variation in effect sizes from methodological variables (meaning to test if our *a priori* decision on sub-group designation influenced outcomes) we included covariates describing how the calculated effect size was included in the response sub-group (whether it was a behavioural, physiological or population response), and also how the calculated effect size was included in the disturbance sub-group (whether it was a pedestrian, vehicle, research or spatial disturbance).

Studies rarely reported treatment-related moderator variables, such as moderators that can influence the impact of disturbance itself. Thus, we could not include them in our meta-regression. For example, studies that assessed the influence of pedestrian and vehicle disturbance did not always consider the distance of the disturber to the animal as a potential moderator variable that could influence the disturbance response (Figs 1 and 2). When only considering pedestrian approaches, studies rarely experimentally accounted for or reported data on disturber group size or angle of approach (Figs 1 and 2), despite the presumed influence of

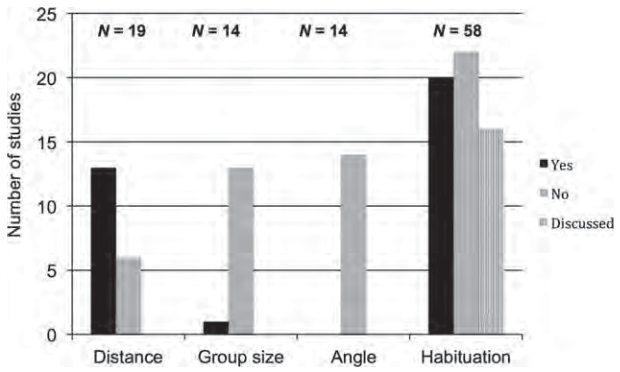

Fig. 2. Studies included in the meta-analysis rarely address the influence of moderator variables on the impacts of disturbance to Antarctic wildlife. Graphed here are pair-wise comparisons included in the meta-analysis (indicated by *N*) for different moderator variables (distance to disturber, disturber group size, disturber angle of approach, species habituation influence) in cases where such moderator variables could influence the outcome of disturbance impacts. The legend indicates the number of studies that addressed ('Yes'), did not address ('No'), or at least discussed the implications of moderator effects ('Discussed'). We excluded studies on devices fitted to animals because animals are handled, and habituation to devices is rarely quantified.

these moderators on wildlife responses (Culik & Wilson, 1991a; Giese, 1998; Holmes *et al.,* 2005). When excluding studies measuring the impact of devices (since animals may never habituate to them; Barron *et al.,* 2010), the majority of studies did not account experimentally for the confounding factors of habituation [66% (38/58)], although 16 studies recognized and discussed its potential influence on interpretation (Fig. 2). As a consequence, we could not assess the influence of distance to or angle of the disturber, disturber group size, or habituation as a potential explanatory variable across all studies in the meta-regression (or indeed, the meta-analysis).

III. RESULTS

Human disturbance to Antarctic wildlife across all studies for all responses showed a statistically significant negative effect [effect size (ES) = −0.39; 95% CI: −0.60 to −0.18; N = 78; Table 2]. No effect for behavioural responses across individual studies was found (ES = −0.22; 95% CI: −0.71 to 0.26; N = 31; Fig. 3), but negative effects were found for physiological (ES = −0.63; 95% CI: −1.10 to −0.16; N = 19; Fig. 4) and population-level responses (ES = −0.38; 95% CI: −0.57 to −0.19; N = 28; Fig. 5). Effect sizes for disturbance sub-groups were negative for pedestrian (ES = −1.28; 95% CI: −2.23 to −0.33; N = 9), vehicle (ES = −1.72; 95% CI: −3.32 to −0.12; N = 5) and research activity (ES = −0.29; 95% CI: −0.47 to −0.11; N = 40), but showed no effect for spatially aggregated disturbances (ES = −0.02; 95% CI: −0.36 to 0.32; N = 24; Table 2). Across all studies, effect sizes were statistically negative for birds (ES = −0.38; 95% CI: −0.61 to −0.16; N = 67), but not for mammals (ES = −0.43; 95% CI: −1.11 to 0.25; N = 11).

When analysing the range of responses reported in the literature, we found no effect for behaviours related to vigilance, for blood chemistry and for hormonal physiological responses (see Table 2). However, there was a

Table 2. Effect sizes (ES), lower (ci.lb) and upper bound (ci.ub) confidence intervals and sample size (N) Tau square (I^2), Q statistic (Q) with its P-value (Qp) for all disturbance and response sub-groups, as well as specific responses (SR)

	Sub-group	ES	ci.lb	ci.ub	N	I^2	Q	Qp
Overall	All	−0.39	−0.60	−0.18	78	97.01	767.88	<0.001
Response	Behavioural	−0.22	−0.71	0.26	31	97.37	367.67	<0.001
	Physiological	−0.63	−1.10	−0.16	19	97.15	151.75	<0.001
	Population	−0.38	−0.57	−0.19	28	92.05	213.28	<0.001
Disturbance	Pedestrian	−1.28	−2.23	−0.33	9	93.03	103.44	<0.001
	Vehicle	−1.72	−3.32	−0.12	5	98.74	103.35	<0.001
	Research	−0.29	−0.47	−0.11	40	92.99	284.46	<0.001
	Spatially aggregated	−0.02	−0.36	0.32	24	95.66	219.02	<0.001
Taxon	Mammal	−0.43	−1.11	0.25	11	99.27	75.14	<0.001
	Bird	−0.38	−0.61	−0.16	67	95.50	674.64	<0.001
SR	Foraging time	−0.21	−0.61	0.19	13	85.55	85.76	<0.001
	Vigilance	−0.27	−1.11	0.57	19	98.78	281.31	<0.001
	Heart rate	−1.42	−2.52	−0.31	8	96.22	117.48	<0.001
	Blood chemistry	−0.02	−0.12	0.08	1	0.00	0.00	1
	Hormones	−0.05	−0.21	0.10	8	18.53	8.75	0.27
	Temperature	−0.75	−1.05	−0.45	1	0.00	0.00	1
	Morphometrics	−0.56	−0.98	−0.15	8	93.30	65.43	<0.001
	Abundance	−0.29	−0.49	−0.09	20	89.48	144.95	<0.001

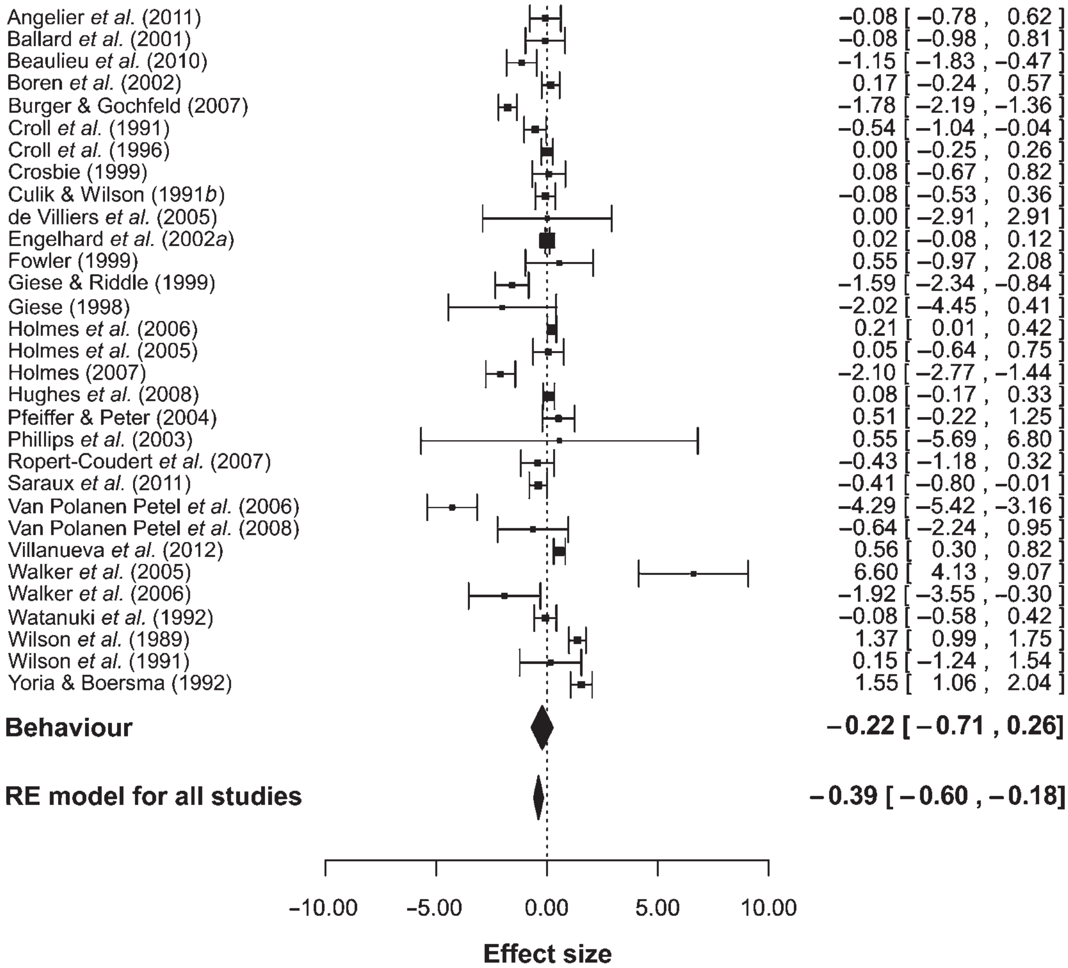

Fig. 3. Forest plot showing the point effect estimates with 95% CI for studies documenting behavioural responses of species to disturbance, with exact values in the right-hand column. Effect sizes per pair-wise comparison are plotted to visualise effect size variations better across studies. Note the variation across effect size direction, and variation in the width of confidence intervals across different pair-wise comparisons. Studies crossing 0, the dotted line of no effect, show non-significant disturbance outcomes. The area of each square indicates the weight given to that study (due to low variance) while the diamonds indicate the overall effect size estimate across sub-groups, and the random effect (RE) meta-analysis across all studies. Diamond widths indicate 95% CI.

negative effect of human disturbance on heart rate physiology, typified by an increase in heart rate under disturbance (ES = −1.42; 95% CI: −2.52 to −0.31; $N = 8$). Abundance, that is, both actual counts of individuals and proxies for abundance such as fledging/hatching success and rates of egg loss, also had a negative effect size (ES = −0.29; 95% CI: −0.49 to −0.09; $N = 20$) and morphometric responses were lower for species under disturbance (ES = −0.56; 95% CI: −0.98 to −0.15; $N = 8$), which are indicative of population decline.

We found significant and high between-study heterogeneity in effect sizes in all response and disturbance sub-groups (minimum $I^2 > 92.05\%$; Q-statistic significant at <0.001; Table 2). Behavioural responses in particular showed high variance in effect size direction and confidence interval width across individual studies (Fig. 3). Variation in effect size direction and confidence interval width is also evident across individual studies of physiological and population response sub-groups (Figs 4 and 5), although to a lesser extent than that of behavioural responses (Fig. 3). Only hormonal responses showed small ($I^2 < 19\%$) and non-significant heterogeneity; heterogeneity could not be established for temperature and blood chemistry as sample size was too low ($N = 1$). The relatively asymmetrical funnel plot (see online Fig. S1) suggests that studies with small (or negative) effect sizes are generally published at a higher frequency. The addition of the most imprecise studies in the cumulative meta-analysis initially caused the cumulative effect size to indicate no effect, with a negative effect from the addition of the 43rd study onwards (see online Fig. S2). Thus some form of publication bias in the material considered for our study cannot be ignored, and is likely contributing

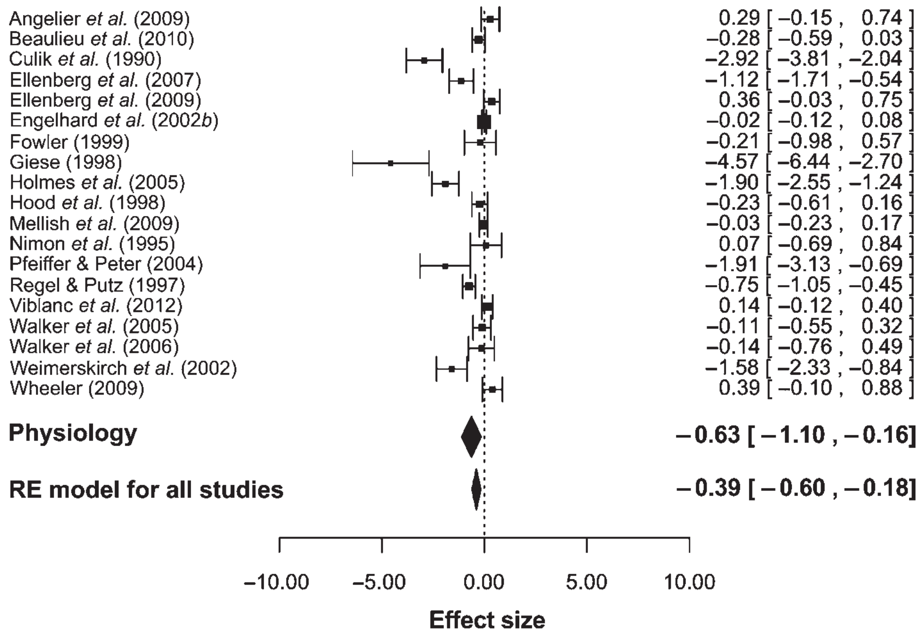

Fig. 4. Forest plot showing the point effect estimates with 95% CI for studies documenting physiological responses of species to disturbance. See Fig. 3 legend for details of interpreting forest plots.

to the high heterogeneity observed (Koricheva *et al.,* 2013).

The meta-regression model could only account for 5.8% of the variation in effect size (Table 3). Residual heterogeneity remained high even after fitting the moderator variables (96.2%). Only latitude was a significant predictor variable. However, some cases included multiple effect sizes per study, and also multiple studies per site (thus identical coordinates are duplicated); the effect was no longer significant when only one effect size per study was selected at random and the meta-regression repeated (data not shown).

IV. DISCUSSION

The random effects model across all responses demonstrates a negative effect of human disturbance on Antarctic wildlife, despite small to medium effect sizes and high and significant heterogeneity. Benchmark values for interpreting 'small', 'medium', and 'large' effects in meta-analysis are 0.2, 0.5 and 0.8, respectively (Cohen, 1988). Effect sizes of this magnitude are common in ecological and evolutionary studies (Møller & Jennions, 2002). In a meta-analysis of the effects of human disturbance on the flight responses of ungulates, Stankowich (2008) also found small effect sizes and high heterogeneity in individual effect scores. Barron *et al.* (2010) found a more consistent negative impact of transmitter devices fitted to birds, but the study still had comparatively low effect sizes. Indeed, high intra- and inter-specific variation in human disturbance impacts, which lower overall effect sizes, are a common feature of these studies (Blumstein *et al.,* 2005; Stankowich & Blumstein, 2005; Stankowich, 2008; Barron *et al.,* 2010). Nonetheless, the overall outcome here is clear – a negative effect of human disturbance on wildlife in the Antarctic.

Our meta-regression model failed to explain the high variation in effect size. Several additional factors not captured in the model might in part explain the high degree of observed, among-study heterogeneity (Figs 3–5). First, outcomes of individual studies might vary due to sampling error. Because recorded responses to human disturbance cannot include all members of a population, estimates of effect might differ from the true estimate (Koricheva *et al.,* 2013). Second, in contrast simply to being a statistical artefact, large variations in effect sizes are commonly found when comparing among studies of human disturbance impacts on wildlife (Blumstein *et al.,* 2005; Stankowich, 2008; Barron *et al.,* 2010). In consequence, this general pattern of variation among taxa in effect sizes probably explains some of the among-study heterogeneity found here. Third, disturbance drivers and measured responses are not necessarily coupled. For example, we found a negative effect of disturbance on wildlife heart rate. However, cryptic physiological changes such as changes in heart rate may occur in a disturbed animal, but not manifest in a behavioural change, such as enhanced vigilance (Gill, Norris & Sutherland, 2001; Beale & Monaghan, 2004*a,b*). If the response measured is not indicative of the actual response, recorded data may underestimate the true contribution of disturbance to the population in question, which again introduces heterogeneity.

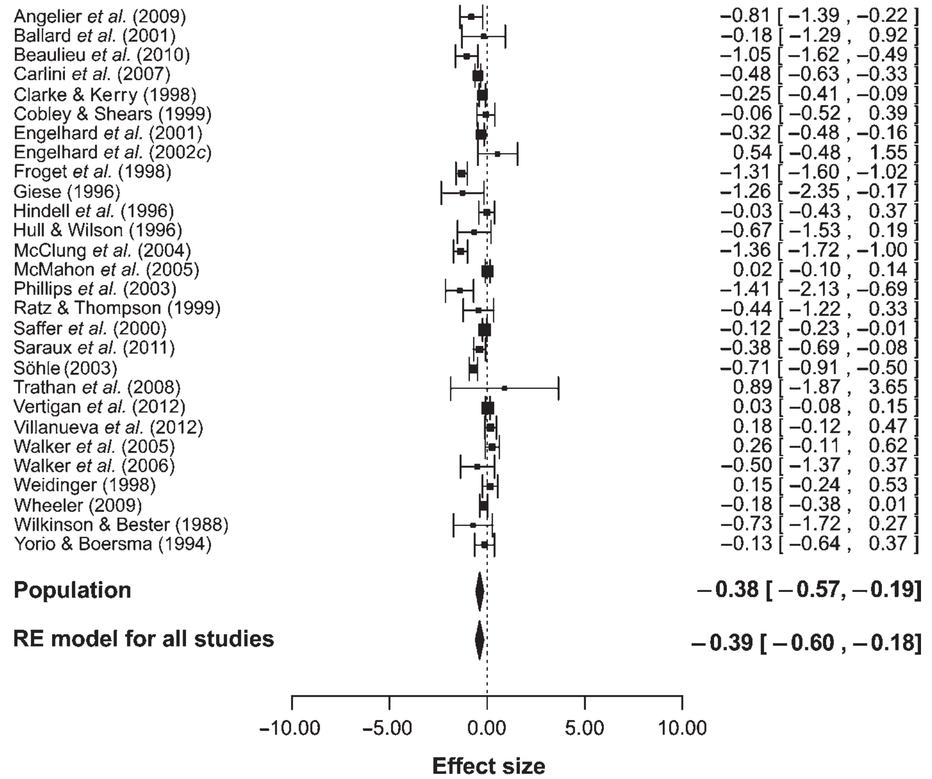

Fig. 5. Forest plot showing the point effect estimates with 95% CI for studies documenting population responses of species to disturbance. See Fig. 3 legend for details of interpreting forest plots.

Table 3. Meta-regression model results for six response variables to explain between-study effect size variation ($N = 78$)

	Deviance explained 5.77%					
	Residual heterogeneity (Tau^2) 96.24%					
	Estimate	SE	zval	pval	ci.lb	ci.ub
Intercept	1.02	0.835	1.222	0.222	−0.616	2.655
Latitude	0.023	0.011	2.155	0.03*	0.002	0.045
Longitude	−0.001	0.001	−1.13	0.26	−0.004	0.001
Species	0.013	0.019	0.679	0.5	−0.024	0.05
Taxon	0.2	0.316	0.633	0.53	−0.42	0.82
Response	−0.082	0.125	−0.653	0.51	−0.326	0.163
Disturbance	−0.113	0.119	−0.954	0.34	−0.346	0.119

Only latitude is a significant predictor variable (*$P < 0.05$), but this significant pattern is removed when only one effect size per study is selected at random and the meta-regression repeated (data not shown). Standard error (SE), standard score (zval), *P*-value (pval), lower (ci.lb) and upper bound (ci.ub) confidence intervals are shown.

Fourth, since moderator variables of disturbance were rarely incorporated, but could introduce variation in effect sizes when not accounted for, their omission from experimental designs might increase heterogeneity in overall effect sizes. Finally, although we did not investigate the likely influence of phylogenetic proximity on variation in effect size (see Section II.4*c*), we cannot discount entirely that it might be responsible for some of the variation found.

We found no significant effect of disturbance on behavioural responses, but it is unclear to what extent behavioural responses in particular may be obscured by moderator variables, which may alter the direction of the response. These include not controlling for the influence and effects of approach speed and angle (Yorio & Boersma, 1994; Martin *et al.*, 2004; Burger & Gochfeld, 2007), animal temperament (Martin & Réale, 2008), distance to disturber (Blumstein *et al.*, 2003, 2005; Pfeiffer & Peter, 2004; de Villiers *et al.*, 2005, 2006), environmental and sampling area effects (Yasué, 2006), and disturber and animal group size (Geist *et al.*, 2005; Holmes, Giese & Kriwoken,

Table 4. Current examples of minimum approach distance guidelines for aircraft, vehicles and pedestrians in Antarctica

		Current guidelines (m)		
Disturbance	Specific disturbance/species	Horizontal	Vertical	Source
Aircraft	Helicopter, one engine	750	750	Harris (2005)
	Helicopter, two engine	1000	1000	Harris (2005)
	Fixed-wing, one or two engine	450	450	Harris (2005)
	Fixed-wing, four engine	1000	1000	Harris (2005)
	All aircraft, bird colonies	930	610	SCAR (2000) and ATCP (2004)
	All aircraft, bird colonies	—	610	GFEA (2013)
Vehicle	All vehicles, all species	200	—	AAD (2014)
	All vehicles, all species	200	—	ANZ (2014)
Pedestrian	Giant petrels and albatrosses	100	—	AAD (2014)
	Giant petrel	50	—	GFEA (2013)
	Breeding/moulting emperor penguin	50	—	AAD (2014)
	Emperor penguin colony	30	—	GFEA (2013)
	Nesting penguin	15	—	Giese (1998)
	Seal pups/fur seal/sea birds	15	—	GFEA (2013)
	Other breeding/moulting birds and seals	15	—	AAD (2014)
	Breeding penguin	10	—	GFEA (2013)
	Non-breeding seal or bird	10	—	ANZ (2014)
	Seal/penguin	5	—	GFEA (2013)
	Non-breeding seal or bird	5	—	AAD (2014)
	Non-breeding seal or bird	5	—	IAATO (2014)

2008; Stankowich, 2008; Van Polanen Petel, Giese & Hindell, 2008; McLeod *et al.,* 2013). Not controlling for habituation in particular may obscure behavioural responses (Bejder *et al.,* 2009; Viblanc *et al.,* 2012), and few studies included such controls (Fig. 2). Furthermore, if behavioural responsiveness is positively related to an animal's condition, which many studies assume, behavioural responses might in any case be an inappropriate and inaccurate assessment of vulnerability (Beale & Monaghan, 2004*a*). Species that show little or no response to disturbance might in fact be those in the poorest condition, and hence 'with the most to lose' (Beale & Monaghan, 2004*a*). Although behavioural responses are an important first and short-term approximation of human disturbance effects (Tuomainen & Candolin, 2011), they might ultimately mask more insidious impacts, such as those on animal physiology and population responses (Gill *et al.,* 2001; Beale & Monaghan, 2004*a*), an interpretation which our data corroborate. As a consequence of the complexity in summarizing the behavioural responses to disturbance, future work should characterize human disturbance by including physiological and population variables, as here we often found both to be negatively impacted by human disturbance.

The majority of studies were conducted on birds rather than mammals, and the meta-analysis revealed a significantly negative effect of disturbance on birds, but no effect for mammals. The reasons for such a difference are unclear. Birds may be more sensitive to disturbance due to underlying differences among taxa in species physiology, habituation potential or life-history traits (Blumstein *et al.,* 2005; Speakman, 2005; Ellenberg *et al.,* 2009; Viblanc *et al.,* 2012). As variance generally increases with low sample sizes (see online Fig. S2), the low sample sizes for mammal pair-wise comparisons found here may, alternatively, have hindered the identification of an effect.

Given our results, we recommend a more precautionary approach to setting minimum approach distance guidelines. Most existing minimum approach guidelines are precautionary for vehicles and boats, but less so for pedestrian approaches (see Table 4), and minimum approach guidelines are not always specified (ATS, 2014). We found that both pedestrian and vehicle disturbance are significant contributors to wildlife disturbance. A recommendation of a 5 m minimum approach distance to non-breeding wildlife is typical, contingent on how the animal behaves (Holmes *et al.,* 2005; AAD, 2014; IAATO, 2014). The existing guidelines also typically recommend that approaching pedestrians stop or increase the distance if the animal shows behavioural signs of distress (e.g. AAD, 2014; ANZ, 2014). Guidelines will, for example, recommend that 'Distances are only a guide – if you detect signs of disturbance, move further away' (AAD, 2014) and to 'Increase [the prescribed] distance if the animal appears disturbed' (ANZ, 2014). However, our work demonstrates clearly that behavioural changes do not necessarily reflect more cryptic and deleterious impacts. The lack of a discernable effect on species behaviour is of particular concern given the demonstrable negative impacts of disturbance on species physiology and population-level attributes. Because current guidelines are based on behavioural cues, the results suggest that, presently, real risks of long-term and negative physiological changes and population declines exist for Antarctic wildlife if current, behaviourally based guidelines are maintained. In consequence, we recommend that pedestrian approach guidelines be revisited. In cases where robust and specific guidance after a systematic review cannot yet be made, as is the case here, it is inappropriate to derive generic implications from individual case studies (Stewart *et al.,* 2007). Additional region- and species-specific studies on the intensity, frequency and type of disturbance in Antarctica, taking into consideration potentially confounding factors, would be most appropriate to determine approach and human conduct guidelines for the regions in question. Ideally, recommendations should be formulated and revised when adequate information becomes available for those sites and species involved (de Villiers, 2008).

Most of the pair-wise comparisons in our database focused on disturbances from research itself, and we found a statistically significant negative effect size for such comparisons. Research activities may alter insect herbivory on plants (Cahill, Castelli & Casper, 2001), and plant seedling communities (Goldsmith *et al.,* 2006; Comita, Goldsmith & Hubbell, 2008), and fitting transmitters to birds reduces their breeding success, morphometrics and can alter their behaviour (Barron *et al.,* 2010). Of critical concern for wildlife disturbance caused by research activities is that disturbance from research can itself compromise the interpretation of results and inferences made from the data obtained. Saraux *et al.* (2011) demonstrated that banding of king penguins (*Aptenodytes patagonicus*) impairs both their survival and reproduction, ultimately affecting their population growth rate and confounding inference on the impact of climate change on the population. Banding carries a long-term costs for penguins (Jackson & Wilson, 2002; Gauthier-Clerc *et al.,* 2004), and transmitters have a negative effect on bird breeding success and behaviour (Barron *et al.,* 2010). While negative effects of research are not ubiquitous in the region (e.g. Wilkinson & Bester, 1988; Angelier, Weimerskirch & Chastel, 2011), our meta-analysis demonstrates that in general, negative research effects on the physiology and populations of wildlife are clear, and may compromise the objectives of the work. Existing guidelines in Antarctica to reduce the impacts of research protocols make only general recommendations to minimize disturbance (e.g. CCAMLR, 2004), but detailed guidelines are used elsewhere effectively to minimize negative effects of instrumentation, viewing, handling and tagging of animals (Murray & Fuller, 2000; Kenward, 2001; Wilson & McMahon, 2006; Casper, 2009; Barron *et al.,* 2010; Buchanan *et al.,* 2012). If a goal for the future scientific conduct of Antarctic ecological research is to reduce its potentially negative impacts on wildlife, and on research outcomes, formalised guidelines will be required. Researchers themselves have a role to play in balancing the benefits of data acquisition against disturbance to animals and associated biases, and to implement best practice guidelines to reduce their potential impact (Jackson & Wilson, 2002; Wilson & McMahon, 2006; Barron *et al.,* 2010; Saraux *et al.,* 2011).

V. CONCLUSIONS

(1) Our findings justify the investment in and expansion of management plans by Antarctic Treaty member countries to reduce human impacts, not only to minimize human disturbance to wildlife, but also to manage general environmental impacts (Tin *et al.,* 2009, 2014; Peter *et al.,* 2013). As with determining minimum approach guidelines, species-specific studies in discrete regions, comprehensively considering confounding factors, will aid in determining the extent and impact of spatially aggregated disturbance, and to develop recommendations on how to reduce it.

(2) Our review raises several research questions that may help improve the evidence base for and therefore the management of wildlife disturbance by humans in the Antarctic (Table 5). A critical challenge for disturbance research is to disentangle the influence of human disturbance from other environmental drivers that may influence species populations (Cobley & Shears, 1999; Micol & Jouventin, 2001; Carlini *et al.,* 2007; Le Bohec *et al.,* 2008; Jenouvrier *et al.,* 2014).

(3) Given the variability of responses to human disturbance, future work will benefit from robust experimental designs to minimize sources of variability in effects (Table 6). Improvements include directly assessing the influence of moderator variables, experimentally manipulating the frequency and intensity of disturbances, and increasing sample sizes to improve statistical power (Table 6). Future meta-analysis will also benefit from comprehensive reporting of sample statistics and variance measures. Widespread and evidence-based guidelines to minimize disturbance can only be made if standardized methodologies in research are adopted across sites and species.

(4) We considered the spatially aggregated disturbance sub-group a possible indicator of longer-term effects of disturbance, because areas with longstanding disturbance are compared to controls. However, why no significant effect was found for the spatially aggregated disturbance group is not entirely clear. As discussed above, high heterogeneity in the responses to disturbance in our database might preclude the identification of a clear effect size direction. Although sample sizes are low, effect sizes for population responses in the spatial disturbance sub-group are negative ($N = 10$), while the remaining behavioural ($N = 10$) and physiological ($N = 4$) effect sizes from that sub-group are positive (data not shown). Thus, the balance of comparisons

Table 5. Conceptual research questions that remain to be answered for future investigations into human disturbance impacts on Antarctic wildlife

Topic	Research questions	Key references
Behaviour	How does behavioural disturbance relate to physiological and population disturbance?	Gill *et al.* (2001) and Beale & Monaghan (2004*a,b*)
	Which behavioural responses, considering species-specific effects, are most indicative of human disturbance?	Bejder *et al.* (2009)
Physiology	What are the long-term physiological consequences of disturbance?	Romero (2004) Viblanc *et al.* (2012) and Dantzer *et al.* (2014)
	Which physiological responses, considering species-specific effects, are most indicative of human disturbance?	Viblanc *et al.* (2012) and Dantzer *et al.* (2014)
Populations	What is the contribution of disturbance to population fluctuations in addition to natural environmental drivers, especially over longer time scales?	Saraux *et al.* (2011)
	Does chronic stress induce population declines?	Romero (2004) and Dantzer *et al.* (2014)
General	What are the linkages between behavioural, physiological and population responses to disturbance?	Gill *et al.* (2001), Beale & Monaghan (2004*a*) and Dantzer *et al.* (2014)
	How do responses interact with global change drivers?	Brook *et al.* (2008) and Saraux *et al.* (2011)
	Under what disturbance regime, both in timing and frequency, does habituation set in?	Bejder *et al.* (2009), Ellenberg *et al.* (2009) and Viblanc *et al.* (2012)
	How can research impacts be reduced?	Murray & Fuller (2000), Kenward (2001), Casper (2009) and Barron *et al.* (2010)
	How can transmitter effects be reduced?	Barron *et al.* (2010)
	What is the impact of human activities to marine animals in Antarctica?	Barber *et al.* (2010)
	What other human activities may cause disturbance to wildlife?	Tin *et al.* (2009) and Peter *et al.* (2013)

Table 6. Recommendations and considerations for future research on human disturbance impacts on Antarctic wildlife

Recommendation	Key references
Account for research disturbance effects, especially transmitter and banding/marking studies.	Murray & Fuller (2000), Kenward (2001), Jackson & Wilson (2002), Casper (2009), Barron *et al.* (2010) and Saraux *et al.* (2011)
Replicated study designs and higher sample sizes to improve statistical power. In some areas, where wildlife is sparse and sites distant from each other in the Antarctic, this may be problematic. At others, such as along the Antarctic Peninsula, for example, this may readily be achieved.	Møller & Jennions (2002) and Lynch *et al.* (2012)
Full reporting of results with variance to allow future meta-analysis.	Koricheva *et al.* (2013)
Standardized methodology to facilitate comparative research. The Expert Group on Birds and Marine Mammals (EGBAMM) of the Scientific Committee on Antarctic Research provides a useful avenue for developing such standard approaches.	Koricheva *et al.* (2013) and EGBAMM (2014)
Better linkages are required between drivers of disturbance and measured responses.	Gill *et al.* (2001) and Beale & Monaghan (2004*b*)
Moderator variables (confounding factors) altering disturbance responses need to be explicitly incorporated (such as: distance to disturbance; group sizes; approach speed; approach angle; habituation).	Blumstein *et al.* (2005) and de Villiers (2008)
Site-based analysis to capture disturbance regimes, regional variation and species-specific effects. These may be especially significant when it is clear that other drivers, such as climate change, sea-ice change and fishing disturbance/impacts are also playing a role.	de Villiers (2008), Lynch *et al.* (2012) and Trathan *et al.* (2014)

in either a positive or negative direction will, in part, preclude identifying a statistically significant effect size. Importantly, population responses to human disturbance cannot be attributed solely to those disturbances, and could also be influenced by natural environmental drivers (Cobley & Shears, 1999; Micol & Jouventin, 2001; Carlini *et al.*, 2007; Saraux *et al.*, 2011; Trivelpiece *et al.*, 2011; Trathan *et al.*, 2014). In consequence, a better understanding of the impacts of longer-term spatially aggregated human disturbance is required, especially for managing Antarctic wildlife populations.

(5) In an Antarctic context, future work will benefit from quantifying the extent to which different vehicles and aircraft impact wildlife. Operators use a range of vehicles and aircraft which vary with local conditions and requirements, and different classes of vehicles may differentially alter wildlife responses (McLeod *et al.,* 2013). Because logistic activities are mainly clustered around research stations, renewed attention is required to the long-term population consequences of disturbance, compared to areas free from such disturbance. Better understanding is also required of the population consequences of long-term physiological stress in wildlife in the Antarctic. Because behavioural responses are poor indicators of human disturbance impacts in the Antarctic region, studies should focus on population and physiological responses (Viblanc *et al.,* 2012). Alternatively, at a minimum, a better appraisal of the relationship between behavioural cues and population and physiological responses is required. Innovative methodological advances from the region also provide the potential for minimizing disturbance in future research, such as remote rovers, disguised as penguin chicks, and equipped to make radio-frequency identification (see Le Maho *et al.,* 2014). Renewed attention is also required to advance understanding of the potentially synergistic interactions between long-term wildlife disturbance regimes in the region, and other drivers of change, such as climate change and pressure from non-native species (Saraux *et al.,* 2011; Trivelpiece *et al.,* 2011; Chown *et al.,* 2012*a*; Trathan *et al.,* 2014). Together with the conceptual research questions and recommendations highlighted in Tables 5 and 6, these are key areas for future work that will enable evidence-based science to underpin guidelines to manage human disturbance in a region undergoing rapidly expanding human activity (Chown *et al.,* 2012*b*).

VI. ACKNOWLEDGEMENTS

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Supplementary database, listing all 62 studies incorporated into the meta-analysis.

Appendix S2. Species included in the meta-analysis.

Appendix S3. Studies excluded from our analyses that underwent detailed assessment ($N = 75$), with reasons for rejection.

Fig. S1. Funnel plot of effect size standard error plotted against effect size.

Fig. S2. Cumulative meta-analysis of the data set sorted by precision.

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