Biological Conservation 211 (2017) 10–19

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Review

Are negative effects of tourist activities on wildlife over-reported? A review of assessment methods and empirical results

Philip W. Bateman[a,*], Patricia A. Fleming[b,*]

[a] Department of Environment and Agriculture, Curtin University, Bentley WA 6845, Perth, Australia
[b] School of Veterinary and Life Sciences, Murdoch University, Murdoch WA 6150, Perth, Australia

ARTICLE INFO

Keywords:
Conservation
Ecotourism
Anthropogenic stressors
Meta-analysis
Behaviour
Habituation

ABSTRACT

There is a general assumption that animal species that face anthropogenic disturbance through tourism suffer some negative impacts as a result. We carried out a meta-analysis of empirical studies of wildlife responses to tourism activities in natural areas to test this assumption. A literature review yielded effect size data for 102 studies representing 99 species. We compare and contrast different measures of response to tourist activities (avoidance responses, time budgets, and physiological responses). Despite most authors interpreting their data as revealing negative impacts of tourist activities on wildlife, we found that behavioural data (flight responses and time budgets) often indicated positive effects of such activities; time budget data are often ambiguous, while physiological data tended to show negative responses. Therefore, how researchers measure the responses of animals, how they interpret the valence of these responses, and the timescale of measure are all important considerations. For example, different measures of physiological response may indicate short term coping responses, while there may be long term physiological change that could influence population dynamics, often beyond the scope of the study. Many species are also able to mitigate the effect of tourist disturbance through habituation and moderation of short term responses, such as avoidance/fleeing responses. In conclusion, therefore, although there could be long term consequences to tourist activities, these impacts are often not readily measurable. Greater consideration of assessment methods to quantify such effects is warranted.

1. Introduction

Tourism in natural environments can have a marked effect on wildlife, especially when animals themselves are the focus of attention. There has been much qualitative discussion on how intrusive or sustainable tourist activities are (e.g. Hunt et al., 2015; Picard, 2015; Wearing et al., 2014), and growing awareness that even ‘benign’ human activities (e.g. observation) influence the biology and behaviour of animals (e.g. Geffroy et al., 2015). Steven et al. (2011) reported that 88% papers exploring the effect of tourist activities on birds qualitatively report negative impacts, although such qualitative statements are often not supported by empirical data.

Objective quantification of effects of tourism disturbance is required to provide a sound basis for guidelines to manage human activity around animals that are either the focus of tourist activities or indirectly impacted by such. One of the issues around quantifying the effects of tourist activities on animals is agreeing on how we measure the impacts (Tarlow and Blumstein, 2007). In this study, we reviewed different methods that have used to quantify the potential impacts of tourism activities on animals (see Box 1 for definitions of tourism activities). We discuss the results and conclusions of empirical studies where an effort has been made to compare animals in the presence of tourist activities with control (non-tourist) groups identified either temporally or spatially. We have included studies where the tourism activities range from ecotourism – where the wildlife species is directly the focus of tourism activities that have the aim of education with the aim to sustaining natural areas – through to incidental impacts of recreational activities in natural areas. We make suggestions regarding data collection for future studies to ensure that we have sufficient empirical quantitative data upon which to make conservation decisions.

2. How do we quantify the impacts of tourist activities?

There are three main categories of data assessing animal responses to tourist activities:

---

* Corresponding authors.
E-mail addresses: bill.bateman@curtin.edu.au (P.W. Bateman), t.fleming@murdoch.edu.au (P.A. Fleming).

http://dx.doi.org/10.1016/j.biocon.2017.05.003
Received 23 August 2016; Received in revised form 27 April 2017; Accepted 3 May 2017

Box 1

Glossary of wildlife tourism terms.

We use the term 'tourist activities' to cover **non-consumptive (wherein the focal organism is not purposefully removed)** recreational human activities in natural environments used by wildlife, including:

Ecotourism – 'responsible travel to natural areas that conserves the environment, sustains the well-being of the local people, and involves interpretation and education' (TIES, 2015). More narrowly, ecotourism has been defined as 'travel with a primary interest in the natural history of a destination' (Fennell, 2015). This form of tourism includes birdwatching, whale watching, shark diving, etc.

Wildlife tourism – A human recreational engagement with wildlife wherein the focal organism is not purposefully removed or permanently affected by the engagement (Duffus and Dearden, 1990).

Natural area tourism – where encounters with and impacts on wildlife can be incidental due to the location of tourism activities, i.e. recreational use of spaces occupied by animals. This form of tourism includes skiing, hiking, biking, swimming, snow-mobiles, sailing, etc.

We did not include:

Consumptive wildlife tourism – A form of leisure travel undertaken for the purpose of hunting or shooting game animals, or fishing for sports fish, either in natural areas or in areas created for these purposes' (Lovelock, 2007).

2.1. *Avoidance responses*

Avoidance responses have been used broadly across wildlife studies (e.g. Blumstein, 2003; Gill and Sutherland, 2000), and have been used to contrast locations with or without tourism activities. An observer approaching a focal animal can simulate how tourists might approach the animal, allowing the testing of different forms of transport (McLeod et al., 2013), approaching in groups (Liao et al., 2005), changing speed or direction of approach (Bateman and Fleming, 2011), carrying different apparatus (e.g. cameras, spear guns; Januchowski-Hartley et al., 2012), or approaching either looking at or away from the animals (Bateman and Fleming, 2014).

An animals' escape response when approached by an observer is arguably the easiest to quantify measure of behavioural responses towards tourists, with measurements that are reasonably objective and highly repeatable, providing metrics that are directly comparable across species, largely irrespective of their different biology (e.g. Blumstein, 2006), for example:

- Alert distance (AD) is the distance between the observer and the animal when it changes its behaviour in response to the approaching observer. AD reflects vigilance and habituation to the continuous presence and behavioural patterns of people; AD has been recorded as a measure of responses to tourists in a range of species (e.g. Amo et al., 2006), and is used as a conservative indicator of tolerance allowing determination of minimum approaching distances (Fernández-Juricic et al., 2001). Distance to cover may similarly reflect vigilance and habituation, and in marine species, so could depth of activity.
- Flight initiation distance (FID) is the distance between the observer and the animal when it moves away from the observer. FID has been recorded for individuals of many species, and is applied in the context of nature-based tourism through the development of setback distances (buffers) around stationary populations e.g. breeding birds (Fernández-Juricic et al., 2005). At a group level, it is possible to record the number (proportion) of individuals fleeing.
- The distance fled (DF) is the displacement of the animal from its original location. DF therefore reflects energy expenditure of escaping disturbance, as well as opportunity costs from moving away from favoured locations. For example, DF has been measured as a response to pedestrians (walking a dog or not) for many bird species (Miller et al., 2001). For animals that leave their territory, young, or nests, the DF can represent a significant energy cost or risk. Measures of how animals flee are also often recorded, including escape speed and protean behaviour (e.g. path sinuosity or directness). Latency to return/resume behaviour is another metric of response to disturbance.
- Avoidance responses are also frequently recorded (e.g. Rode et al., 2007) where animals vacate areas (measured as e.g. duration of encounter, changing residency patterns, number of individuals present) or shift activity patterns (e.g. spending less time around the disturbance, change home range area, avoid paths used by people, shift their percent daytime activity) to reduce encounters with tourists. For example, interaction bout length has been recorded in primates (McKinney, 2014) and cetaceans (Senigaglia et al., 2016), the presence of tourists causes a greater number of take-offs in roosting fruit bats (Cardiff et al., 2012), while ungulates avoid waterholes where tourists have been (Wakefield and Attum, 2006).

2.2. *Time budgets*

An animal's time budget can indicate changes in maintenance or vigilance behaviour due to disturbance. Time budgets can therefore capture an animal's opportunity costs (e.g. less time spent foraging/feeding, resting, grooming, nursing/attending nest, engaging in social behaviour or play), increases in wariness/vigilance or locomotion, increased aggression with conspecifics, or expression of displacement 'comfort' behaviour (e.g. stereotypies, Burger and Gochfeld, 1993). Many studies record vigilance as a measure of wariness of animals towards disturbance. Vigilance can be evident as the animal stopping other activities, for example discontinuing foraging, showing alert, erect postures, or increased head and body turns (recorded for birds on nests). For example, caribou *Rangifer tarandus* spend more time vigilant in the presence of tourists on skis or snowshoes (Duchesne et al., 2000), while Magellanic Penguins *Spheniscus magellanicus* from colonies exposed to tourist activities showed fewer head turns than penguins from colonies with less human visitation (Villanueva et al., 2012).

2.3. *Physiological and breeding responses*

Disturbance through tourist activities can negatively influence an individual's physiological or physical state. An immediate physiological response to threat is the fight-or-flight response: a general stimulation of the sympathetic nervous system in response to perceived risk. For example, heart rate is influenced by stimulation of the sympathetic nervous system as well as circulating epinephrine (adrenalin) levels. Heart rate telemetry using dummy eggs on nests revealed elevated heart rates for penguins exposed to a 'benign' human presence (e.g. Ellenberg et al., 2013). Significant increases in heart rate would cause increased energy expenditure even if there was no overt behavioural reaction to the disturbance evident.

The hypothalamic-pituitary-adrenal (HPPA) axis is part of the vertebrate neuroendocrine system that responds over a longer time period to stress, and circulating hormones of the HPPA axis – adrenocorticotropic hormone (ACTH) or glucocorticoids – are often used as markers for physiological stress in animals. For example, tourist trips to see hoatzin *Opisthocomus hoazin* in their breeding season can cause increases in corticosterone concentration in fledgling birds (Müllner, 2004), while groups of howler monkeys *Alouatta pigra* exposed to tourists show faecal cortisol concentrations around twice that of 'non-tourist' groups (Behie et al., 2010).

Stressed animals may divert energy reserves away from the immune system, and become immunocompromised, evident through immune challenge (humoral or cell-mediated), monitoring level of leukocytes (evident as changes in white blood cell parameters), or the ratio of heterophil to lymphocytes (Tarlow and Blumstein, 2007). Immune suppression can result in animals carrying higher numbers of pathogenic organisms and showing higher rates of parasite shedding. For example, wall lizards *Podarcis muralis* at tourist sites exhibit lower body condition, higher tick load, lower cell-mediated immune response, and reduced reproductive output (Amo et al., 2006). Southern stingrays *Dasyatis americana* at tourist sites display sub-optimal health: lower haematocrit, total serum protein concentrations, and oxidative stress (Semeniuk et al., 2009).

Impacts of tourist activities can also manifest as increased metabolic rates, reduced growth rates, impaired responses to injuries/healing wounds, reduced investment in rearing young, and reduced reproductive success. For example, visitors disturb birds by standing close to their nest for too long, causing delays in post-foraging landing and consequently reducing growth rate in chicks; Yellow-eyed Penguins breeding at sites with more tourist presence have lower chick fledging weights, and because survival is positively associated with mass at fledging, this suggests long term population consequences (McClung et al., 2004).

3. Methods – meta-analysis of past tourism studies

We reviewed studies that considered animals' reactions to tourists including recreational use of spaces occupied by animals (see PRISMA flow diagram; Supplementary material). We identified these studies through Google Scholar searches for key terms (e.g. 'ecotourism', 'tourism', 'ecotourist', 'tourist', 'ecotourism + wildlife', 'tourism + wildlife', 'wildlife + human') and then further searched for key term combinations such as 'ecotourism + FID', 'tourism + FID', 'ecotourism + wildlife (or specified taxon) + reproductive success' and other such iterations.

These search terms yielded returns of between 217 and 50,000 hits. We searched either all the returns or the first 10 pages (i.e. a minimum of 100 returns) and downloaded any papers that mentioned effects of tourism on animal behaviour, welfare, breeding etc., or differences between tourist and non-tourist sites. We excluded similar papers that were, for example, focussed on similar questions in urban areas, or hunting and non-hunting areas. This left us with approximately 300 papers which we reviewed in detail. Many studies on ecotourism do not measure impacts of both tourism with non-tourism within the same study and these papers were therefore discarded. Of those that do, where possible, data were extracted from text directly, re-calculated from data presented (e.g. standard deviation calculated from presentation of standard errors), or estimated from graphs using calipers. Finally, 102 published studies had empirical data for 38 categories of measures where Cohen's *d* effect size could be calculated.

We attributed a valence for each response measured (Table 1) such that negative *d* values indicated a negative impact of tourism (e.g. more avoidance responses, more time spent in negative valence behaviour, greater cortisol concentrations, etc.). For species-specific time budget and physiological responses, we relied on the author's interpretation of the valence of each measure. We grouped effect sizes together for common categories (Table 2) and calculated average effect sizes for each category for each study. We calculated an effect size for each different measure for each species because these would reveal different aspects of the animal's biology as well as different temporal scales of responses. For example, red blood cell parameters indicate oxygen-carrying capacity or dehydration, while white blood cell values represent immune function. Therefore, in part, these response categories can be considered independent measures. Where a number of responses were recorded within a study, we standardised for the valence of each (Table 1) and then averaged the valence-standardised effect sizes for each response category (Supplementary material Table S1). In addition to representing the averaged *d* values, for graphical presentation, we also categorised *d* values into categories indicating small $< |0.3|$, medium $|0.3|–|0.8|$, and large $> |0.8|$ effects.

We tested whether there were taxonomic or body size impacts on effect sizes by carrying out a mixed-model ANOVA with Class, Order, and Family as random factors and log(average body mass) as a covariate.

We noted where the author(s) had made a qualitative statement about the effect of tourist activities on their focal animal ('positive', 'negative', or 'neutral'/'not specified') (including interpretation presented by Steven et al., 2011). We also recorded whether the study made a spatial or temporal comparison.

4. Results and interpretation of studies

The 102 studies describe responses to tourist activities for 99 species. The majority were birds (48 species) and mammals (37 species), with few studies on other taxa: reptiles: 5 species, bony fish (Actinopterygii) 2 species, cartilaginous fish (Chondrichthyes): 7 species, invertebrate: 1 species (Supplementary data Table S1). The majority of studies recorded few response measures (mean 3.74 ± 5.93 SD response measures, median = 2, range 1–53), with a total of 490 raw response measures recorded across all studies. When averaged by 38 response categories (e.g. all nesting time budget behaviour grouped, Bouton et al., 2005), we had a total of 265 averaged effect sizes for further analyses (data given in Table S1).

Around half of the 102 studies (46%) compared between tourism and control sites, and 49% compared between time points; only five studies (5%) used both a temporal and spatial experimental design. There was an even split between temporal and spatial experimental designs for studies that recorded avoidance responses ($\chi^2_1 = 0.61$, $p = 0.435$) or time budgets ($\chi^2{}_1 = 2.64$, $p = 0.104$), but more studies recording physiological responses used a spatial experimental design ($\chi^2{}_1 = 6.96$, $p = 0.008$) (Fig. 1).

The three main response measures showed no significant difference in average effect sizes (Kruskal-Wallis test: $H_{2,n\,=\,157} = 2.52$ $p = 0.284$) (Table 2). Only few studies included measures across the three categories, and therefore there was little power to determine correlations between the response categories (avoidance responses vs. time budgets: $r_9 = 0.294$, $p = 0.3796$; avoidance responses vs. physiological responses: $r_7 = -0.202$, $p = 0.603$; time budgets vs. physiological responses: $r_6 = 0.587$, $p = 0.126$).

There was no significant effect of body mass or taxonomic classification level on overall averaged effect size (Table 2). There were differences in avoidance responses by taxonomic Order ($F_{14,51} = 2.85$, $p = 0.003$; Table 2, Fig. 2a). The majority of avoidance response measures in birds (all flighted species) were positive, indicating birds exposed to tourist activities allowed an approaching person to come closer before moving away (Table 3). By contrast, the majority of mammals showed behaviour that suggested they increased avoidance of tourism disturbance. The reptile and fish species we had data for demonstrated mixed responses. There were no clear body mass or taxonomic patterns for time budgets (Table 2); some stand out data (Fig. 2b) indicated nesting penguins (Sphenisciformes) show marked habituation to tourism in terms of reduced alert/vigilance behaviour, while turtles (Testudines) show marked reduction in foraging/feeding in response to the presence of swimmers/divers. There were no clear body mass or taxonomic patterns for physiological responses (Table 2); the majority of physiological data was captured for cetaceans (included

Table 1
Criteria for identifying a negative influence of tourist activities applied in this review. These criteria were identified a priori for comparison with empirical data.

Method of assessment	Criteria associated with negative valence
Avoidance responses	• Increased wariness evident for antipredator responses: ○ longer alert distance, longer FID, greater number of individuals fleeing, longer distance fled, more protean escape behaviour (e.g. path sinuosity), greater escape speed, longer latency to return/resume behaviour • More avoidance responses: ○ Greater depth of activity (marine species), shorter distance to cover maintained, decreased duration of encounter, avoidance of a particular site, reduced percent daytime activity, reduced residency (e.g. greater space use, home range area, distances from paths, fewer individuals present)
Time budgets	• More time spent in negative valence behaviour: ○ increased body movement/activity, locomotion, alert/vigilance (e.g. head raised, head turning), aggression (e.g. threatening or submissive behaviour) • Greater incidence of displacement behaviour ○ e.g. comfort grooming, sparring • Less time spent in positive valence behaviour: ○ foraging/feeding, inactive resting, social behaviour (e.g. sexual interactions, play, allo-grooming), grooming (self-grooming), nursing/attending nest
Physiological responses	• More negative physiological state: ○ increased heart rate, greater plasma glucocorticoid (cortisol/corticosterone) concentrations, increased metabolic rate (e.g. shorter inter-breath interval), mineral imbalance, more injuries or slower wound healing, changes in white blood cell or other blood parameters, greater parasite load • Reduced investment in growth and reproduction: ○ slower growth rates, reduced nest success/reproduction rate, smaller young, smaller body size/mass/condition

in Cetartiodactyla), penguins and turtles (Fig. 2c), with varying responses.

Avoidance responses (especially FID) are often recorded as measures of effects of tourist activities, with a multitude of measures measured across different studies in a consistent manner (Table 3). Immediate avoidance measures generally show outcomes that we have interpreted as having positive valence, with animals exposed to tourist activities allowing an approaching person to come closer before moving away (i.e. shorter AD, FID, and DF) or moving away more slowly (all positive d values; Table 3). Negative d values were recorded for medium term avoidance responses (i.e., distance to cover, depth of activity, latency to return/resume behaviour, duration of encounter, percent daytime activity). In the long term, there was a negative effect on the number of individuals remaining present, but an increase in residency, suggesting that there may be a smaller number of individuals that elect to remain for longer around tourist sites.

Time budget data showed varying impacts of tourist activities (Table 3). Animals generally spent less time spent immobile, resting, or foraging/feeding in the presence of tourist activities. However other time budget measures yielded ambiguous results (e.g. attending young or the nest $d = 0.00 \pm 0.39$, n = 5 studies), with increases in both intuitively positive valence behaviour (i.e. more grooming, comfort behaviour, social behaviour) as well as negative valence behaviour (i.e. more locomotion and aggression). Notably, there was an overall reduction in vigilance in response to exposure to tourism ($d = 0.26 \pm 1.81$, n = 12).

There was a smaller range of effect sizes for physiological measures than for avoidance responses or time budget data (Fig. 3c). Physiological measures were also more likely to show overall negative effects of tourist activities; the strongest negative effects were recorded for measures of injuries/healing wounds, energy balance (e.g. circulating levels of glucose, cholesterol, and triglycerides), nest success/reproductive rate, heart rate, blood parameters (red blood cells, haematocrit and proteins), and white blood cell counts (representing aspects of immune function). Notably, changes in body mass (e.g. growth rate in fledglings) ($d = -0.12 \pm 0.74$, n = 9), metabolic rate ($d = -0.04 \pm 0.54$, n = 9), glucocorticoids ($d = -0.03 \pm 0.74$, n = 10) and parasite load ($d = 0.13 \pm 0.42$, n = 3), showed little

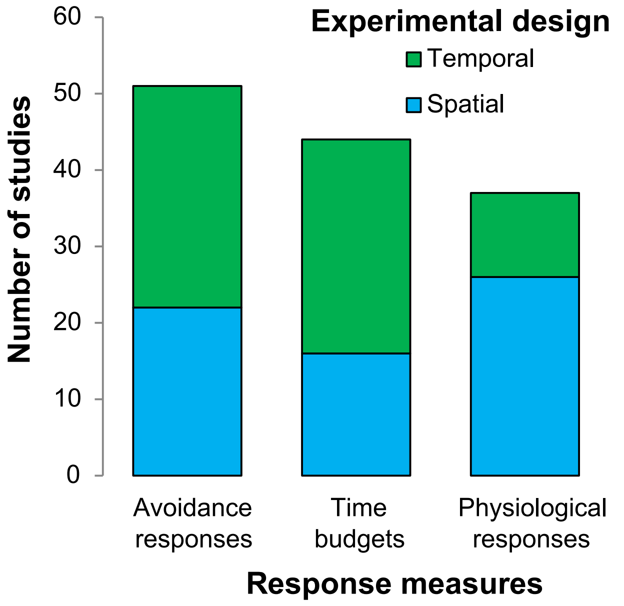

Fig. 1. Distribution of temporal or spatial study designs among the three categories of response measure. 102 published empirical studies are represented, although some studies used both temporal and spatial designs and are so are represented twice, or capture data on more than one species.

Table 2
Results of mixed-effects ANOVA testing for an effect of body mass and taxonomic level on responses to tourism impacts.

	Effect	Averaged d			a. Avoidance responses			b. Time budgets			c. Physiological responses		
			F	p		F	p		F	p		F	p
Log(avg. body mass)	Fixed	$F_{1,1}$	3.63	0.294	$F_{1,7}$	1.24	0.305	$F_{1,2}$	0.12	0.766	$F_{1.2}$	0.80	0.485
Taxon (Class)	Random	$F_{5,18}$	0.73	0.609	$F_{5,15}$	0.83	0.547	$F_{5,10}$	1.89	0.182	$F_{3,4}$	0.73	0.588
Taxon (Order)	Random	$F_{19,104}$	1.13	0.332	$\mathbf{F_{14,51}}$	**2.85**	**0.003**	$F_{9,32}$	0.73	0.682	$F_{10,22}$	1.18	0.354

Bold text indicates statistical significance.

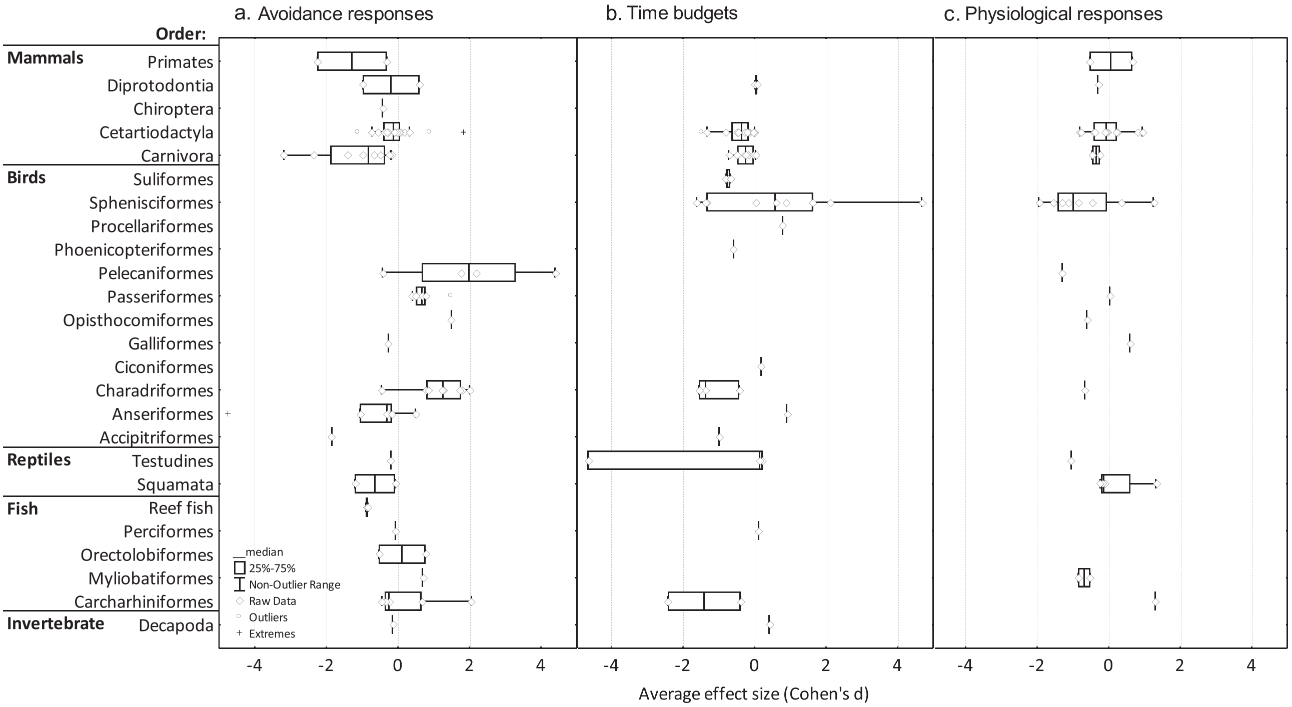

Fig. 2. Distribution of effect sizes for each of the three response measures. Diamonds represent the average effect sizes for each individual study (99 species from 102 published empirical studies).

pattern.

The majority of studies interpret their data as indicating a 'negative' influence of tourism, ecotourism, or recreation activities on wild animals (Table 4). Of the 480 measures where we could calculate effect sizes and the authors had made a clear indication of the valence of their results, 68% were interpreted by the authors as indicating negative responses, even though 31% of these actually showed positive valence *d* values. 23% of measures were interpreted as neutral, although we calculated positive *d* values for 37% of these measures. Only 9% of measures were interpreted by the authors as showing a 'positive' response to tourist activities.

5. Discussion

Most of the reported positive impacts of tourist activities focus largely on financial benefits, education and community awareness

Table 3

Summary results for 265 measures of animal responses towards tourist activities averaged for 38 response categories. Short term changes capture immediate responses by individuals towards disturbance, medium term changes reveal indirect changes, while long term responses reveal life-time changes for individuals or populations, and capture the greatest levels of ecological disturbance. Numbers are the average Cohen's *d* value (number of measures across studies) (see Table S1 for further detail).

Level of ecological disturbance →					
Response time **Immediate/direct responses**		**Medium term/indirect responses**		**Long term responses**	
Avoidance responses					
AD	0.79 (3)	Dist to cover	− 0.14 (2)	No. individuals present	− 0.8 (19)
FID	0.94 (25)	Depth of activity	− 0.2 (1)	Residency	0.22 (7)
Fleeing/not	− 1.18 (7)	Latency to return/resume behaviour	− 0.08 (4)		
DF	0.19 (8)	Duration of encounter	− 1.03 (3)		
Escape speed	0.11 (9)	Percent daytime activity	− 0.28 (3)		
Protean behaviour	− 0.28 (7)				
Time budgets					
Immobile	− 0.30 (8)	Foraging/feeding	− 0.56 (24)	Time at water surface	− 0.82 (2)
Locomotion	− 0.44 (16)	Grooming	0.17 (7)	Not at water surface	− 0.17 (3)
Alert/vigilance	0.26 (12)	Comfort behaviour	0.35 (5)	Nursing/attending nest	0.00 (5)
Vocalisation	0.31 (2)	Social behaviour	0.08 (9)		
Resting	− 0.68 (13)	Aggression	− 0.24 (12)		
		Play	− 0.53 (1)		
Physiological responses					
Heart rate	− 0.68 (5)	Mineral balance	0.09 (1)	Parasite load	0.13 (3)
Metabolic rate	− 0.04 (9)	Blood parameters	− 0.39 (2)	Body mass/size/condition	− 0.12 (9)
		WBC parameters (immune function)	− 0.37 (1)	Nest success/reproductive rate	− 0.77 (4)
		Injuries/healing wounds	− 1.74 (2)		
		Glucocorticoids	− 0.03 (10)		
		Energy balance	− 0.78 (2)		

Table 4

Comparison between the author(s) qualitative interpretation of their data and effect sizes for the same. Grey highlights where there is consensus between the author's interpretation and the valence of the data. Values are the count out of 300 measures reported across the studies reviewed.

			Authors' qualitative interpretation		
Interpretation of empirical data			Negative	Neutral	Positive
Negative effects	Large	$d < -0.8$	86	9	0
	Medium	$d = -0.3$ to -0.8	76	9	1
	Small	$d = 0$ to -0.3	64	28	2
Positive effects	Small	$d = 0$ to 0.3	43	24	11
	Medium	$d = 0.3$ to 0.8	30	27	13
	Large	$d > 0.8$	27	14	16

(Green and Higginbottom, 2000). By contrast, the effects of tourist activities on wildlife are more often reported as negative. However, we found that the negative interpretation of tourism activities is not always supported by empirical data: the majority of studies where we could extract effect sizes and valence show neutral or even positive effects (i.e. habituation) in animals towards human presence. The interpretation of response data needs to be carefully considered in light of an understanding of the type of measure recorded, the species' biology, and the context and environment within which such measures are collected. The valence of animal responses can also be ambiguous, as we noted for much of the time budget (e.g. comfort behaviours) and physiological data (e.g. mineral balance), and interpreting these responses require considerable knowledge of the species' biology. For example, understanding the relevance of expression of specific behaviour (e.g. sparring, head turning, stepping, Burger and Gochfeld, 1993) or changes in white blood cell populations (Semeniuk et al., 2009) is required to allocate a valence to these measures.

5.1. Avoidance responses

Reduced flight response of animals through habituation to tourists is the general response across reviewed studies, particularly in flighted birds. Flight in response to being approached by a person incurs energetic and opportunity costs for the animal; animals should therefore modulate their flight responses according to perceived risk (Ydenberg and Dill, 1986). This pattern of reduced flight response is therefore likely to reflect habituation towards humans to reduce energetic and opportunity costs incurred through unnecessary flight, which has consequences for individual survival and reproduction fitness measures (Cooper and Blumstein, 2015). Only a few species appear to become sensitised to increased disturbance (e.g. Tarlow and Blumstein, 2007), mostly mammal species.

Modulation of flight responses can become so extreme that for many species living in relatively safe sites (such as predator-free islands), functional anti-predator behaviour is eliminated through selection. Animals living on islands become extremely tame, or 'predator-naïve', allowing close approach by people (e.g. Blumstein and Daniel, 2005). This makes island species particularly appealing targets for nature-based tourism ventures, where some species will accept hand-feeding or even tolerate being touched (e.g. Hines, 2011; Worrell et al., 2016).

5.2. Time budgets

Time budgets reveal important information about how an animal spends its time and how this can be influenced by tourist activity. We found contradictory evidence for the prediction that animals would spend more of their time in behaviour identified as negative for their overall welfare and less time in maintenance behaviour. This may indicate either that time budgets are often not sufficiently sensitive to detect responses to increased disturbance, or that there are issues with interpretation of the valence of specific behaviour. Time budgets can also be influenced by provisioning of animals, with an abundance of food resulting in decreased foraging times (Saj et al., 1999) and therefore more time to allocate to other behaviour, further complicating interpretation of time budget responses. Most notably, there was an overall reduction in vigilance in response to exposure to tourism, with many species that are regularly visited showing decreased vigilance (e.g. Villanueva et al., 2012).

Time budgets appear to be highly context- and species-specific, limiting the interpretation of comparisons. For example, consider species that differ in diet, activity patterns, or mobility. Determining the valence of specific behaviours can also be reasonably subjective; e.g. some authors consider standing/immobility as a negative response, when it could also reflect a positive or neutral response such as resting or inactivity (e.g. Wheeler et al., 2013).

5.3. Physiological and breeding responses

Empirical data for physiological responses is clearly of importance for understanding long-term consequences of tourist activities on animal populations. Physiological measures, such measures of injuries/healing wounds, energy balance (e.g. circulating levels of glucose, cholesterol, and triglycerides), heart rate, blood parameters (red blood cells, haematocrit and proteins), and white blood cell counts (representing aspects of immune function) offer the greatest capacity to interpret the valence of behavioural responses, while longer term responses, such as nest success/reproductive rate and population survival, are important measures of ultimate fitness consequences. The majority of physiological studies reviewed demonstrated negative effects of tourist activities on animals, although we note that the range of responses was much smaller than that for behavioural measures (Fig. 3), likely because physiological responses generally function within parameters as animals seek to maintain homeostasis.

Glucocorticoids have been considered a useful measure of stress in animals; however, glucocorticoids respond to a myriad of short and long term changes within the animal's body, only some of which are relevant to the reason they are being measured. Immunocompetence has rarely been used as a measure of animal responses towards tourist activities. Reproductive success is another important measure of a species' ultimate fitness. Carney and Sydeman (1999) reviewed 64 investigations concerning effects of human disturbance on nesting waterbirds and concluded that although most studies found significant negative effects on physiology, reproductive behaviour, reproductive success, and population trends of waterbirds, these effects were not always substantiated when careful measures and empirical data were collated. Similarly, we found empirical data on reproductive success for only four species for inclusion in this review.

6. Future approaches to understanding animal responses to tourist activities

In carrying out this review, it was clear that methods used by researchers substantially influence their conclusions regarding whether tourist activities are perceived as benign or not. Wildlife responses to disturbance from tourist activities can be influenced by a range of factors (Hammitt and Cole, 1998) that require consideration at the time of measurement:

6.1. Group size

Seeing and being able to interact with animals increases the willingness of tourists to contribute towards conservation (e.g. Tisdell and Wilson, 2001). Intuitively, large groups of animals are likely to optimise nature-based tourism experiences, increasing the chances of people seeing the animals, although few surveys of tourist satisfaction indicate large numbers of animals as an attraction (Van Der Merwe and Saayman, 2008). Many nature-based tourist interactions occur at sites where animals group for breeding purposes, because it is spectacular and one is more likely to see animals that do not move away from their

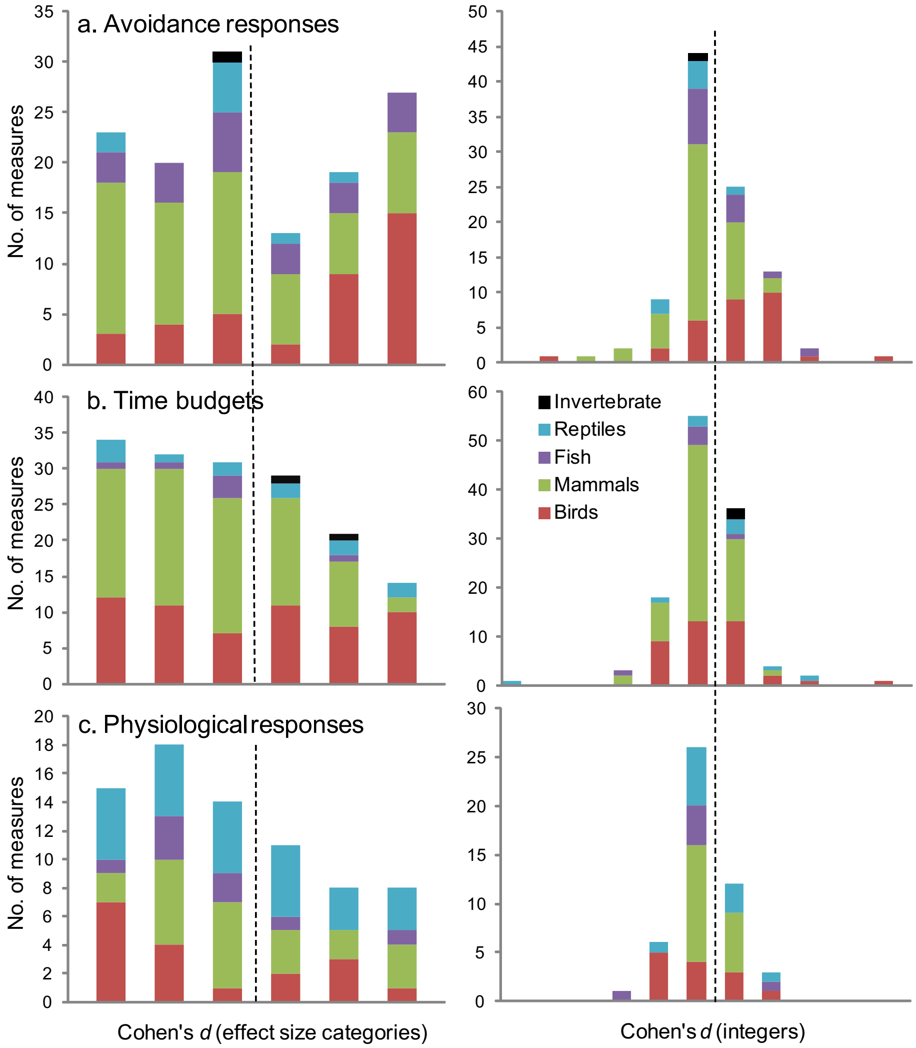

Fig. 3. Summary of effect sizes for 99 species (490 raw response measures from 102 published empirical studies) examining the effects of tourist activities on animal responses. Negative *d* values to the left of the dotted lines indicate negative effects of tourist activities; positive *d* values suggest positive effects (according to interpretation shown in Table 1). Left hand panel show the breakdown of studies according to Cohen's effect size categories (small < |0.3|, medium |0.3|–|0.8|, and large > |0.8| effects); right hand panel are integer values.

nest sites. However, animals are most vulnerable at this time due to the energetic requirements associated with raising young, the young or the parents are unable to move away from the disturbance, or the young show inappropriate responses to disturbance. Similarly, disturbance of groups of resting animals also causes them to increase energy consumption; for example, Indiana bats *Myotis sodalis* in winter hibernacula showed the greatest weight loss in caves with the most human visitation (Johnson et al., 1998).

Some have argued that animals are more robust to tourism disturbance when they are in larger groups (Newsome et al., 2001) because individuals may devote less time to vigilance through collective vigilance when in large groups (Blumstein and Daniel, 2003). However, group size can influence flight responses in different ways, confounding interpretation of group size effects. For example, degu *Octodon degus* display shorter FID in response to human approach when they are foraging socially (Lagos et al., 2009), while Yellow-legged gulls *Larus michahellis* are more reluctant to fly away when disturbed in dense nesting groups, presumably due to risk of nest predation by conspecifics if they move (Martínez-Abraín et al., 2008). Furthermore, in large groups, predator avoidance can be induced by the behaviour of other members of the group, before the predator is seen. This response has been termed the Trafalgar Effect (Treherne and Foster, 1981) and would be particularly problematic for tourism activities around flocks of resting birds (e.g. Fernández-Juricic et al., 2005). Analyses therefore need to account for size of observed animal groups and should not make assumptions about the direction of group size effects (Elgar, 1989).

6.2. Environmental factors - season, time of day and distance to protective cover

Environmental factors such as time of day, season, and distance to protective cover (e.g. Andersen et al., 2012) can also affect the perceived level of threat an animal feels in response to human or predator approach, and will influence results for the effects of tourist activities.

Daily and seasonal changes in physiological responses due to patterns of energy storage and mobilisation, as well as seasonal breeding patterns, influence an animal's responses to disturbance. Additionally, the influence of body size and sex of the animal influence their energy balance and therefore allocations towards responses. For example, flight responses (AD and FID) are often influenced by the time of day. Nocturnally-feeding animals, such as red kangaroos *Macropus rufus* and quokkas have shorter FID in the evening, before overnight foraging periods, possibly because intraspecific competition for food resources is greater and energy levels lower when the animals have not yet fed; by contrast, after a night of foraging, they have more energy to devote towards vigilance behaviour (Wolf and Croft, 2010; Worrell et al., 2016). Sanderlings *Calidris alba* on a Florida beach similarly had shorter FIDs and fled less often when feeding at night, with the longest FIDs at dusk (Burger and Gochfeld, 1991).

Seasonal breeding and nursing times have been correlated with increased vigilance levels and longer FID in some studies (Wolf and Croft, 2010), but shorter FID in other studies, possibly due to increased energy burdens associated with fleeing (Andersen et al., 2012; Blumstein et al., 2001). Seasonal differences in animal responses towards tourists can therefore reflect energy reserves and disturbing animals at times when they are more nutritionally-stressed might increase both their risk perception and the intensity of the negative influence.

The proximity to cover increases the level of disturbance for the animal and influences their responses to tourists. For example, Van der Zande et al. (1984) found a stronger effect of recreation on birds in open deciduous than closed conifer plantations, while Pierce et al. (1993) found approaching boats to be more disturbing to waterbirds in open water than for birds among reeds or other vegetation. Nature-based tourism relies on the animals being visible – making "elusive animals … susceptible to regular, proximate, and protracted human viewing" (Knight, 2009, p 167). Nature-based tourism therefore promotes construction of walkways, viewing platforms, etc. or eliminating the dense shrubbery or mature trees with hollow branches or more subtle cover requirements of many species in an effort to make the animals more visible (e.g. Guillemain et al., 2007). Hides reduce the impact of human presence on target animals, effectively making the observers invisible, thus reducing or negating the burden of monitoring for target animals, and intuitively should have the least impact.

6.3. Opportunity costs can outweigh benefits of leaving high-disturbance sites

Feeding animals is fairly common practice in many ecotourism ventures (Murray et al., 2016). Such activity can cause animals to move from areas of food availability in response to disturbance (e.g. Johnson et al., 2005), but where animals are provisioned, it can cause animals to congregate (e.g. Hodgson et al., 2004) and decrease foraging times (e.g. Saj et al., 1999). Being able to detect an effect of tourist activities through foraging behaviour can therefore be difficult.

The effects of human presence are not always overtly negative, and there are confounding effects of provisioning on different measures (Corcoran et al., 2013). Human refuse can subsidise high population densities, and rubbish dumps have been promoted as ecotourism sites for brown *Ursus arctos* and black bears *U. americanus* (Gunther, 1994), or spotted hyaenas *Crocuta crocuta* (Yirga et al., 2016). However, this provisioning also influences physiology, home range, sociality and breeding success of animals (Bateman and Fleming, 2012), which can have negative long term consequences (e.g. Beckmann and Lackey, 2008). For example, feeding the animals in close proximity is part of the attraction of shark ecotourism and influences species composition and depth of shark activity (Fitzpatrick et al., 2011; Meyer et al., 2009).

Grouping behaviour as a consequence of provisioning will also influence flight responses of animals and the detection of tourism impacts. Although shorter FID in a group situation may be due to a higher perceived level of safety (McNamara and Houston, 1992), it may also be a result of increased competition for food. High competition between conspecifics increases the opportunity cost an animal would face if it fled a resource-rich site in response to predator approach (Blumstein et al., 2002).

6.4. Experimental design

Measures appropriate for assessing the effect of tourist activities should ideally rely on remote monitoring. When the method requires that we capture and handle animals to collect data, we risk confounding the effects of tourist activities with the impact of the handling itself. The challenge will always be to measure physiology without influencing behaviour, as many physiological parameters require blood sampling and are therefore invasive and disruptive in their own right. Remote surveillance methods, such as recording heart rate through the use of 'dummy eggs' (Ellenberg et al., 2006) avoid the issues of animal handling and may therefore be a more robust measure of long-term stress responses. We found ambiguous results for analysis of faecal corticosterone, although this has been used in multiple studies previously (e.g. Behie et al., 2010) (but see Goymann, 2012 for caveats of sampling methods).

Study design is also an important consideration for future researchers. Studies that have compared animals at different sites (where tourists are present/absent) are subject to confounding site factors (e.g. cover, foraging resources, terrain) that influence outcomes of the study. Animals may also self-select to remain in proximity to high levels of disturbance, and therefore the personality mix across sites would not be the same (Worrell et al., 2016); since personality traits influence vulnerability to risks (e.g. Santos et al., 2015), this would affect survival. Finally, appropriate level of replication is often not achievable using a spatial experimental design. Studies that have compared animals from the same sites over time are more robust to confounding factors due to spatial heterogeneity. For example, there may be variation in numbers of tourists over time (e.g. Duchesne et al., 2000) that enables comparison between times with high and low levels of tourism: seasons (e.g. skiing season, summer tourism season at beach resorts etc.), weekends compared with week days (e.g. Stalmaster and Kaiser, 1998), or perhaps days when the site is closed to tourists. However, we note that these short-term changes would not be able to detect long-term patterns in animal responses and therefore there is a place for both spatial and temporal replication studies.

We were able to attribute all the studies for which we collected data under the three categories of measures we recorded, although there may be other measures that are appropriate to different contexts. Fluctuating asymmetry and mate choice could also act as indicators of long-term human disturbance (Tarlow and Blumstein, 2007), although we found no data for an effect of tourist activities on these measures. Other aspects of avoidance responses may also contribute valid information; for example for animals in groups, where it is difficult to record responses for a focal animal, 'responsiveness' (the proportion of a group responding to a stimulus; e.g. Blaxter et al., 1981), the proportion of animals moving in a particular direction, or 'response latency' (the interval of time between stimulus presentation and the first detectable movement) can be measured instead (reviewed by Fleming and Bateman, 2015).

7. Conclusions

Measuring the impact of tourist activities on wildlife is often hampered by the complex effects of such activities on animal responses. There may also be conflicting selection pressures, varying in intensity and direction, acting on animals as a consequence of the nature of the relationship between humans and animals at a particular site. For example, provisioning causes increased habituation to humans and alters the behaviour and physiology of animals. The nature of human interactions with animals may also vary across time, with benign observers of animals interspersed with extractive action, e.g. by hunters or fishers. Geffroy et al. (2015) argue that habituation through ecotourist activities can expose animals to potentially dangerous situations, creating a 'human shield' such that they will become susceptible to non-benign human activities and to predation by other species. Arlinghaus et al. (2015) point out that consumptive tourism such as hunting and fishing will have the opposite effect, resulting in a 'timidity syndrome' for target species, such as fish, where changes in escape behaviour (greater wariness) is a powerful indicator of fishing intensity or poaching (e.g. Januchowski-Hartley et al., 2013). Habituation in itself is therefore not necessarily benign or neutral, and "the widely held assumption that habituation has a positive or neutral outcome for animals can lead to inappropriate decisions about the threats human interactions pose to wildlife" (Bejder et al., 2009).

We clearly need objective empirical data to support conservation actions, with the valence of measures clearly identified a priori and not argued on a case by case basis. Where species are subject to tourist activities, these data are needed to ensure that we are aware of and can control for potential negative impacts. Steven et al. (2011) indicate that potential negative impacts of human behaviour on birds vary in duration, intensity, extent and timing, ranging from benign impacts at low levels of disturbance, to significant – potentially long-term – effects at high levels of human disturbance. We identified response measures that capture this range of animal responses towards tourist activities (Table 3), and which therefore vary in their capacity to capture different levels of ecological impact. We support Tarlow and Blumstein (2007) in concluding that there is no single optimal method to quantify anthropogenic stressors, and add that in addition to the precise goals and fiscal constraints of a project, the context, species, and level of temporal change to be measured are also considerations.

Although many studies conclude that there are negative effects of tourist activities on animal responses (e.g. Steven et al., 2011), our meta-analysis suggests that there is over-reporting of negative effects of tourist activities on wildlife species, with short-term responses (especially avoidance responses) suggesting capacity of some animals to cope with disturbance associated with tourism. Buckley et al. (2016) support the contention that tourist activities may be less problematic than feared, highlighting how benefits can outweigh impacts, with some threatened species showing extended survival times (expected time to extinction) as a consequence of tourism. Even if tourist activities have deleterious impacts on individual animals, they can have net positive impacts by providing revenue to support species and habitat conservation over extensive areas for long periods of time (e.g. Krüger, 2005; Wunder, 2000). Conservation in the presence of tourism requires empirical data for informed action, with appropriate assessment methods that capture relevant responses for the study species and take into account the context and environment being tested. Development and application of robust assessment methods, as well as long term monitoring of animal responses, is warranted, and broad application of such approaches may enable further comparison in the future.

Acknowledgements

Thanks to Curtin University and Murdoch University for funding support. We would also like to acknowledge Mr J. Treays for his continuing encouragement during manuscript preparation: "This isn't the way out, this is the way in".

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2017.05.003.

References

Amo, L., López, P., Martı, J., 2006. Nature-based tourism as a form of predation risk affects body condition and health state of *Podarcis muralis* lizards. Biol. Conserv. 131, 402–409.

Andersen, S.M., Teilmann, J., Dietz, R., Schmidt, N.M., Miller, L.A., 2012. Behavioural responses of harbour seals to human-induced disturbances. Aquat. Conserv. Mar. Freshwat. Ecosyst. 22, 113–121.

Arlinghaus, R., Alós, J., Klefoth, T., Laskowski, K., Monk, C.T., Nakayama, S., Schröder, A., 2015. Consumptive tourism causes timidity, rather than boldness, syndromes: a response to Geffroy et al. Trends Ecol. Evol. 31, 92–94.

Bateman, P.W., Fleming, P.A., 2011. Who are you looking at? Hadeda ibises use direction of gaze, head orientation and approach speed in their risk assessment of a potential predator. J. Zool. (Lond.) 285, 316–323.

Bateman, P.W., Fleming, P.A., 2012. Big city life: carnivores in urban environments. J. Zool. (Lond.) 287, 1–23.

Bateman, P.W., Fleming, P.A., 2014. Does human pedestrian behaviour influence risk assessment in a successful urban adapter? J. Zool. (Lond.) 294, 93–98.

Beckmann, J.P., Lackey, C.W., 2008. Carnivores, urban landscapes, and longitudinal studies: a case history of black bears. Hum.-Wildl. Conflicts 2, 168–174.

Behie, A.M., Pavelka, M.S.M., Chapman, C.A., 2010. Sources of variation in fecal cortisol levels in howler monkeys in Belize. Am. J. Primatol. 72, 600–606.

Bejder, L., Samuels, A., Whitehead, H., Finn, H., Allen, S., 2009. Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. Mar. Ecol. Prog. Ser. 395, 177–185.

Blaxter, J., Gray, J., Denton, E., 1981. Sound and startle responses in herring shoals. J. Mar. Biol. Assoc. UK 61, 851–870.

Blumstein, D.T., 2003. Flight-initiation distance in birds is dependent on intruder starting distance. J. Wildl. Manag. 67, 852–857.

Blumstein, D.T., 2006. Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. Anim. Behav. 71, 389–399.

Blumstein, D.T., Daniel, J.C., 2003. Foraging behaviour of three Tasmanian macropodid marsupials in response to present and historical predation threat. Ecography 26, 585–594.

Blumstein, D.T., Daniel, J.C., 2005. The loss of anti-predator behaviour following isolation on islands. Proc. Roy. Soc. Biol. Sci. 272, 1663–1668.

Blumstein, D.T., Daniel, J.C., McLean, I.G., 2001. Group size effects in quokkas. Aust. J. Zool. 49, 641–649.

Blumstein, D.T., Daniel, J.C., Ardron, J.G., Evans, C.S., 2002. Does feeding competition influence tammar wallaby time allocation. Ethology 108, 937–945.

Bouton, S.N., Frederick, P.C., Rocha, C.D., Barbosa Dos Santos, A.T., Bouton, T.C., 2005. Effects of tourist disturbance on Wood Stork nesting success and breeding behavior in the Brazilian Pantanal. Waterbirds 28, 487–497.

Buckley, R.C., Morrison, C., Castley, J.G., 2016. Net effects of ecotourism on threatened species survival. PLoS ONE 11 (2), e0147988. http://dx.doi.org/10.1371/journal.pone.0147988.

Burger, J., Gochfeld, M., 1991. Human activity influence and diurnal and nocturnal foraging of sanderlings (*Calidris alba*). Condor 93, 259–265.

Burger, J., Gochfeld, M., 1993. Tourism and short-term behavioural responses of nesting masked, red-footed, and blue-footed, boobies in the Galapagos. Environ. Conserv. 20, 255–259.

Cardiff, S.G., Ratrimomanarivo, F.H., Goodman, S.M., 2012. The effect of tourist visits on the behavior of *Rousettus madagascariensis* (Chiroptera: Pteropodidae) in the caves of Ankarana, northern Madagascar. Acta Chiropterol. 14, 479–490.

Carney, K.M., Sydeman, W.J., 1999. A review of human disturbance effects on nesting colonial waterbirds. Waterbirds 22, 68–79.

Cooper, W.E.J., Blumstein, D.T., 2015. Escaping From Predators: An Integrative View of Escape Decisions and Refuge Use. Cambridge University Press, Cambridge.

Corcoran, M.J., Wetherbee, B.M., Shivji, M.S., Potenski, M.D., Chapman, D.D., Harvey, G.M., 2013. Supplemental feeding for ecotourism reverses diel activity and alters movement patterns and spatial distribution of the southern stingray, *Dasyatis americana*. PLoS ONE 8, e59235.

Duchesne, M., Côté, S.D., Barrette, C., 2000. Responses of woodland caribou to winter ecotourism in the Charlevoix Biosphere Reserve, Canada. Biol. Conserv. 96, 311–317.

Duffus, D.A., Dearden, P., 1990. Non-consumptive wildlife-oriented recreation: a conceptual framework. Biol. Conserv. 53, 213–231.

Elgar, M.A., 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. Biol. Rev. 64, 13–33.

Ellenberg, U., Mattern, T., Seddon, P.J., Jorquera, G.L., 2006. Physiological and reproductive consequences of human disturbance in Humboldt penguins: the need for species-specific visitor management. Biol. Conserv. 133, 95–106.

Ellenberg, U., Mattern, T., Seddon, P.J., 2013. Heart rate responses provide an objective evaluation of human disturbance stimuli in breeding birds. Conserv. Physiol. 1 (cot013).

Fennell, D.A., 2015. Ecotourism, fourth ed. Routledge (Taylor & Francis Group), London and New York.

Fernández-Juricic, E., Jimenez, M.D., Lucas, E., 2001. Alert distance as an alternative measure of bird tolerance to human disturbance: implications for park design. Environ. Conserv. 28, 263–269.

Fernández-Juricic, E., Venier, M.P., Renison, D., Blumstein, D.T., 2005. Sensitivity of wildlife to spatial patterns of recreationist behavior: a critical assessment of minimum approaching distances and buffer areas for grassland birds. Biol. Conserv. 125, 225–235.

Fitzpatrick, R., Abrantes, K.G., Seymour, J., Barnett, A., 2011. Variation in depth of whitetip reef sharks: does provisioning ecotourism change their behaviour? Coral Reefs 30, 569–577.

Fleming, P.A., Bateman, P.W., 2015. Fish and amphibians. In: Cooper, W.E.J., Blumstein, D.T (Eds.), Escaping From Predators: An Integrative View of Escape Decisions and Refuge Use. Cambridge University Press, Cambridge (Chapter 6).

Geffroy, B., Samia, D.S.M., Bessa, E., Blumstein, D.T., 2015. How nature-based tourism might increase prey vulnerability to predators. Trends Ecol. Evol. 30, 755–765.

Gill, J.A., Sutherland, W.J., 2000. Predicting the consequences of human disturbance from behavioural decisions. In: Gosling, L.M., Sutherland, W.J. (Eds.), Behaviour and Conservation. Cambridge University Press, Cambridge, pp. 51–64.

Goymann, W., 2012. On the use of non-invasive hormone research in uncontrolled, natural environments: the problem with sex, diet, metabolic rate and the individual. Methods Ecol. Evol. 3, 757–765.

Green, R.J., Higginbottom, K., 2000. The effects of non-consumptive wildlife tourism on free-ranging wildlife: a review. Pac. Conserv. Biol. 6, 183–197.

Guillemain, M., Blanc, R., Lucas, C., Lepley, M., 2007. Ecotourism disturbance to wildfowl in protected areas: historical, empirical and experimental approaches in the Camargue, Southern France. Biodivers. Conserv. 16, 3633–3651.

Gunther, K.A., 1994. Bear management in Yellowstone National Park, 1960–93. In: International Conference of Bear Research and Management. 9. pp. 549–560.

Hammitt, W.E., Cole, D.N., 1998. Wildland Recreation: Ecology and Management, second ed. John Wiley, New York.

Hines, K.N., 2011. Effects of ecotourism on endangered northern Bahamian Rock Iguanas (*Cyclura cychlura*). Herpetol. Conserv. Biol. 6, 250–259.

Hodgson, A.J., Marsh, H., Corkeron, P.J., 2004. Provisioning by tourists affects the behaviour but not the body condition of Mareebe rock-wallabies (*Petrogale mareeba*). Wildl. Res. 31, 451–456.

Hunt, C.A., Durham, W.H., Driscoll, L., Honey, M., 2015. Can ecotourism deliver real economic, social, and environmental benefits? A study of the Osa Peninsula, Costa Rica. J. Sustain. Tour. 23, 339–357.

Januchowski-Hartley, F.A., Nash, K.L., Lawton, R.J., 2012. Influence of spear guns, dive gear and observers on estimating fish flight initiation distance on coral reefs. Mar. Ecol. Prog. Ser. 469, 113.

Januchowski-Hartley, F.A., Graham, N.A.J., Cinner, J.E., Russ, G.R., 2013. Spillover of fish naïveté from marine reserves. Ecol. Lett. 16, 191–197.

Johnson, S.A., Brack Jr., V., Rolley, R.E., 1998. Overwinter weight loss of Indiana bats (*Myotis sodalis*) from hibernacula subject to human visitation. Am. Midl. Nat. 139, 255–261.

Johnson, C.J., Boyce, M.S., Case, R.L., Cluff, H.D., Gau, R.J., Gunn, A., Mulders, R., 2005. Cumulative effects of human developments on Arctic wildlife. Wildl. Monogr. 160, 1–36.

Knight, J., 2009. Making wildlife viewable: habituation and attraction. Soc. Anim. 17, 167–184.

Krüger, O., 2005. The role of ecotourism in conservation: panacea or Pandora's box? Biodivers. Conserv. 14, 579–600.

Lagos, P., Meier, A., Tolhuysen, L., Castro, R., Bozinovic, F., Ebensperger, L., 2009. Flight initiation distance is differentially sensitive to the costs of staying and leaving food patches in a small-mammal prey. Can. J. Zool. 87, 1016.

Liao, J., Blumstein, D.T., Libby, S., Geist, C., 2005. Does intruder group size and orientation affect flight initiation distance in birds? Anim. Biodivers. Conserv. 28, 69–73.

Lovelock, B., 2007. Tourism and the Consumption of Wildlife: Hunting, Shooting and Sport Fishing. Routledge.

Martínez-Abraín, A., Oro, D., Conesa, D., Jiménez, J., 2008. Compromise between seabird enjoyment and disturbance: the role of observed and observers. Environ. Conserv. 35, 104–108.

McClung, M.R., Seddon, P.J., Massaro, M., Setiawan, A.N., 2004. Nature-based tourism impacts on yellow-eyed penguins *Megadyptes antipodes*: does unregulated visitor access affect fledging weight and juvenile survival? Biol. Conserv. 119, 279–285.

McKinney, T., 2014. Species-specific responses to tourist interactions by white-faced capuchins (*Cebus imitator*) and mantled howlers (*Alouatta palliata*) in a Costa Rican wildlife refuge. Int. J. Primatol. 35, 573–589.

McLeod, E.M., Guay, P.-J., Taysom, A.J., Robinson, R.W., Weston, M.A., 2013. Buses, cars, bicycles and walkers: the influence of the type of human transport on the flight responses of waterbirds. PLoS ONE 8, e82008.

McNamara, J.M., Houston, A.I., 1992. Evolutionary stable levels of vigilance as a function of group size. Anim. Behav. 43, 641–658.

Meyer, C.G., Dale, J.J., Papastamatiou, Y.P., Whitney, N.M., Holland, K.N., 2009. Seasonal cycles and long-term trends in abundance and species composition of sharks associated with cage diving ecotourism activities in Hawaii. Environ. Conserv. 36, 104–111.

Miller, S.G., Knight, R.L., Miller, C.K., 2001. Wildlife responses to pedestrians and dogs. Wildl. Soc. Bull. 29, 124–132.

Müllner, 2004. Breeding Ecology and Related Life-history Traits of the Hoatzin, *Opisthocomus hoazin*, in a Primary Rainforest Habitat. Universität Würzburg.

Murray, M.H., Becker, D.J., Hall, R.J., Hernandez, S.M., 2016. Wildlife health and supplemental feeding: a review and management recommendations. Biol. Conserv. 204, 163–174.

Newsome, D., Moore, S.A., Dowling, R.K., 2001. Natural Area Tourism: Ecology, Impacts and Management. Channel View Publications, Sydney.

Picard, D., 2015. Making ecotourism sustainable: refocusing on economic viability. Lessons learnt from the “regional strategic action plan for coastal ecotourism development in the South Western Indian Ocean”. J. Sustain. Tour. 23, 819–837.

Pierce, G.J., Spray, C.J., Stuart, E., 1993. The effect of fishing on the distribution and behaviour of waterbirds in the Kukut area of Lake Songkla, Southern Thailand. Biol. Conserv. 66, 23–34.

Rode, K.D., Farley, S.D., Fortin, J., Robbins, C.T., 2007. Nutritional consequences of experimantally introduced tourism in brown bears. J. Wildl. Manag. 71, 929–939.

Saj, T., Sicotte, P., Paterson, J.D., 1999. Influence of human food consumption on the time budget of vervets. Int. J. Primatol. 20, 977–994.

Santos, C.D., Cramer, J.F., Pârâu, L.G., Miranda, A.C., Wikelski, M., Dechmann, D.K.N., 2015. Personality and morphological traits affect pigeon survival from raptor attacks. Sci. Report. 5.

Semeniuk, C.A.D., Bourgeon, S., Smith, S.L., Rothley, K.D., 2009. Hematological differences between stingrays at tourist and non-visited sites suggest physiological costs of wildlife tourism. Biol. Conserv. 142, 1818–1829.

Senigaglia, V., Christiansen, F., Bejder, L., Gendron, D., Lundquist, D., Noren, D.P., Schaffar, A., Smith, J.C., Williams, R., Martinez, E., 2016. Meta-analyses of whale-watching impact studies: comparisons of cetacean responses to disturbance. Mar. Ecol. Prog. Ser. 542, 251–263.

Stalmaster, M.V., Kaiser, J.L., 1998. Effects of recreational activity on wintering bald eagles. Wildl. Monogr. 137, 3–46.

Steven, R., Pickering, C., Castley, J.G., 2011. A review of the impacts of nature based recreation on birds. J. Environ. Manag. 92, 2287–2294.

Tarlow, E.M., Blumstein, D.T., 2007. Evaluating methods to quantify anthropogenic stressors on wild animals. Appl. Anim. Behav. Sci. 102, 429–451.

TIES, 2015. ed. T.I.E. Society.

Tisdell, C., Wilson, C., 2001. Wildlife-based tourism and increased support for nature conservation financially and otherwise: evidence from sea turtle ecotourism at Mon Repos. Tour. Econ. 7, 233–249.

Treherne, J.E., Foster, W.A., 1981. Group transmission of predator avoidance behaviour in a marine insect: the Trafalgar effect. Anim. Behav. 29, 911–917.

Van Der Merwe, P., Saayman, M., 2008. Travel motivations of tourists visiting Kruger National Park. Koedoe 50, 154–159.

Van der Zande, A.N., Berkhuizen, J.C., Van Latesteijn, H.C., Ter Keurs, W.J., Poppelaars, A.J., 1984. Impact of outdoor recreation on the density of a number of breeding bird species in woods adjacent to urban residential areas. Biol. Conserv. 30, 1–39.

Villanueva, C., Walker, B.G., Bertellotti, M., 2012. A matter of history: effects of tourism on physiology, behaviour and breeding parameters in Magellanic penguins (*Spheniscus magellanicus*) at two colonies in Argentina. J. Ornithol. 153, 219–228.

Wakefield, S., Attum, O., 2006. The effects of human visits on the use of a waterhole by endangered ungulates. J. Arid Environ. 65, 668–672.

Wearing, S.L., Cunningham, P.A., Schweinsberg, S., Jobberns, C., 2014. Whale watching as ecotourism: how sustainable is it? Cosmopolitan Civ. Soc. 6, 38–55.

Wheeler, M., de Villiers, M.S., Altwegg, R., 2013. Effect of human disturbance on the behavioural responses and offspring survival of grey-headed albatrosses *Thalassarche chrysostoma* at Subantarctic Marion Island. Afr. J. Mar. Sci. 35, 533–543.

Wolf, I.D., Croft, D.B., 2010. Minimizing disturbance to wildlife by tourists approaching on foot or in a car: a study of kangaroos in the Australian rangelands. Appl. Anim. Sci. 126, 75–84.

Worrell, T., Admiraal, R., Bateman, P.W., Fleming, P.A., 2016. Are tourism and conservation compatible for ‘island tame’ species? Anim. Conserv. http://dx.doi.org/10.1111/acv.12301.

Wunder, S., 2000. Ecotourism and economic incentives—an empirical approach. Ecol. Econ. 32, 465–479.

Ydenberg, R.C., Dill, L.M., 1986. The economics of fleeing from predators. Adv. Study Behav. 16, 229–249.

Yirga, G., Leirs, H., De Iongh, H.H., Asmelash, T., Gebrehiwot, K., Deckers, J., Bauer, H., 2016. Spotted hyena (*Crocuta crocuta*) concentrate around urban waste dumps across Tigray, northern Ethiopia. Wildl. Res. 42, 563–569.