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Determinants of uncertainty in wildlife responses to human disturbance

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ABSTRACT

Outdoor recreation is increasing in intensity and space. Areas previously inaccessible are now being visited by ever-growing numbers of people, which increases human–wildlife encounters across habitats. This has raised concern among researchers and conservationists as, even in non-aggressive encounters, animals often perceive humans as predators and mount physiological and behavioural responses that can have negative consequences. However, despite all the research in recent decades, not many general patterns have emerged, especially at the level of populations, and many studies have yielded seemingly contradictory or inconclusive results. We argue that this is partly due to incomplete knowledge of the number and complexity of factors that may modulate the responses of animals. Thus, we aim to provide a conceptual approach intended to highlight the reasons that make it difficult to detect general patterns. We present a comprehensive compilation of factors modulating animal responses to humans at increasing levels (from sensory detection and immediate behavioural and physiological reactions, to changes in fitness and population trends), which may help understanding the uncertainty in the patterns. We observed that there are many modulating factors, which can be categorized as reflecting characteristics of the recreational activity itself (e.g. intensity of human presence), of the animals concerned (e.g. age or antipredatory strategy), and of the spatio-temporal context (e.g. habitat or timing of the encounter). Some factors appear to have non-linear and complex effects, which, if not considered, may lead to erroneous conclusions. Finally, we conclude that the difficulty in finding general patterns will be amplified at higher levels (i.e. at the level of populations), since as we proceed from one level to the next, the number of potential modulating factors accumulates, adding noise and obscuring direct associations between recreation and wildlife. More comprehensive knowledge about which (and how) factors affect animal responses across levels will certainly improve future research design and interpretation, and thus, our understanding of human recreational impacts on wildlife.

Key words: human disturbance, recreational activities, vertebrates, adrenocortical response, flight initiation distance, stress response, survival, reproduction, spatial use, population growth.

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I. INTRODUCTION

Outdoor recreational activities have increased dramatically over the past decades (Boyle & Samson, 1985; Balmford *et al.*, 2009). Natural habitats and species that remained relatively undisturbed in the past are now being visited by an ever-increasing number of tourists (Balmford *et al.*, 2009; Buckley, 2009; Carney & Sydeman, 1999). The development of technologies and transportation has allowed humans to reach areas that were previously inaccessible to most people, such as Antarctica, underwater habitats, or rainforests (Sinclair & Jayawardena, 2010; Tisdell, 2010; Ríos-Jara *et al.*, 2013). This trend, together with the ever-decreasing amount of 'natural' areas, calls for a deeper understanding of the effects that human–nature interactions may impose on wildlife species around the world (Buckley, 2004*b*; Bejder, 2005; Arlettaz *et al.*, 2007; Price, 2008). Many authors have investigated various responses of animals to human disturbance; however, most have focused on single species or on single locations (van der Zande & Vos, 1984; Harper & Eastman, 2000; Bolduc & Guillemette, 2003; Thiel *et al.*, 2008). Most studies measured changes in behaviour or hormones as a direct response to human disturbance without further investigating possible consequences for demographic rates, population size or species resilience (Gill, Norris & Sutherland, 2001; Stankowich & Blumstein, 2005; Breuner, Patterson & Hahn, 2008; Bonier *et al.*, 2009).

Despite the interest and concern directed towards this subject in the last few decades, not many general patterns have emerged. The findings to date are often inconclusive or in disagreement, especially concerning consequences of human disturbance for animal fitness parameters or population trends (Burger, Gochfeld & Niles, 1995; Price, 2008; Bonier *et al.*, 2009). We suggest that this difficulty in finding patterns is in part due to an incomplete understanding of the mechanisms linking animal responses to human disturbance and, perhaps more importantly, to insufficient knowledge of the factors modulating the response mechanisms. We also suggest that these factors sometimes modify animal responses to disturbance in complex non-linear ways that have been largely overlooked. Moreover, the combined effect of several modulating factors could largely obscure the effects of human activities. Therefore, to obtain a better insight into the effect of human recreational activities on wildlife, a comprehensive understanding of the modulating factors is necessary. Our objective in this review is to present an overview of the modulating factors and mechanisms that underlie responses of wildlife to encounters with humans at multiple levels of complexity.

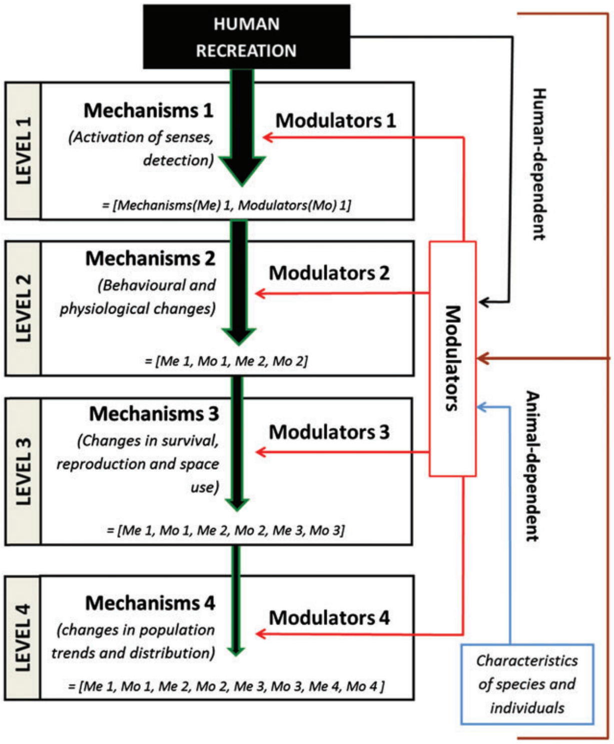

Fig. 1. Conceptual model showing the different levels in the process of interaction between recreationists and wildlife. The resultant responses of animals to human disturbance can be modulated by factors depending on the source of the disturbance (i.e. characteristics of human activity), on properties of the animal, and on the spatio-temporal context (e.g. habitat, climate, timing). Decreases in the width of the green/black arrows, as we go down the diagram, represent the dilution of the association between human disturbance and animal response, due to confounding effects of the accumulation of modulating factors across levels.

To do so, we present a conceptual scheme (Fig. 1) that integrates the different levels in human–wildlife interactions, beginning with detection of recreationists by animals, and followed by immediate physiological or behavioural responses, consequences at the level of individual fitness and habitat use, and subsequent impacts on populations or species. It is not our intention to describe exhaustively the mechanisms of response of disturbed animals (for that see, for example, Sapolsky, Romero & Munck, 2000; Romero, 2004; Bejder, 2005; Breuner *et al.*, 2008; Bejder *et al.*, 2009; Bonier, 2012), but rather to focus on factors that may alter the expected patterns of response. At each level we first present a synthesis of the mechanisms of response; we then identify factors that may modulate those mechanisms, and the type of effects they may cause (i.e. amplification or attenuation, in a linear or non-linear manner), according to what has been described, so far, in the literature (Table 1 and Fig. 2).

We classify the modulating factors into three different categories: (*i*) factors dependent on the humans themselves (e.g. number and frequency of people visiting an area or the nature of the recreational activity), (*ii*) intrinsic characteristics of the animals being disturbed, such as their antipredatory strategy or sex, and (*iii*) modulators depending on the spatio-temporal context in which the disturbance takes place (e.g. season, climate or habitat). Although the modulating factors and mechanisms act at specific levels, these levels are not independent of each other (Fig. 1).

Table 1. Summary of factors modulating animal responses to human recreation activities at different levels

Levels	Mechanisms	Modulators								
		Human			**Intrinsic**			**Spatio-temporal context**		
LEVEL 1[a]	Visual, hearing, olfactory activation	Size (e.g. human group size)	+	[1]	Sensory abilities (e.g. larger *versus* smaller species)	+	[2–4]	Time of day (changes in sensorial abilities and vigilance during the day)	A	[5–7]
		Colouration (conspicuity)[b]	+	[8–10]	Vigilance	+	[11–13]	Habitat characteristics (vegetation density and topography)	−	[14–16]
		Noise (volume)	+	[17,18]	Previous experience (i.e. learn to better recognize and be more vigilant)	+	[19–21]	Climate (cloud, rain, etc. reducing disturbance detection)	−	[22–24]
		Odour	+	[25–28]	Social aggregation	+	[13,29]	Relative position of disturbance to animal (e.g. perching height)	+	[30,31]
		Rate of movement	+	[32,33]						
		Proximity	+	[14,34]						
		Human			**Intrinsic**			**Spatio-temporal context**		
LEVEL 2[a]	Behavioural changes (Behav), physiological responses, i.e. corticosteroid reactivity (Cort), heart rate (HR)	Size (e.g. human group size)	+	[1,35]	Antipredator strategy: passive (hiding, crypticity) *versus* active (flushing, fighting)	B	[36–38]	Time of day (circadian, ultradian)	K	[39–42]
		Colouration (difference from animal)[b]	+	[10]	Previous experience (with humans and natural predators)	C	[37,43–49]	Time of year (e.g. breeding season, moulting)	L	[40,50–52]
		Noise (volume, type)	+	[18,53,54]	Cognitive aptitudes	−	[55]	Habitat characteristics (vegetation density)	−	[14,16,56–58]
		Speed of movement	+	[59,60]	Flushing performance[c]	D	[37,48,61–66]	Climate (i.e. direct effect of temperature)	−	[14,65]
		Proximity	+	[37,67]	Offspring value and parental care (as determined by, for example, mating system, breeding season length and survival rates)	E	[68–73]	Relative position of disturbance to animal (e.g. perching height)	−	[58,74–76]
		Directness of human approach and gaze	+	[59,60,77,78]	Social aggregation	F	[14,37,79–81]	Predation pressure	+	[82–84]
		Unpredictability	+	[34,85–87]	Mass-specific metabolic rates	+	[88]	Concomitant stressful events (e.g. extreme weather agonistic or predator encounters)	+	[89–92]

Table 1. Continued

Levels	Mechanisms	Modulators								
		Type (i.e. aggressiveness or similarity to predators, hearing *versus* seeing humans)	+	[25,93–95]	Sex and reproductive status (e.g. effects through sexual hormones)	G	[64,75,96–107]			
					Body condition (e.g. due to high density of conspecifics, poor habitat)	H	[72,108–110]			
					Coping style (due to selection, neonatal development, perinatal stress exposure, social rank, etc.)	I	[111–114]			
					Age (developmental)^d	J	[72,75,84,115–121]			
		Human			**Intrinsic**			**Spatio-temporal context**		
LEVEL 3	Decrease in reproduction, decrease in survival, space-use changes, chronic stress	Intensity (amount of visitors)	+	[122,123]	Social aggregation	M	[124–128]	Timing of the disturbance (e.g. periods of higher vulnerability of nest abandonment, HPA axis maturation)	+	[129–131]
		Frequency or continuity	+	[126,132–134]	Cognitive aptitudes (smarter animals will learn to recognize faster non-consumptive recreation activities, avoiding chronic stress)	–	[55,135]	Habitat quality (e.g. food availability, offspring concealment) and its value relative to alternative areas.	–	[43,136–138]
					Energetic constraints (limited compensation for disturbance-induced energy loss; e.g. migratory birds)	+	[118–120]	Predation pressure	+	[130,139]
					Body condition (body reserves to buffer negative effects of disturbance)	N	[43,138,140,141]	Climate (i.e. harsh weather and climatic conditions)	+	[129,142–144]
					Coping style (due to selection, neonatal development, perinatal stress exposure, social rank, etc.)	O	[43,90,145]			
					Previous investment in an area	P	[43,138]			
		Human			**Intrinsic**			**Spatio-temporal context**		
LEVEL 4	Decreases in demographic rates leading to population decreases, increased extinction risk and changes in distribution	Spatial and temporal scale	+	[146–148]	Life-history traits (e.g. a higher number of reproductive attempts, higher survival may compensate for negative medium-term responses)	–	[149–151]	Concomitant deterioration of habitat^e	+	[152–154]
		Ecological generality of the disturbance	Q	[155–158]	Site fidelity and philopatry (low plasticity or learning ability to avoid disturbed areas)	R	[159–162]	Concomitant changes in disturbance-independent factors (e.g. climate change, migration patterns, invasions overriding the effects of human disturbance)	T	[163–167]

Table 1. Continued

Levels	Mechanisms	Modulators		
		Social aggregation	+	[125,168]
		Density (through release from density-dependent negative effects)	−	[169–171]
		Meta-population dynamics (disturbed population is a source or a sink)	S	[172–174]
		Capacity to adapt (genetic/phenotypic variation, and phenotypic plasticity)[f]	−	[175–177]

Sign columns indicate the direction of the effect of a given factor. For the more complex effects a capital letter is assigned which corresponds to a graph in Fig. 2, depicting the shape of the relationship. We only included mechanism, effects and trends which have been already described in, suggested in, or emerge through combining, previous studies.

References: 1, Geist *et al.* (2007); 2, Jones *et al.* (2007); 3, Kiltie (2000); 4, Blumstein *et al.* (2004); 5, Amo *et al.* (2011); 6, Gordon *et al.* (2010); 7, Elbaz *et al.* (2013); 8, Cuthill *et al.* (2005); 9, Gomez & Thery (2007); 10, Gutzwiller & Marcum (1997); 11, Fernandez-Juricic & Schroeder (2003); 12, Blumstein (2006); 13, Beauchamp (2010); 14, Fernandez-Juricic *et al.* (2002); 15, Whittingham *et al.* (2004); 16, Lazarus & Symonds (1992); 17, Margalida *et al.* (2011); 18, Karp & Root (2009); 19, Utne-Palm (2001); 20, Kelley & Magurran (2003); 21, Knight & Knight (1986); 22, Martin (2011); 23, Hilton *et al.* (1999); 24, Carere *et al.* (2009); 25, Bates *et al.* (2007); 26, Fedosenko & Blank (2005); 27, Dupuch, Magnan & Dill (2004); 28, Roth *et al.* (2008); 29, Schaik *et al.* (1983); 30, Carlson (1985); 31, Moreno (1984); 32, Ewert *et al.* (2001); 33, Siegel (1972); 34. Miller *et al.* (2001); 35, Burger & Gochfeld (1991); 36, Espmark & Langvatn (1985); 37, Stankowich & Blumstein (2005); 38, Steen *et al.* (1988); 39, Llewelyn *et al.* (2010); 40, Romero & Remage-Healey (2000); 41, Sarabdjitsingh *et al.* (2012); 42, Tillmann (2009); 43, Bejder *et al.* (2009); 44, Müllner *et al.* (2004); 45, Ikuta & Blumstein (2003); 46, Rödl *et al.* (2007); 47, Bateman *et al.* (2014); 48, Ydenberg & Dill (1986); 49, Helfman (1989); 50, Stankowich (2008); 51, Riou *et al.* (2010); 52, Romero (2002); 53, Burger & Gochfeld (1998); 54, Waynert *et al.* (1999); 55, Lendvai *et al.*, 2013; 56, Camp *et al.* (2012); 57, Dill & Houtman (1989); 58, Tadesse & Kotler (2012); 59, Cooper (1997); 60, Bateman & Fleming (2011); 61, Iriarte-Diaz (2002); 62, Bishop (2005); 63, Losos (1990); 64, Braña (1993); 65, Cooper *et al.* (2009); 66, Møller *et al.* (2013); 67, Weston *et al.* (2012); 68, Bókony *et al.* (2009); 69, Breuner (2010); 70, Warner (1998); 71, Lendvai & Chastel, 2008; 72, Breuner *et al.* (2008); 73, Silverin & Wingfield (1998); 74, MacArthur *et al.* (1982); 75, Steidl & Anthony (1996); 76, Thiel *et al.* (2007); 77, Bateman & Fleming (2014); 78, Stankowich & Coss (2006); 79, Ramp *et al.* (2005); 80, Kikusui *et al.* (2006); 81, Pride (2005); 82, St Clair *et al.* (2010); 83, Januchowski-Hartley *et al.* (2011); 84, Berger *et al.* (2007); 85, Desire *et al.* (2002); 86, Boissy (1995); 87, Taylor & Knight (2003); 88, Jessop *et al.* (2013); 89, Romero *et al.* (2000); 90, Romero (2004); 91, Thaker *et al.* (2009*a*); 92, Thaker *et al.* (2010); 93, Martinetto & Cugnasse (2001); 94, González *et al.* (2006); 95, Gabrielsen & Smith (1995); 96, Cartledge & Jones (2007); 97, Solomon (2009); 98, Tilbrook *et al.* (2006); 99, Peczely (1979); 100, Wingfield & Sapolsky (2003); 101, Jiang *et al.* (2013); 102, O'Reilly & Wingfield (2001); 103, Irschick *et al.* (2005); 104, Torner & Neumann (2002); 105, Albrecht & Klvana (2004); 106, Malo *et al.* (2011); 107, Wynne-Edwards & Timonin (2007); 108, Beale & Monaghan (2004*a*); 109, Stillman & Goss-Custard (2002); 110, Moore & Jessop (2003); 111, Thaker *et al.* (2009*b*); 112, Atwell *et al.* (2012); 113, Schoech *et al.* (2011); 114, Carere *et al.* (2010); 115, Reeder & Kramer (2005); 116, Jacobsen (1979); 117, Wilcoxen *et al.* (2011); 118, Ingram (2000); 119, Walker, Boersma & Wingfield (2005); 120, Goutte *et al.* (2010); 121, Møller (2014); 122, Thiel *et al.* (2008); 123, Niles & Clark (1989); 124, Buckley (2004*b*); 125, Carney & Sydeman (1999); 126, Robert & Ralph (1975); 127, Burger (1988); 128, Serrano *et al.* (2004); 129, Buckley (2011); 130, Bolduc & Guillemette (2003); 131, Kapoor *et al.* (2006); 132, Wheeler *et al.* (2009); 133, Harper & Eastman (2000); 134, French *et al.* (2011); 135, Carrete & Tella (2011); 136, Lambert & Kleindorfer (2006); 137, Weidinger (2002); 138, Gill *et al.* (2001); 139, Gutzwiller *et al.* (2002); 140, Weimerskirch (1999); 141, Weimerskirch *et al.* (2002); 142, Martin & Wiebe (2004); 143, Cowles (1956); 144, Carr & Lima (2012); 145, Fowler (1999); 146, Finney *et al.* (2005); 147, Lima (1993); 148, Riffell *et al.* (1996); 149, Church *et al.* (2007); 150, Lima (2009); 151, Heppell *et al.* (2000); 152, Buckley (2004*a*); 153, Cole & Landres (1995); 154, Braunisch *et al.* (2010); 155, Møller (2012); 156, Hebblewhite *et al.* (2005); 157, Price (2008); 158, Skagen *et al.* (1991); 159, Yohannes *et al.* (2007); 160, Igual *et al.* (2007); 161, Stamps & Krishnan (1999); 162, Schlaepfer *et al.* (2002); 163, Foden *et al.* (2013); 164, Ozgul *et al.* (2010); 165, Schaefer, Jetz & Böhning-Gaese (2008); 166, Dextrase & Mandrak (2006); 167, Tablado & Revilla (2012); 168, Burger (1981); 169, Mallord *et al.* (2007); 170, Sinclair & Pech (1996); 171, McGowan *et al.* (2011); 172, Brawn & Robinson (1996); 173, Pulliam (1988); 174, Dias (1996); 175, Lande & Shannon (1996); 176, Carvalho (1993); 177, Dufty *et al.* (2002).

[a] In many cases previous research does not allow us to distinguish between the effects of human recreation on detection (level 1) from the effects on short-term behavioural/physiological response (level 2; see for example the human factor 'size' for which we cited the same reference). Nevertheless, when possible, we emphasized this difference. A good example is the intrinsic factor 'social aggregation'. A larger group size facilitates the detection of humans and other predators; however, the effect of group size on the decisions of the animals to flush away after detecting the disturbance is likely to be the opposite. Some authors have found that animals in larger groups show a lower physiological response to stressors and tolerate for longer the approaching human before flushing, when comparing alert distances, which we use as a proxy of detection, with flight initiation distance (FID). This could be due either to the dilution of risk in larger groups, or to group-dependent antipredator strategies, such as in some fish species. In any case at too large aggregation densities the pattern can start to reverse and increases in arousal and general stress could increase again in some species.

[b] Animals tend to see humans wearing bright/conspicuous colours earlier; however once detected the reaction of the animals towards those humans depends on their own coloration pattern. Some authors have shown that animals tolerate humans better when dressed in colours similar to their own.

[c] As the economics of fleeing predicts, animals should escape only when the cost of staying is greater than the cost of flushing away. In this line, animals with a lower ability to flush, such as gravid females or newborn individuals with reduced mobility, rely on crypsis/hiding and allow closer approach. As performance increases, FID also increases; however, FID decreases again in individuals whose escaping ability is much higher than the risk of staying (e.g. In some species, the better locomotor performance of adults, allows them to rely more on last-minute escaping strategies than in the case of juveniles of the same species).

[d] We chose to consider age using a developmental perspective and not directly as days after birth in order to take into account the differences in physiological maturation between altricial and precocial species (e.g. varying timing of the hypothalamic— pituitary— adrenal axis hyporesponsive period).

[e] It is important to understand the difference between direct effects of human presence (e.g. tourists visiting penguin colonies) and the additional anthropogenic effects through habitat deterioration (e.g. construction of roads or ski resorts).

[f] Adaptation to humans will be positive for a species, provided that it does not entail a concomitant relaxation of the anti-predator response to other non-human/real predators. Otherwise, excessive boldness may be counterproductive for the species.

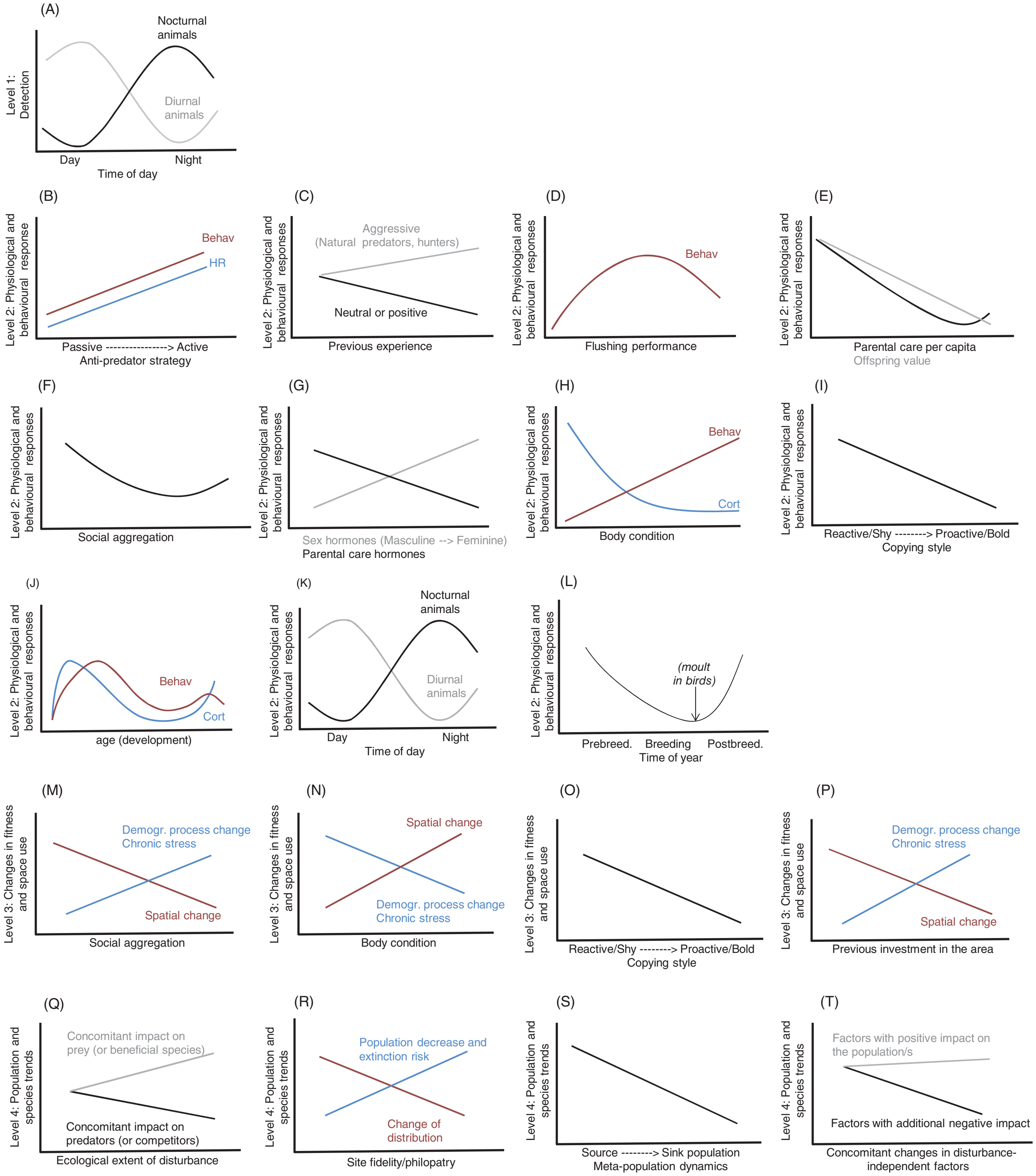

Fig. 2. Schematic representation of complex associations between detection or responses of animals to direct human presence and some modulating factors. Letters correspond to the relationship marked with the same letter in Table 1, where supporting references can be found. As in Table 1, we only included relationships that have been documented in, suggested in, or can be inferred from combining, the existing literature. Black and grey lines summarize the trends when all mechanisms within a given level respond similarly to a factor; coloured lines indicate mechanism-specific associations to a factor (e.g. specific physiological responses or behavioural responses within level 2). Cort = adrenocortical response; HR = heart rate; Behav = flushing/escaping distance; Demogr. = demographic.

That is, responses at a certain level will only happen if the responses at previous levels have already taken place (e.g. human disturbance can only have negative effects on demographic rates if animals detect people and react to them). This dependence on previous levels entails the accumulation of modulating factors across levels, which will generally lead to a weakening of the association between disturbance and animal responses at higher levels (see Fig. 1).

To support this conceptual model, we focus mainly on studies of the effects of human recreation on vertebrate species, especially birds, given the large representation of this taxon in the disturbance literature (e.g. Keller, 1996; Carney & Sydeman, 1999; Buckley, 2004*a*; Price, 2008; Steven, Pickering & Castley, 2011). We also used complementary literature from other fields, such as predation ecology, urban wildlife, or laboratory-induced stress (e.g. Lima, 1993; Møller, 2012; Elbaz *et al.*, 2013). Our approach focuses on disturbance caused by recreational activities with the least alteration of the habitat (such as people walking or cross-country skiing). In this way, we hope to extract the direct responses of animals to the presence of humans. Anthropogenic activities associated with substantial habitat modifications, such as the construction of tourist resorts or roads, will be assumed to amplify (i.e. modulate) the impact of recreationists, and are included, therefore, as modulating factors. We hope that the comprehensive overview given here about the scope and influence of modulating factors will serve to help future researchers identify variables that need to be taken into account in the design and interpretation of studies and, thereby, to provide a better understanding of the effect of recreational activities on wildlife.

II. LEVEL 1: SENSORY DETECTION OF HUMAN APPROACH

(1) Mechanisms

As suggested by previous research, wild species may perceive humans as predators (Frid & Dill, 2002; Beale & Monaghan, 2004*b*); however, for this to happen, animals must first detect them. What are the cues and mechanisms used by vertebrate animals to detect the presence of humans? Wildlife perceive humans (as well as predators) visually, auditorially, and olfactorially (Utne-Palm, 2001; Smith, Kane & Popper, 2004; Whittingham *et al.*, 2004; Bates *et al.*, 2007; Hagelin & Jones, 2007; Fernandez-Juricic *et al.*, 2012), although, as we will see later, the type and threshold of the sensory response will vary according to factors such as the intensity of the human signal, the taxon, and the environment. Detection of human presence is typically characterized by an immediate orienting reflex (also called 'alert' position) in which the animals cease their current activity (feeding, singing, etc.) and focus their senses on the anthropogenic stimulus, increasing vigilance to gather further information about the potential threat and assess the danger (Sokolov *et al.*, 1963; Gabrielsen, Blix & Ursin, 1985; Knight & Gutzwiller, 1995).

(2) Modulators

Many factors may modify the ability of animals to detect recreationists (Table 1 and Fig. 2). First, detection likelihood depends on the obviousness of the anthropogenic presence in itself, such as the number of people approaching, clothing colour (Cuthill *et al.*, 2005; Gomez & Thery, 2007), noise level (Karp & Root, 2009; Margalida *et al.*, 2011), odour (e.g. presence or absence of pet species) (Miller, Knight & Clinton, 2001; Bates *et al.*, 2007; Roth, Cox & Lima, 2008), distance (Miller *et al.*, 2001; Fernandez-Juricic, Jimenez & Lucas, 2002), and speed of movement (Siegel, 1972; Ewert *et al.*, 2001). That is, animals will more easily sense humans if they are in larger groups, conspicuously dressed, louder, smell stronger, and are moving fast or in close proximity.

Second, the intrinsic properties of the species and individuals being approached will also affect the likelihood of detection. Among these intrinsic characteristics are variation in sensory abilities (e.g. raptors have better vision than other bird species, larger animals have a larger range of detection than smaller ones) (Kiltie, 2000; Jones, Pierce & Ward, 2007), vigilance effort (which may vary with an individual's body condition or reproductive status) (Fernandez-Juricic & Schroeder, 2003; Beauchamp, 2010), previous experience (i.e. individuals may learn better to recognize human presence) (Utne-Palm, 2001; Kelley & Magurran, 2003), and degree of gregariousness (animals in larger social groups usually have a structured sentinel system leading to a higher overall vigilance level and probability of detection) (Schaik *et al.*, 1983; Beauchamp, 2010). The last category of factors influencing detection is related to the spatio-temporal context of human–wildlife interaction. For example, time of the day, habitat characteristics, weather conditions and relative position of the animal to the recreational activity will determine whether animals detect people or not. Time of day will influence not only light levels and other environmental characteristics that may influence the ability to detect humans, but also the level of awareness and sensory ability of animals (e.g. nocturnal animals have senses and activity patterns better adapted for night life while it is the opposite for diurnal species) (Gordon, Dickman & Thompson, 2010; Amo, Caro & Visser, 2011; Elbaz *et al.*, 2013). Characteristics of the habitat (i.e. vegetation density and pronounced topography), together with weather conditions, such as precipitation or fog, will also limit the detection ability of animals, as they may decrease visibility, odour and sound transmission (Lazarus & Symonds, 1992; Hilton, Ruxton & Cresswell, 1999; Fernandez-Juricic *et al.*, 2002; Whittingham *et al.*, 2004; Carere *et al.*, 2009; Martin, 2011). Finally, the position of people relative to the animal may also affect detection, that is, for instance animals resting/nesting high in trees may have a larger range of visibility than ground dwellers (Moreno, 1984; Carlson, 1985).

III. LEVEL 2: PHYSIOLOGICAL AND BEHAVIOURAL RESPONSES TO HUMAN PRESENCE

(1) Mechanisms

When human presence is detected, the sensory response (and the corresponding alert reflex) may be followed by a behavioural and physiological anti-predatory response (Gabrielsen & Smith, 1995; Berger *et al.*, 2007; Blumstein, 2010), depending on the degree to which human presence is perceived as a threat. Behaviourally, this reaction may be passive or active. That is, upon perception of a threat, an individual will evaluate the situation and respond accordingly by relying on staying still and not being seen (i.e. hide or freeze and remain cryptic) or by actively escaping from or fighting the threat (Lima & Dill, 1990; Lima, 1993; Bracha, 2004).

At the physiological level, there are almost instantaneous increases in the secretion of acetylcholine and catecholamines from the autonomic nervous system (Fisher, 1990; Knight & Gutzwiller, 1995; Sapolsky *et al.*, 2000; Romero & Butler, 2007), and corticotropin-releasing hormone (CRH) from the hypothalamus in the brain (Sapolsky *et al.*, 2000; Reeder & Kramer, 2005). These secreted substances contribute importantly to passive or active behavioural reactions by decreasing or increasing locomotion, cardiovascular activity, oxygen consumption, glucose mobilization, and body temperature (Fisher, 1990; Knight & Gutzwiller, 1995; Wingfield *et al.*, 1997; Sapolsky *et al.*, 2000). They also produce temporary interruptions of reproductive behaviour and appetite during stressful events (Sapolsky *et al.*, 2000; Wingfield & Sapolsky, 2003). Simultaneously, there is an activation of the immune system through the release of cytokines in preparation for potential injuries and infections (Wingfield *et al.*, 1997; Sapolsky *et al.*, 2000; Wingfield & Sapolsky, 2003; Romero, Dickens & Cyr, 2009).

In addition to its role in the immediate arousal reaction, the release of CRH triggers the slower adrenocortical stress response (Sapolsky *et al.*, 2000; Romero, 2004) through the activation of the hypothalamic–pituitary–adrenal (HPA) axis (or the homologous hypothalamic–pituitary–interrenal axis, depending on the vertebrate taxon) (Sapolsky *et al.*, 2000; Rollins-Smith, 2001; Øverli *et al.*, 2007; Gasser, Lowry & Orchinik, 2009; Wingfield, 2013). Thus, hypothalamic CRH promotes the secretion of adrenocorticotropic hormone (ACTH) from the pituitary gland (also called hypophysis) which in turn stimulates the adrenal cortex to increase production of corticosteroids (CORT; mainly cortisol in fish and most mammals and corticosterone in birds, reptiles, amphibians, and many rodents) (Sapolsky *et al.*, 2000; Romero, 2004; Reeder & Kramer, 2005). The stress-induced levels of CORT start to be detected in plasma a few minutes after disturbance and exert numerous effects throughout the body. These effects will depend on the abundance and distribution of CORT receptors in different organs (Bellingham, Sar & Cidlowski, 1992; Kapoor *et al.*, 2006; Crespi *et al.*, 2013; Lattin *et al.*, 2015) and the action of CORT binding globulins (a plasma protein that binds CORT with high affinity and can regulate CORT delivery and availability at specific sites) (Breuner & Orchinik, 2002; Malisch & Breuner, 2010; but see Schoech *et al.*, 2013).

CORT produces its effect through both rapid and delayed mechanisms (Sapolsky *et al.*, 2000; Gasser *et al.*, 2009). In the former case, CORT acts through non-genomic pathways and, in the course of minutes, induces changes in concentrations of monoamines (e.g. catecholamines) in some brain areas. It also alters brain cell excitability and activation that result in autonomic output and rapid changes in behaviour (Gasser *et al.*, 2009; Groeneweg *et al.*, 2011; Sarabdjitsingh, Joëls & De Kloet, 2012). The delayed effects, on the other hand, entail genomic processes, such as gene transcription and protein formation, and produce effects hours and days after the disturbance (Sapolsky *et al.*, 2000; Romero, 2004; Wingfield, 2013). All these effects of CORT serve to improve survival under threatening situations by redirecting energy and attention away from non-essential processes, to help the body to return to homeostasis after the perturbation is over, and to prepare the animal for subsequent stressors and energy expenditures (Wingfield & Sapolsky, 2003; Tarlow & Blumstein, 2007; Wingfield, 2013). In this sense, stress-induced CORT contributes to the inhibition of reproductive behaviour and physiology, the facilitation of locomotor responses, the enhancement of stress-related memory and learning, and the increase of energy availability (e.g. by promoting gluconeogenesis, fat and protein catabolism, and decreasing peripheral glucose uptake by non-essential tissues). CORT also acts to suppress stress-induced immune responses to prevent them from overshooting and to down-regulate the HPA axis itself through negative feedback (Sapolsky *et al.*, 2000; Gasser *et al.*, 2009; Breuner, 2010).

(2) Modulators

The physiological and behavioural responses to human presence will also be modulated by anthropogenic, intrinsic and context-dependent factors (Table 1 and Fig. 2). In regard to human-dependent factors, the perception of risk increases when animals are approached by people: (*i*) in large groups (Burger & Gochfeld, 1991; Geist *et al.*, 2007); (*ii*) wearing coloured clothing that differs markedly from the animal's colouration (Gutzwiller & Marcum, 1997); (*iii*) involved in activities that generate considerable noise (Burger & Gochfeld, 1998; Waynert *et al.*, 1999; Karp & Root, 2009); and (*iv*) engaged in activities characterized by rapid movements (Cooper, 1997; Bateman & Fleming, 2011). Perceived risk also increases when humans get closer to animals (Stankowich & Blumstein, 2005; Weston *et al.*, 2012), and move and look directly towards them (Cooper, 1997; Stankowich & Coss, 2006; Carter *et al.*, 2008; Bateman & Fleming, 2011, 2014). Predictability of the disturbance is another key factor to take into account. Animals are more distressed by recreationists appearing suddenly in an unpredictable way (Boissy, 1995; Miller *et al.*, 2001; Desire, Boissy & Veissier, 2002; Taylor & Knight, 2003). Activities that are more aggressive or similar to predation, such as consumptive recreation (e.g. hunting, capture, and handling), or presence of predator-like animals (e.g. dogs), will also influence animal risk assessment (Gabrielsen & Smith, 1995; Martinetto & Cugnasse, 2001; González *et al.*, 2006; Bates *et al.*, 2007; Bateman *et al.*, 2014). Some research has also shown that animals may be more reactive to the visual presence of humans than to anthropogenic noise (Gabrielsen & Smith, 1995).

Other modulating factors are the characteristics of the animals being approached (Table 1 and Fig. 2). For example, certain species have more passive antipredatory strategies, such as hiding and crypticity, while others opt for active strategies like flushing or fighting (Espmark & Langvatn, 1985; Steen, Gabrielsen & Kanwisher, 1988; Stankowich & Blumstein, 2005). Factors such as previous experience (Ikuta & Blumstein, 2003; Müllner, Eduard Linsenmair & Wikelski, 2004; Rödl *et al.*, 2007) and cognitive ability (Lendvai *et al.*, 2013) will also influence the way in which animals distinguish non-dangerous humans from real threats, affecting the response exhibited. Prior interactions with human activities or natural predation might increase stress responses in further encounters (i.e. sensitization of individuals exposed to hunting, noxious anthropogenic stimuli or high natural predation pressure) (Bejder *et al.*, 2009; Bateman *et al.*, 2014). However, human-induced stress response can be low when animals are naïve to predation risk due to the lack of natural predators or when individuals have been habituated to harmless anthropogenic stimuli (Ydenberg & Dill, 1986; Helfman, 1989; Bejder *et al.*, 2009). The ability to escape (flushing performance in Table 1 and Fig. 2D) may affect animal reactivity (Ydenberg & Dill, 1986; Losos, 1990; Iriarte-Diaz, 2002; Bishop, 2005; Møller, Vágási & Pap, 2013). That is, even if they perceive a high risk, animals with extremely poor flushing abilities (e.g. gravid females or newborn offspring) will rely on hiding, thereby showing reduced behavioural responses compared to animals better able to escape (Braña, 1993; Stankowich & Blumstein, 2005). However, animals with better flushing performance and/or fitter may be 'confident' of their ability to escape and, therefore may tolerate a closer approach, exhibiting a minimal behavioural response (Ydenberg & Dill, 1986; Cooper, Hawlena & Pérez-Mellado, 2009; Blumstein, 2010; Møller *et al.*, 2013).

The behavioural and physiological response of parents with dependent offspring have been shown to be less strong if the value of the offspring is high. Offspring value is high if there is little chance for the individual to reproduce again, and *vice versa*, which may depend, for example, on sex, mating system, survival likelihood (i.e. individual age and the chance of future reproduction), and environmental conditions (Silverin & Wingfield, 1998; Warner, 1998; Lendvai & Chastel, 2008; Bókony *et al.*, 2009; Breuner, 2010; Schmid *et al.*, 2013). Antipredator responses will also vary with social aggregation, which is expected to decrease the perceived danger by single individuals (i.e. risk dilution and coordinated defence strategies) at least up to a certain group size. However, at even larger group sizes this trend may switch, since the higher overall stress and lower arousal thresholds (e.g. more likely alarm calls) of highly dense groups may increase responsiveness (Fernandez-Juricic *et al.*, 2002; Pride, 2005; Ramp, Russell & Croft, 2005; Stankowich & Blumstein, 2005; Kikusui, Winslow & Mori, 2006). Other properties that may affect the physiological and psychological state of individuals, and therefore their stress response, are mass-specific metabolic rates (i.e. faster metabolism favours stress reactivity) (Jessop, Woodford & Symonds, 2013), sex and hormone profiles, body condition, coping style, and developmental age (i.e. from foetus to adults). Sex hormones and hormones involved in parental care play an important role in modulating the physiological and behavioural stress response. For example, oestrogens are related to higher adrenocortical reactivity, while prolactin reduces parental stress responses, thereby favouring offspring care and survival (Peczely, 1979; Steidl & Anthony, 1996; Tilbrook *et al.*, 2006; Wynne-Edwards & Timonin, 2007; Solomon, 2009; Malo, Acebes & Traba, 2011). Poor body condition (i.e. typical of high anxiety levels, high densities, or poor habitats) favours self-maintenance mechanisms, energy-saving behaviours and a higher adrenocortical response (Moore & Jessop, 2003; Beale & Monaghan, 2004*a*; Breuner *et al.*, 2008). Individuals may exhibit considerable variability in stress reactivity (i.e. the intensity and duration of their response to a given stressor). These variations in 'coping style' have both genetic and environmental influences, such as perinatal exposure to stressors and corticosteroids (Carere, Caramaschi & Fawcett, 2010; Schoech, Rensel & Heiss, 2011). The coping style will be reflected both in the behavioural and the physiological response to disturbance. That is, shyer individuals are generally more fearful and, thus, are likely to mount a higher adrenocortical response and flush (or hide) earlier than bolder individuals (Thaker, Lima & Hews, 2009*b*; Carere *et al.*, 2010; Atwell *et al.*, 2012). Physiological and behavioural responses to disturbance will vary non-linearly with developmental age. During early development, which occurs mostly prenatally (or in ovo) in precocial species and extends further into postnatal (or posthatch) life in altricial species, there is a hypo-responsive period of the HPA axis when CORT responses are low (Berger *et al.*, 2007; Breuner *et al.*, 2008; Wada & Breuner, 2010). This has been suggested to protect developing animals from the detrimental effects of high CORT levels, which could cause permanent alterations of the HPA axis, may cause damage to memory and cognitive functions, and reduce growth rates (Kitaysky *et al.*, 2003; Hayward & Wingfield, 2004; Breuner *et al.*, 2008; Rensel, Boughton & Schoech, 2010; Wada & Breuner, 2010). Later the HPA axis responsiveness increases and reaches relatively high levels during juvenile and early-adulthood periods. Some studies have shown that HPA reactivity may, to a certain degree, decrease again during adulthood (Table 1, Fig. 2J). That is, juvenile individuals and younger adults would show a higher adrenocortical response than experienced adults (Berger *et al.*, 2007; Breuner *et al.*, 2008; Wilcoxen *et al.*, 2011). With senescence; however, the trend appears to switch once more and the responsiveness of the HPA axis tends to increase (Goutte *et al.*, 2010; Wilcoxen *et al.*, 2011). Behavioural responses also often show a complex non-linear relationship with age (Table 1, Fig. 2J). Behavioural responses may be lower (more passive) in newborn and senescent individuals, due to locomotor and energetic limitations (Knight & Gutzwiller, 1995; Berger *et al.*, 2007; Seltmann *et al.*, 2012). At 'intermediate' ages, flushing responses will show a U-shaped relationship, with juvenile and older adults (but not senescent) age classes tending to escape earlier than middle-aged adults (Berger *et al.*, 2007; Seltmann *et al.*, 2012; Møller, 2014).

Animal responses to human activities can also vary depending on the spatio-temporal context (Table 1, Fig. 2). We observe that these responses often vary throughout the day and year (Fig. 2J, K), i.e. depending on circadian and circa-annual variations in physiology, activity and motivation (e.g. nocturnality *versus* diurnality, territory establishment *versus* moulting or migratory phase) (Romero & Remage-Healey, 2000; Stankowich, 2008; Tillmann, 2009; Llewelyn, Webb & Shine, 2010; Riou *et al.*, 2010). In addition, in recent years smaller-scale cycles have been described for at least some species, in which within a given daily cycle individuals experience ultradian HPA axis pulsatility (Sarabdjitsingh *et al.*, 2012). The stress response of a given individual will, thus, be time-specific and depend on the phase of the ultradian cycle when human disturbance occurs. Habitat characteristics will also affect reactions towards human presence, since apart from their effect on food availability, and thus, body condition, they differ in refuge availability for animals exposed to human recreation. Wildlife having options to hide or retreat to refuges (e.g. dense canopy, cavities or steep slopes), will 'feel' safer and react differently from individuals or species found in more open habitats and that have to traverse larger distances for protection (Lazarus & Symonds, 1992; Fernandez-Juricic *et al.*, 2002; Camp *et al.*, 2012; Tadesse & Kotler, 2012).

Weather can also directly affect animal behavioural responses. For example, higher ambient temperatures tend to increase an animal's 'tolerance' to approaching people, due to their faster capacity of reaction when warmer. In addition, animals may want to limit their stress responses to, to some extent, avoid excessive heat build-up due to stress-related increases in metabolism and movement (Fernandez-Juricic *et al.*, 2002; Cooper *et al.*, 2009). Other contextual factors that determine the psychological and physiological excitability of animals are the relative position of the animal to humans (e.g. animals 'feel' safer when located higher or closer to escape routes) (MacArthur, Geist & Johnston, 1982; Steidl & Anthony, 1996; Thiel *et al.*, 2007; Tadesse & Kotler, 2012), predation pressure (Berger *et al.*, 2007; St Clair *et al.*, 2010; Januchowski-Hartley *et al.*, 2011), and simultaneous stressful events, such as extreme weather or agonistic encounters with conspecifics (Romero, Reed & Wingfield, 2000; Romero, 2004). Increases in the latter two usually lead to high levels of awareness and baseline CORT that, in turn, may lower response thresholds to disturbance (Thaker, Lima & Hews, 2009*a*; Thaker *et al.*, 2010).

IV. LEVEL 3: IMPACTS OF RECREATIONAL ACTIVITIES ON FITNESS AND SPACE USE

(1) Mechanisms

If individuals respond behaviourally or physiologically to the presence of recreationists, their fitness (reproductive output and survival as proxies) and habitat use may be compromised. This can happen both through single disturbance events and through more continuous or frequent disturbances (Bowles, 1995; Knight & Gutzwiller, 1995; Wingfield *et al.*, 1997; Frid & Dill, 2002; Buckley, 2011). Regarding the negative effects of single disturbances on fitness, one of the most common cases is when parents are flushed, leaving eggs or newborn offspring unattended. The temporarily abandoned offspring or eggs may then be depredated, starve, or die from thermal stress (Ellison & Cleary, 1978; Anderson & Keith, 1980; Major, 1990; Buckley, 2011). Some predators may even specialize in this type of opportunistic hunting (Kury & Gochfeld, 1975; Strang, 1980; Knight & Cole, 1995). Disturbance-related single panic reactions may cause accidental self-injury or damage to conspecifics and progeny, thus decreasing survival and reproductive output (Bowles, 1995; Buckley, 2011). An understudied phenomenon is that single disturbance events during settling periods (e.g. dispersal and territory formation) might cause significant changes in habitat use or even lead to abandonment (Buckley, 2004*b*, 2011).

If disturbances are frequent or continuous, they may also cause negative effects through chronic stress (i.e. continuous activation of HPA axis and disruption of negative feedback, which impedes the return to basal CORT levels), longer-term changes in activity budget patterns, behaviour (e.g. movement patterns) and energy expenditure (Knight & Gutzwiller, 1995; Wingfield *et al.*, 1997; Frid & Dill, 2002; Romero, 2004). Note that this might not apply in cases in which habituation occurs [see Level 2 (Section III) for further information on the modulating effect of previous experience on animal responses to humans]. Chronic high levels of stress hormones can lead to infertility, an offspring sex-ratio biased towards the less costly sex, immunosuppression, weight and muscle loss, growth inhibition, damage to the central nervous system with accompanying impairment of cognitive functions, among others (Sapolsky *et al.*, 2000; Elenkov, 2004; Wikelski & Cooke, 2006; Breuner, 2010). Regularly disturbed areas may also be avoided or used only when humans are not present, altering spatial use and/or activity patterns (Tuite, Owen & Paynter, 1983; Pfister, Harrington & Lavine, 1992; Bejder *et al.*, 2006, 2009). This can lead to a shift in home range and displace wildlife into suboptimal habitats, either permanently or temporarily, with all the possible consequences for animal body condition and fitness (Olsson *et al.*, 2007; Paquet & Darimont, 2010; Kerley, Kowalczyk & Cromsigt, 2012). Finally, waste of energy, as a consequence of recurrent disturbance can lower body condition of animals and, in turn, compromise survival and reproduction, especially if it occurs during periods of high energetic needs, such as migration, harsh winter conditions, breeding or moult (Madsen, 1995; Buckley, 2004*b*; Barshep *et al.*, 2013).

(2) Modulators

The impact of human intrusion on fitness and habitat use will not be the same for all individuals and situations, but will be modified by the characteristics of the disturbance itself, the properties inherent to the species or individuals, and the circumstances around the disturbance event. Human recreation will tend to have a higher impact on breeding success, survival, habitat selection and/or chronic stress when it causes more frequent or intense behavioural or physiological responses. This is the case for animals in areas with frequent, continuous or intense human use (i.e. higher number of people using an area at the same time) and that fail to habituate to the disturbance (Robert & Ralph, 1975; Niles & Clark, 1989; Harper & Eastman, 2000; Thiel *et al.*, 2008; Wheeler, Villiers & Majiedt, 2009; French *et al.*, 2011).

The outcome of disturbance at this intermediate level will vary among species and individuals. Social aggregation may modulate the effects of disturbance, since gregarious species are more likely to suffer self-injury and injure conspecifics during panic behaviour (Robert & Ralph, 1975; Carney & Sydeman, 1999; Buckley, 2004*a*). The spatial response to human recreation will likely differ between gregarious and solitary taxa, since habitat selection of gregarious species will depend not only on characteristics of the habitat (and degree of disturbance) but also on group decisions and social attraction that might increase the reluctance to abandon a certain area (Burger, 1988; Serrano *et al.*, 2004). Higher cognitive ability will most likely also play an important role in helping animals to recognise quickly and, thus, habituate to non-dangerous human activities and reduce the likelihood of suffering chronic stress and decreased fitness (Carrete & Tella, 2011; Lendvai *et al.*, 2013). In addition, individual coping style may influence the speed of recovery after a stressful perturbation, leading to differences in long-term stress levels (Fowler, 1999; Romero, 2004; Bejder *et al.*, 2009). That is, animals with a more reactive HPA axis, i.e. generally shyer, possess less efficient negative feedback systems to facilitate the return of CORT to baseline levels and, as a result, will be more prone to suffer chronic stress.

As mentioned above, human disturbance causing increases in energy expenditure or decreases in food intake may lead to decreases in animal survival and reproduction, especially in periods of harsh weather conditions or during periods crucial for reserve accumulation (e.g. during premigratory staging) (Madsen, 1995; Buckley, 2004*b*; Barshep *et al.*, 2013). This will predominantly affect individuals and species that are energetically constrained, reducing their limited capacity to compensate for additional expenditures. An example of this are species which are limited by the capacity of their digestive tract (e.g. grouse species in winter feeding on coniferous needles) or performing costly activities (e.g. moulting, breeding) (Smith, 1976; Millar, 1978; Koteja, 1996; Sedinger, 1997). Other cases are, for instance, animals whose survival and reproduction depend on especially high rates of energy accumulation, such as long-distance migrating birds or animals storing energy for wintering (MacKinnon, 1972; Piersma, 1990). If their fuel deposition rate is lowered through human activities, their time schedule may be delayed, causing reproduction and survival to be compromised (Madsen, 1995; Buckley, 2004*b*; Klaassen *et al.*, 2006). Similarly, individuals in suboptimal condition (e.g. living in a suboptimal habitat, harsh climatic conditions, low social rank, and/or suffering from parasites or disease) will have a lower capacity to buffer the deleterious effects of acute or prolonged disturbances. These animals will not be able to compensate with additional broods after stress-induced failures or will produce smaller, more vulnerable offspring (Weimerskirch, 1999; Weimerskirch *et al.*, 2002). Interestingly, poor body condition may impede the abandonment of disturbed areas as only individuals with enough energy reserves will be able to search for new suitable habitat (Gill *et al.*, 2001; Bejder *et al.*, 2009). The degree of psychological and energetic investment in settling in a given area may also determine the willingness and likelihood of abandoning it after being disturbed by recreationists. The more an individual invests in an area, the less prone will it be to leave, even though this attachment may lead to chronic stress, since it will continue to be exposed to human visitation (Gill *et al.*, 2001; Bejder *et al.*, 2009).

Finally, timing and environmental characteristics will also influence the fitness and spatial consequences of human–wildlife encounters. For example, disturbance will have a higher impact on survival, reproduction and spatial use if it occurs during especially vulnerable moments (e.g. during territory establishment or when nestlings are small and more vulnerable to predation or to anxiety-induced HPA axis alterations) (Bolduc & Guillemette, 2003; Kapoor *et al.*, 2006; Buckley, 2011). Additionally, apart from the effect of habitat quality on body condition mentioned above, habitat quality may induce spatial-use changes, namely a trade-off between the quality of the current habitat and that of alternative areas. If alternative habitats are poor or not available, animals may be reluctant to abandon an area despite human activities (Gill *et al.*, 2001; Weidinger, 2002; Lambert & Kleindorfer, 2006; Bejder *et al.*, 2009). Relatively high predation pressure can also aggravate the detrimental effects of human activities (Gutzwiller, Riffell & Anderson, 2002; Bolduc & Guillemette, 2003). For example, human-induced momentary abandonment of offspring might have a higher impact in cases in which the number of predators and their probability of accessing the offspring are higher (e.g. ground breeding location *versus* trees or cliffs). Bad weather and harsh climate will also aggravate the impact of human disturbance on animal fitness. Difficult weather conditions will increase both the energetic expenditure associated with escaping and the likelihood of mortality of unattended and unprotected offspring (Cowles, 1956; Buckley, 2004*b*, 2011; Carr & Lima, 2012). Similarly, harsh climatic conditions will limit the capacity to compensate for the effects of disturbance, given that such conditions are usually associated with poorer body condition, lower resource availability, and shorter breeding seasons (Wingfield, 1984; Martin & Wiebe, 2004).

V. LEVEL 4: CONSEQUENCES OF HUMAN DISTURBANCE FOR ANIMAL POPULATIONS AND SPECIES

(1) Mechanisms

If human activities reduce the fitness of at least some individuals of a population and/or change their habitat use, population demographic processes (rates of reproduction, survival, immigration, and emigration) may be negatively affected. Thus, population growth rate may decrease and even reach negative values. This reduction in population growth rates may, in turn, result in reductions in population size, increased probability of local extirpation, and potential changes in distribution (Tuite *et al.*, 1983; Pfister *et al.*, 1992; Stevens & Boness, 2003; Bejder *et al.*, 2006; Gill, 2007; Lusseau & Bejder, 2007).

(2) Modulators

Even though the association between demographic processes and population growth seems straightforward, the final impact will vary depending on characteristics of the recreational activity, of the animals and of the context (Table 1, Fig. 2). Regarding recreational activity, both the spatial and temporal scale, as well as the pervasiveness of human disturbance will affect the fate of populations. That is, if the effect of disturbance is widespread throughout a larger portion of a population or species range, and/or occurs over long periods of the year, then we would expect greater decreases in population growth rate than if disturbance only affects a small part of the population locally or occurs only occasionally (Lima, 1993; Riffell, Gutzwiller & Anderson, 1996; Finney, Pearce-Higgins & Yalden, 2005). If human presence has a large ecological effect, that is, if it affects several taxa simultaneously, disturbance-induced decreases of competitor or predator species might indirectly favour species expected to be negatively affected by humans. Conversely, the direct effect of recreation on a given species may be further aggravated if human activities concurrently reduce other species on which they depend (e.g. human-induced reductions of prey availability will indirectly affect predators) (Skagen, Knight & Orians, 1991; Hebblewhite *et al.*, 2005; Price, 2008; Møller, 2012).

The effect of human activities at the population level will also vary according to the properties of the populations and species themselves. Differences in life-history traits (e.g. survival rates, number of reproductive attempts, generation times) will determine how quickly the population changes in the face of reductions in reproduction or survival caused by human recreation. For example, some species will be more sensitive to decreases in survival, while other will be more responsive to declines in reproduction (Heppell, Caswell & Crowder, 2000; Saether & Bakke, 2000; Oli & Dobson, 2003; Church *et al.*, 2007; Lima, 2009). That is, some species dynamics will be able to buffer or compensate losses due to disturbance better than others. Higher degrees of philopatry and site fidelity of a species (Yohannes, Hobson & Pearson, 2007) will further modulate the consequences of disturbance. That is, the reluctance to abandon a disturbed area due to site fidelity in some species may produce an evolutionary or ecological trap (Stamps & Krishnan, 1999; Schlaepfer, Runge & Sherman, 2002; Igual *et al.*, 2007; Yohannes *et al.*, 2007), leading to negative population trends. Human recreation can also have stronger effects on social species than on solitary ones, since disturbances in areas where animals aggregate (e.g. bird colonies) will affect most individuals simultaneously, which is further aggravated by the usually higher site fidelity in gregarious species (Burger, 1981; Carney & Sydeman, 1999).

Additionally, characteristics such as population density or meta-population dynamics are expected to have an important role in modulating the effect of disturbance at the population and species level. For example, small populations, which are more vulnerable to stochasticity, are more likely to be affected by human disturbances, even by single events, that result in reductions in reproductive output, habitat-use changes, or increased mortality that affect only a few individuals (Lande, 1993; Lacy, 2000; McGowan *et al.*, 2011). On the other hand, in populations with high densities entailing negative density dependence, the detrimental effects of human disturbance could go unnoticed *via* release of density dependence (Sinclair & Pech, 1996; Mallord *et al.*, 2007). When two or more populations are connected as a meta-population system, recreational activities affecting sink populations are expected to have a smaller impact because the population is maintained primarily by immigration from other sources. Conversely, in those instances in which disturbance affects source populations, the overall meta-population system might suffer the consequences (Pulliam, 1988; Brawn & Robinson, 1996; Dias, 1996).

An important modulator of the consequences of disturbance at this level is the capacity of a given species or population to adapt to humans, as demonstrated by the many species that thrive in urban environments. That is, populations and species with a greater genetic and phenotypic variability (e.g. variability of coping styles), as well as phenotypic plasticity, will be able to adjust more easily to human presence by replacement of sensitive individuals by less sensitive (usually bolder and less fearful) individuals (Carvalho, 1993; Lande & Shannon, 1996; Dufty, Clobert & Moller, 2002). However, adaptation to humans may come at a cost. For example, reduction of fear will only be positive at the population level if it does not increase the probability of being depredated by non-human predators or result in a reduction in reproduction (Dahlgren, 1990; Smith & Blumstein, 2008).

Finally, regardless of the species or human activities, there exist many other factors that may modify or obscure the demographic consequences of human disturbance by causing similar or opposing effects. First, we emphasize that, in most cases, human recreation is associated with habitat deterioration (e.g. construction of roads or ski resorts) and it is often difficult to separate the influence of direct human presence from that of habitat degradation. Thus, habitat modification associated with some recreational activities may negatively affect populations by decreases in both habitat quality and foraging opportunities. Clearly, this might obscure or even worsen the consequences of stress due to direct interactions with people (Cole & Landres, 1995; Buckley, 2004*b*; Braunisch, Patthey & Arlettaz, 2010). Environmental changes independent of human disturbance may influence population-level responses to recreation. Factors with potentially positive effects on populations, such as, for example, increases in reproduction, carrying capacity, or immigration rates due to climate change, might increase population growth rate obscuring or compensating for any negative effects of disturbance (Ozgul *et al.*, 2010; Tablado & Revilla, 2012). On the other hand, factors that negatively impact populations or species, such as biological invasions, changes in land use, or detrimental effects of climate change on ecosystems and migration patterns, might further exacerbate negative effects of disturbance on populations or species (Dextrase & Mandrak, 2006; Foden *et al.*, 2013).

VI. CONCLUSIONS

(1) From this synthesis, we conclude that the difficulties in finding general patterns in the field of recreational disturbance are due to three main reasons. First, for all levels of response there are many diverse factors likely to modulate the impact of human outdoor activities on wildlife, and the combined influence of these factors within each level may obscure or confound the effects of disturbance. That is, the impact of human disturbance not only depends on the intensity and type of the recreational activity, but also on the characteristics of the species, and the context in which interactions occur. For instance, whether individuals respond behaviourally, physiologically, or not will depend on their assessment of the risk imposed by humans, their options to hide or escape, and the potential consequences on their offspring's and their own welfare. The impact of recreational activities will also vary among populations or species depending on a combination of factors (e.g. extent of human activities, species ecology and context characteristics) which may or may not allow them to compensate for or adapt to disturbance.

(2) Second, the difficulty in finding general patterns is due to the fact that some modulators might affect wildlife responses in complex non-linear ways, such as the bell-shaped dependence of behavioural response on flushing performance (see Fig. 2D) (Ydenberg & Dill, 1986; Losos, 1990; Iriarte-Diaz, 2002). Many such relationships may be non-linear; however, they still need to be explored. In other instances, factor complexity results from contrasting effects at different levels of response. For instance, group size and predator (human) detection are positively related (Schaik *et al.*, 1983; Beauchamp, 2010). However, at the next level, this relationship may not be positive because animals in groups may feel safer than single animals and, therefore, exhibit a dampened behavioural or physiological reaction to humans (Fernandez-Juricic *et al.*, 2002; Kikusui *et al.*, 2006). Moreover, the same modulating factor may have contrasting impacts even within the same level of response, depending on the response mechanism. This entails a lack of correlation between different measures of stress response, such as differences in behavioural *versus* physiological responses (Killen *et al.*, 2013). This would be, for example, the case for body condition. Better body condition tends to increase active behavioural responses (e.g. flushing distance), however, the physiological response tends to be dampened (i.e. HPA axis reactivity) as body condition improves (Beale & Monaghan, 2004*a*; Breuner *et al.*, 2008).

(3) Third, another complication in finding general patterns of the impacts of human disturbance on wildlife exists because of the accumulation of modulating factors across different levels of response which may confound the patterns, especially at higher levels (such as reproductive success, survival, or population and species trends) (Burger *et al.*, 1995; Gill *et al.*, 2001; Price, 2008; Bonier *et al.*, 2009). The more levels of response (i.e. from Level 1 to 2 to 3, etc.), the more factors accumulate, adding uncertainty to the probability of finding generalizable associations (Fig. 1). That is, even if negative reactions to human disturbance are clearly observed at lower levels, we cannot readily infer detrimental consequences at the demographic level since the influence of many factors (e.g. habitat quality, previous experience, climate, or density dependence) may confound the expected effect at the population level.

(4) All the modulators and relationships considered here, as well as those yet to be considered may explain why few studies have shown general patterns for the relationships between direct human disturbance and wildlife. However, this should not discourage researchers in the field of human disturbance. We rather hope to have set, with this synthesis, a comprehensive basis that may be used as a future approach and reference for identifying the type of factors that may affect animals' responses to human disturbance and the complexity of their effects. There is a need for more research to validate across populations and taxa the generality of some of the modulating effects presented herein. Inclusion, or at least acknowledgement, of factors that may modulate responses to disturbance in a given system, and consideration of the complexity and likely interactions of such factors will facilitate improved study designs and interpretation of findings. We are confident that doing so will improve our understanding of the complex nature by which human recreation influences wildlife.

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