

Christoph Randler

Disturbances by dog barking increase vigilance in coots *Fulica atra*

Received: 21 December 2005 / Accepted: 27 May 2006 / Published online: 8 July 2006
© Springer-Verlag 2006

Abstract Animals frequently interrupt their activity to look up and to scan their surrounding environment for potential predators (vigilance). As vigilance and other activities are often mutually exclusive, such behaviours are at the expense of feeding, sleeping or preening. Authors of many wildlife disturbance studies found that people with free-running dogs provoked the most pronounced disturbances (e.g. greater flushing distances and more birds affected). However, dogs on leash may also negatively affect wild animals, and barking dogs may lead to an increase in vigilance. In this study, I tested this hypothesis in coots (*Fulica atra*) using three different playback procedures: (1) dog barks, (2) conspecific coot alarm calls and (3) chaffinch song. The trials were conducted in spring and autumn 2005 at three study sites in southwestern Germany. During the dog playbacks, vigilance increased significantly from 17 to 28%. This increase in vigilance is comparable to the presence of a natural predator. As expected, vigilance also increased significantly during conspecific coot alarm calls but not during playbacks of the chaffinch song control. Two main findings result from the study: (1) coots respond to acoustic traits of dogs and may be able to acoustically recognise this predator and (2) this increase in vigilance might have implications for conservation, especially when considering buffer zones around sensitive areas.

Keywords Auditory stimuli · Disturbances by dogs · Human disturbances · Predator recognition · Recreation

Introduction

During feeding and preening, animals frequently interrupt their activities to look up within different time intervals to detect a given stimulus (Beauchamp 2003). During this

vigilance behaviour, the animals scan their surrounding environment for potential predators (for reviews, see Elgar 1989; Roberts 1996; Treves 2000; Beauchamp 2003). As vigilance and other activities are often mutually exclusive (see Lima and Bednekoff 1999, for exception), such vigilance behaviour is at the expense of feeding, sleeping or preening and, therefore, incurs costs. Observational and experimental studies have shown that most wild animals increase their vigilance in the presence of a predator independently whether these predators were detected or experimentally presented via visual (Pöysä 1987), acoustical (Randler 2006) or chemical traits (Monclús et al. 2005). In domestic animals, the time spent being vigilant is used as a measure of fear towards new stimuli (Welp et al. 2004).

Human-caused disturbance stimuli are considered a form of predation risk (Frid and Dill 2002) and these disturbances often negatively affect wildlife (Pomerantz et al. 1988; Skagen et al. 1991; Holmes et al. 1993; Klein 1993; Klein et al. 1995; Hill et al. 1997; Blumstein et al. 2005; but see as an exemption, e.g. wildlife in parks and on islands that do not show a predator-specific reaction towards humans). Apart from other human disturbances, free-ranging or unleashed dogs (*Canis familiaris*) present a major threat and disturbance factor in many animal species and at different localities during all season (see, for overview, Sime 1999; Miller et al. 2001; for parks in Madrid, see Fernandez-Juricic and Telleria 2000). Dogs are often present in natural, suburban and recreational areas as companions of humans seeking recreation and physical or wildlife-related activities. Therefore, dogs account for a large proportion of disturbances (e.g. Fernandez-Juricic and Telleria 2000; Randler 2003). Authors of many wildlife disturbance studies concluded that people with dogs, dogs on leash or loose dogs provoked the most pronounced disturbances, e.g. greatest flushing distances, longest duration and highest numbers of individuals affected (Sime 1999; Randler 2003). Dogs are canid-like predators, and canids are natural, evolutionary predators of many, if not all, wildlife species (Sime 1999). Concerning birds, the presence of dogs has an impact on incubating birds (Keller

C. Randler (✉)
Institute of Biology I, University of Leipzig,
Johannisallee 46,
04103 Leipzig, Germany
e-mail: Randler@uni-leipzig.de

1989; Yalden and Yalden 1990), on breeding display ('lekking'; Baydack 1986), on foraging (Hoopes 1993) and on roosting (Keller 1991). Disturbances by pedestrians usually cause flushing responses at a given distance and these distances were greater when the pedestrians were accompanied by dogs (Burger 1986; Hanson and Grant 1991; Ingold et al. 1993; Randler 2003). Furthermore, greylag geese *Anser anser* seem able to distinguish between dogs on leash and free-ranging dogs (M. Weisser, unpublished data) and swan geese *Anser cygnoides* were found to react differently towards dogs of different sizes (Randler 2003). Despite much observational evidence, studies on experimental disturbances using dogs are scarce (Gabrielsen and Smith 1995; Sime 1999).

As a consequence, dogs are often excluded in natural areas or in wildlife sensitive regions. If exclusion is impossible, dogs should be walked on a lead. However, dogs on leash may also negatively affect wild animals, e.g. if these species would respond to dog barking. Hence, barking dogs—although on a lead—may be also be perceived as a kind of predation. Dogs on leash seldom bark but mostly do when stimulated by their owners. Barking may lead to an increased vigilance at the expense of other activities even if the dog itself is invisible to the disturbed subjects. This might also negatively affect the time budgets of animals. However, free-ranging dogs mostly flush their potential prey rather than provoking a higher vigilance. Nevertheless, when free-ranging dogs are farther away, vigilance may also increase despite the fact that the dog does not provoke a flushing response, because fleeing is traded off against remaining in the place (Ydenberg and Dill 1986).

The quality of the behavioural approach in the study of the impact of human disturbances and its population consequences has been vividly discussed (Gill et al. 2001; Blumstein et al. 2005). However, the large body of vigilance studies showed that this parameter seems to be a good metric to estimate possible consequences on fitness because vigilance is traded off against other activities such as feeding, preening or resting. A higher amount of vigilance is supposed to negatively affect an individual's foregoing. Nevertheless, there are only a handful of studies that examine fitness consequences in terms of lifetime reproductive success of anti-predator behaviour (Lind and Cresswell 2005). Nonetheless, measuring vigilance as a variable seems to be a useful approach because an increase in vigilance detracts an animal from other activities. This might not always have consequences for fitness and may represent a relationship with a pronounced threshold above which fitness consequences may be serious. Yasué (2005) further emphasises the importance of examining behavioural changes. Many studies focus only on displacement (flight initiation distances) rather than on less obvious measures such as behavioural changes (see, for a review, Thomas et al. 2003).

In this study, I tested whether coots responded to an acoustic stimulus of a predator (dog barks) with an increased vigilance. The anti-predator and vigilance behaviour of coots is well studied (Randler 2004, 2005a,b)

and this species is therefore suitable for such an investigation.

Materials and methods

Species and study sites

Coots are waterbirds (Rallidae, order Gruiformes) and widely dispersed and abundant in freshwater lakes and streams throughout the northern hemisphere. The species usually forages both on land and in the water, mainly on plants or molluscs, and is of medium size (approximately 24.5 cm in length, 600–1,265 g; Glutz von Blotzheim et al. 1973). The natural predators of coots are either aerial, such as goshawk *Accipiter gentilis*, peregrine *Falco peregrinus*, black kite *Milvus migrans*, marsh harrier *Circus aeruginosus* (Glutz von Blotzheim et al. 1973), or terrestrial (fox *Vulpes vulpes* and stoat *Mustela erminea*; Glutz von Blotzheim et al. 1973).

I obtained samples from three different habitats in southwestern Germany: (1) Ehmetsklinge ($8^{\circ}55'$ W, $49^{\circ}09'$ N; 227 m asl), (2) Breitenauer See ($9^{\circ}23'$ W, $49^{\circ}08'$ N; 230 m asl) and (3) Monrepos ($9^{\circ}10'$ W, $48^{\circ}56'$ N; 238 m asl). All habitats are used by humans for recreation during all season, and Ehmetsklinge and Breitenauer See were used for bathing and swimming purpose during the summer (i.e. between the end of May and September according to weather conditions). At both sites, dogs are excluded between 1 April and 31 August (Ehmetsklinge) and between 15 April and 30 September (Breitenauer See). In all three habitats, domestic dogs (*C. familiaris*) could be considered as a kind of predator as coot fled into the water when unleashed dogs occurred (personal observation). The flushing distance at where escape responses occurred was approximately 50 m. Field work was restricted to the time span when the dogs were present.

Playback procedure

I used preening coots and not feeding individuals as it was often impossible to follow a specific individual feeding in a dense flock during the two playback procedures. Furthermore, vigilance during feeding may be mediated by saturation and food density (Elgar 1989; Beale and Monaghan 2004; Yasué 2005) or by competition (Beauchamp 2003; Randler 2005b). Preening coots were usually found in shallow water approximately 1 m from the waterline. Therefore, the distance to a refuge does not influence the behaviour. I randomly chose one preening coot from a flock and videotaped 30-s pre-stimulus, 30-s stimulus and 30-s post-stimulus sequences. I videotaped the coots using a JVC GR-PD1 digital video camera with a $\times 16$ zoom lens mounted onto a tripod. The coots had habituated to human visitors so concealment was unnecessary and the videotaping was carried out from a place where there was no obvious influence on the birds' behaviour (~ 25 m).

To test the hypothesis that the coots may increase their vigilance as a response to dog barks, I used three different playbacks. First, the playback of dog barks was used as treatment stimulus. These barks were obtained from the British Sound Library. I used dog barking from five different recordings and created five playback tapes to avoid pseudo-replication (Kroodsma 1989).

Second, the coot alarm calls were obtained from different sound recordings (Roché 1995; Kosmos 2002; Schulze 2003). These calls were recorded in Europe at different locations, mainly in France (J.C. Roché, personal communication; K.-H. Dingler, personal communication). The coot calls were edited to minimise background noises using a Grundig 437 CD player and AIWA CX-Z87M cassette recorder. I created four different coot playback tapes.

Third, the territorial song of the chaffinch *Fringilla coelebs* is considered a non-threatening sound and was used as a control stimulus. This song was also obtained from a commercial sound recording (Roché 1995). Chaffinches are common songbirds breeding in the vicinity of all three locations, and they produce relatively loud songs. Furthermore, chaffinches are present all year round. This control is necessary to test whether the coots would respond to any loud sounds in their environment (Shriner 1998).

In addition, behavioural recordings without playback were sampled during a period of 30 s before and after the broadcasting of the different stimuli. The playbacks were broadcast using a small portable Toshiba MCR 103 cassette recorder. The different playback tapes were standardised at approximately 75 dB measured at a 1-m distance from the speaker using a Lutron SL 4001 digital sound level meter with A-level weighting [dog barking, 76.6 ± 0.6 (range 75–78 dB; $N=5$); coot, 73.9 ± 2.4 (range 67–78 dB; $N=4$); chaffinch 80 dB ($N=1$)].

The trials were conducted within two seasons, in spring between 8 February 2005 and 2 March 2005 and in autumn between 31 August 2005 and 4 November 2005 always in the morning between 0745 and 1200 hours central European time, outside the period when dogs were forbidden. I used a matched-pair design (Kroodsma 1989). This experimental design holds many environmental variables constant and is described as a within-subject procedure by Kroodsma (1989).

I usually started the matched-pair comparison with the playback of dogs ($N=14$ and in $N=4$ with coot first) because I expected the conspecific stimulus to be strongest, thus providing the greatest potential for carryover in response to subsequent stimuli (Martin and Martin 2001). Afterwards, I waited until the coots resumed to a baseline level of vigilance (see, Karpanty and Grella 2001) before broadcasting the next stimulus.

Although the populations of coots were not individually marked, it is highly unlikely that the same coot has been sampled more than once. The maximum counts of coots were $N=20$ at Monrepos, $N=50$ at Ehmetsklinge and $N>100$ at Breitenauer See. Two or three trials were usually carried out per day (between one and five on 1 day; mean

2.35 ± 0.26 trials/day; median 2). However, these trials were temporarily—and sometimes spatially—separated from each other. The coot used the total area for feeding but only a few places for preening. Therefore, preening individuals changed within the same day because coots left the preening areas after 2 to 10 min to resume feeding elsewhere. I numbered the experimental trials per day (1=first experimental treatment, 2=second), but the number of trials per day per site did not correlate significantly negatively with vigilance time as would be expected when habituation had occurred (Kendall-Tau, always $P>0.05$). Therefore, the results do not seem to be affected by habituation.

Data handling and statistics

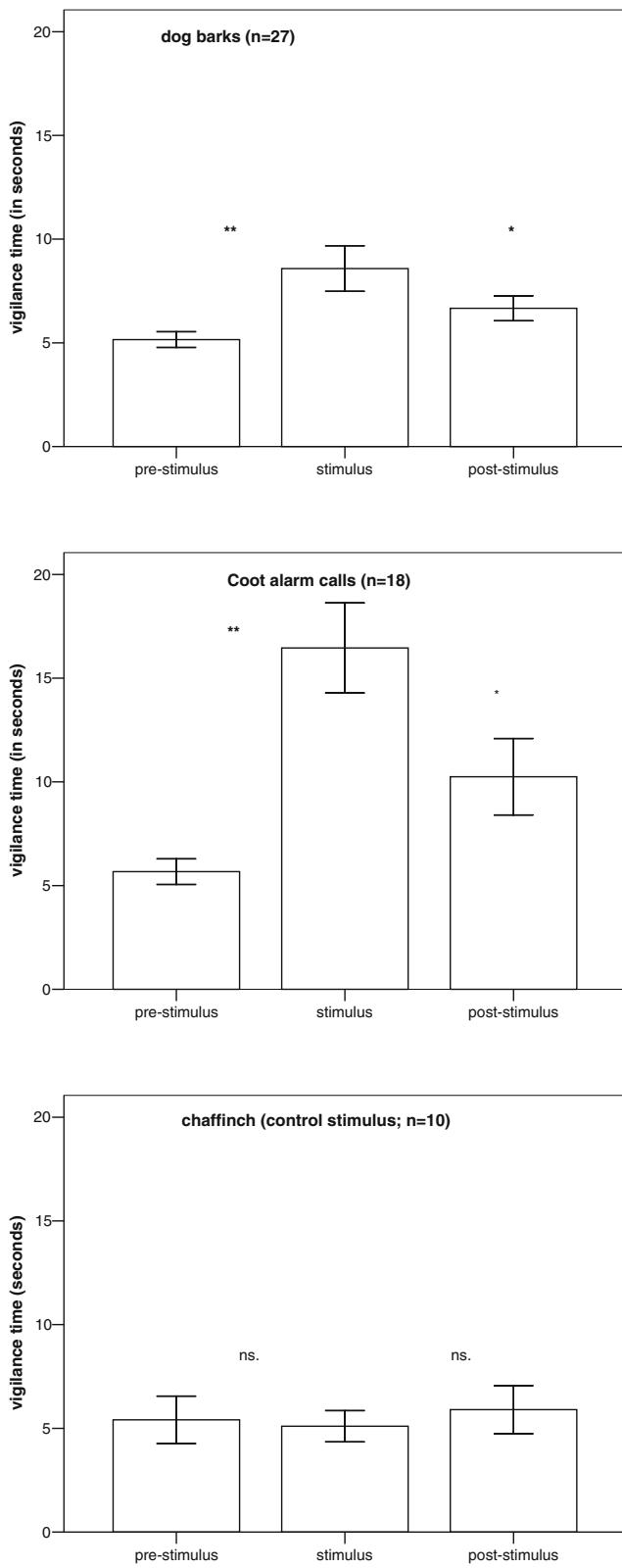
I counted scanning events (number of head-up scans) and the total scan duration. All data were measured with a precision of 0.1 s and are based on the three 30-s trials (pre-playback, playback and post-playback period). I did not use the results concerning scanning events, because scanning events are helpful when they are rather short (see, for a review, Randler 2005a,b) and when coots showed only short scan durations (as is usual without playbacks). However, during playbacks, coots increased their vigilance because they increased their scan durations, i.e. some individuals looked up and they remained vigilant until the playback ended. Furthermore, the total amount of vigilance seems the most relevant factor because it influences time budgets significantly. As some coots left the area during the post-stimulus period, I interpolated data when at least 15 s could be sampled. I sampled a total of 37 different coots: 27 received dog playbacks and 18 therefrom additionally received coot playbacks (matched pairs). Out of the initial 27 individuals, nine left the preening area before the second stimulus was broadcast. An additional independent sample of ten coots received the chaffinch (control) playback.

To quantify the responses towards the different stimuli, I subtracted the baseline level of vigilance (pre-stimulus) from the vigilance level during the stimulus presentation for each individual coot and used the behavioural change for comparison.

I used matched-paired *t* test to compare pre-playback, playback and post-playback stimuli, because the same individuals were used (three 30-s periods). To compare dog barks and chaffinch song, I used the independent *t* test.

Results

During playbacks of dog barks, coots increased their time spent being vigilant significantly from (means \pm SE) 5.1 ± 0.37 to 8.5 ± 1.10 s ($t=3.339$, $df=26$, $P=0.003$; Fig. 1). Expressed in percent, vigilance increased from 17 to 28% during the playback of dog barks. Vigilance also increased during conspecific coot alarm calls from 5.6 ± 0.61 to 16.4 ± 2.17 s ($t=4.784$, $df=17$, $P<0.001$; Fig. 1), but not during



◀ **Fig. 1** Coots responded to dog barks and coot alarm calls with a significant increase in vigilance, but not during playbacks of chaffinch song. Vigilance remained higher in the post-playback period after coot and dog playbacks. The figures are based on three 30-s stimuli (before, during and after the playbacks; mean±SE). * $P<0.05$, ** $P<0.01$. The statistical comparisons are made between pre-playback periods and playback stimuli, and between pre-playback and post-playback periods

barks ($t=2.352$, $df=24$, $P=0.027$) but not after the chaffinch song ($t=1.671$, $df=8$, $P=0.133$). After subtracting the baseline pre-playback vigilance (see “Materials and methods”), coots responded with a significantly longer vigilance to conspecific calls compared to dog barking ($t=3.090$, $df=17$, $P<0.007$), suggesting that conspecific calls elicit a stronger reaction. Compared to the chaffinch control, coots responded with longer time spent vigilant during dog barking ($t=2.081$, $df=35$, $P=0.045$).

Discussion

When exposed to coot alarm calls and dog barks, coots increased their vigilance. This could be interpreted as anti-predator behaviour (Pöysä 1987; Welp et al. 2004; Caro 2005). There was no significant response towards the chaffinch song broadcast at the same volume. This indicates that coots were not simply responding to any loud sounds in their environment (Shriner 1998). Two main findings result from the study: (1) coots respond to acoustic traits of a ‘novel’ predator in evolutionary terms and may have developed some kind of acoustic predator recognition and (2) this response—an increase in vigilance time—might have implications for conservation.

The response, although highly significant, did not elicit escape reactions as did with that of an approaching dog (personal observation). This might support the “seeing is believing” hypothesis (van der Veen 2002), namely, that the information about a potential predator received by an acoustical cue could not be validated by vision and, therefore, no strong escape response was provoked. The animals seem to respond stronger towards visual stimuli compared to acoustic ones (Blumstein et al. 2000). Fleeing also incurs costs and should be under selection pressure (Ydenberg and Dill 1986). Furthermore, the vigilance behaviour of the coots may have been influenced by flock size and by site. The sample size is too small to test these hypotheses. Nevertheless, in the matched-pair comparisons, flock size was similar within each trial, suggesting that the increase in vigilance generally persists over different flock sizes, but this aspect would be worth further experiments, and I suppose that the percentage of increase in vigilance may depend on flock size (negative correlation).

playbacks of chaffinches which served as a control (5.4 ± 1.14 vs 5.1 ± 0.75 s; $t=0.320$, $df=9$, $P=0.756$, n.s.). During the 30-s post-playback period, vigilance remained higher compared to the pre-stimulus period after the broadcast of coot alarm calls ($t=2.80$, $df=14$, $P=0.014$) and of the dog

Implications for conservation

Although Fernandez-Juricic et al. (2001a) showed that habituation to disturbances by dogs occur in highly

urbanised habitats, this may not hold true in more natural areas. As animals rarely have perfect information about their predators, they are expected to overestimate rather than underestimate predation risk to maximise fitness (Frid and Dill 2002). Habituation, although it generally occurs, is often partial and negligible (Frid and Dill 2002) and may be restricted to highly urbanised areas, such as urban parks (Fernández-Juricic et al. 2001a, 2004; but see as an exemption, e.g. wildlife on islands that do not show a predator-specific reaction towards humans). When considering buffer zones around sensitive areas (e.g. Rodgers and Smith 1997), the detrimental effects of such acoustic “environmental pollution” by barking dogs should be taken into account and buffer zones, therefore, should be much wider than could be inferred from flushing distances. If buffer zones were established by conservation managers, e.g. by using flushing distances of sensitive species, another (wider) buffer zone is needed where dogs were excluded to avoid disturbances imposed by barking. Furthermore, in sensitive areas, it should be discussed whether dogs should be generally excluded, rather than allowing people to walk them on leash. Although coots are not threatened species, these results could be representative for endangered species as well.

Flushing distances are usually considered a good measurement for the planning of buffer zones (Anderson 1988; Madsen 1988; Blumstein et al. 2003), although not an unquestioned one (e.g. Gill et al. 2001; Beale and Monaghan 2004). Apart from flushing distances, other measurements related to anti-predator behaviour or disturbance reactions, such as vigilance (Fernández-Juricic et al. 2001b, 2004), therefore, deserve further attention. While Fernández-Juricic et al. (2001b, 2004) already introduced differences between flushing distance and states of alertness/vigilance, the total time spent being vigilant might be also important. For example, in the teal *Anas crecca*, the individuals increase their vigilance (proportion of time spent scanning) in the presence of a predator from 36.2 to 54.3% during feeding with head submerged, from 29.6 to 36.2% when feeding with head and neck submerged and from 30.5 to 46.9% when feeding by up-ending (Pöysä 1987). During the dog playbacks, vigilance increased from 17 to 28%. However, vigilance behaviour also occurs in natural ecosystems without the presence of humans and is a part of the daily activity pattern. In evolutionary terms, vigilance should not always have negative impacts on the fitness or the survival of the individual bird. However, every individual should have optimised its trade-off between vigilance and other activities (Ydenberg and Dill 1986). There exists perhaps a critical threshold above which an increase in vigilance acts as detrimental. This might be the case during cold and short days during winter when energetic requirements are rather high (see, e.g., studies in geese; Owen et al. 1992) or during feeding young, when an increased vigilance detracts, e.g. male geese from feeding, resulting in significant mass loss (Weisser and Randler 2005). More studies are needed to quantify these effects.

However, disturbance might also result in non-visible behaviour, e.g. in the freezing response, which also incurs stress provoked by hormonal or physiological processes (Gabrielsen et al. 1985; Gabrielsen and Smith 1995; Fowler 1999). Time spent being vigilant during disturbances may be a useful measurement of a behavioural response, bridging the gap between flushing distances on the one side and physiological responses, which are more difficult to measure, on the other.

Acknowledgements I would like to thank especially Richard Ranft from the British Sound Library for supplying audio material. This study was partly funded by grant #1430 5771 of the University of Education Ludwigsburg and by a grant from the Federal Ministry for Education und Research Germany (JP CR). The experiments comply with the current law in Germany. I am grateful to two anonymous reviewers for their helpful comments which added to the clarity of the manuscript.

References

- Anderson DW (1988) Dose-response relationship between human disturbance and brown pelican breeding success. *Wildl Soc Bull* 16:339–345
- Baydack RK (1986) Sharp-tailed grouse response to lek disturbance in the Cranberry Sand Hills of Manitoba. Colorado State University, Fort Collins, Colorado
- Beauchamp G (2003) Group-size effects on vigilance: a search for mechanisms. *Behav Processes* 63:111–121
- Beale CM, Monaghan P (2004) Behavioural response to human disturbance: a matter of choice? *Anim Behav* 68:1065–1069
- Blumstein DT, Daniel JC, Griffin AS, Evans CS (2000) Insular tammar wallabies (*Macropus eugenii*) respond to visual but not acoustic cues from predators. *Behav Ecol* 11:528–535
- Blumstein DT, Anthony LL, Harcourt A, Ross G (2003) Testing a key assumption of wildlife buffer zones: is flight initiation distance a species-specific trait? *Biol Conserv* 110:97–100
- Blumstein DT, Fernandez-Juricic E, Zollner PA, Garity SC (2005) Inter-specific variation in avian responses to human disturbances. *J Appl Ecol* 42:943–953
- Burger J (1986) The effect of human activity on shorebirds in two coastal bays in northeastern United States. *Environ Conserv* 13:123–130
- Caro T (2005) Anti-predator defence in mammals and birds. Chicago University Press, Chicago
- Dimond S, Lazarus J (1974) The problem of vigilance in animal life. *Brain Behav Evol* 9:60–79
- Elgar MA (1989) Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol Rev* 64:13–33
- Fernández-Juricic E, Telleria JL (2000) Effects of human disturbances on spatial and temporal feeding patterns of Black-birds *Turdus merula* in urban parks in Madrid, Spain. *Bird Study* 47:13–21
- Fernández-Juricic E, Jimenez MD, Lucas E (2001a) Bird tolerance to human disturbances in urban parks of Madrid (Spain): management implications. In: Marzluff JM, Bowman R, Donnelly R (eds) Avian ecology and conservation in an urbanizing world. Kluwer, Dordrecht, pp 259–274
- Fernández-Juricic E, Jimenez MD, Lucas E (2001b) Alert distances as an alternative measure of bird tolerance to human disturbance: implications for park design. *Environ Conserv* 28:263–269
- Fernández-Juricic E, Vaca R, Schroeder N (2004) Spatial and temporal responses of forest birds to human approaches in a protected area and implications for two management strategies. *Biol Conserv* 117:407–416

- Fowler GS (1999) Behavioural and hormonal responses of Magellanic penguins (*Spheniscus magellanicus*) to tourism and nest site visitations. Biol Conserv 90:143–149
- Frid A, Dill LM (2002) Human-caused disturbance stimuli as a form of predation risk. Cons Ecol 6(1):11 (<http://www.consecol.org/vol6/iss1/art11>)
- Gabrielsen GW, Smith EN (1995) Physiological responses of wildlife to disturbances. In: Knight RL, Gutzwiller K (eds) Wildlife and recreationists. Coexistence through management and research. Island, Washington, DC
- Gabrielsen GW, Blix AS, Ursin H (1985) Orienting and freezing response in incubating ptarmigan hens. Physiol Behav 3: 925–934
- Gill JA, Norris K, Sutherland WJ (2001) Why behavioural responses may not reflect the population consequences of human disturbances. Biol Cons 97:265–268
- Glutz von Blotzheim UN, Bauer KM, Bezzel E (1973) Handbuch der Vögel Mitteleuropas. Bd. 5, Galliformes et Gruiformes. Frankfurt/Main: Akademische Verlagsgesellschaft
- Hanson P, Grant TA (1991) The effects of human disturbance on trumpeter Swan breeding behaviour. Wildl Soc Bull 19: 248–257
- Hill D, Hocking D, Price D, Tucker P, Morris R, Treweek J (1997) Bird disturbance: improving the quality and utility of disturbance research. J Appl Ecol 34:275–288
- Holmes TL, Knight RL, Stegall L, Craig GR (1993) Responses of wintering grassland raptors to human disturbances. Wildl Soc Bull 21:461–468
- Hoopes EM (1993) Relationship between human recreation and piping plover foraging ecology and chick survival. Ph.D. thesis, University of Massachusetts, Amherst, MA
- Ingold P, Huber B, Neuhaus P, Mainini B, Marbacher H, Schnidrig-Petrig R, Zeller R (1993) Tourism and sports in the Alps—a serious problem for wildlife? Rev Suisse Zool 100:529–545
- Karpanty SM, Grella R (2001) Lemur responses to diurnal raptor calls in Ranomafana National Park, Madagascar. Folia Primatol 72:100–103
- Keller V (1989) Variation in the response of great crested grebes *Podiceps cristatus* to human disturbance—a sign of adaptation? Biol Conserv 49:31–45
- Keller V (1991) Effects of human disturbances on eider ducklings *Somateria mollissima* in an estuarine habitat in Scotland. Biol Conserv 58:213–228
- Klein ML (1993) Waterbird behavioural responses to human disturbances. Wildl Soc Bull 21:31–39
- Klein ML, Humphrey SR, Franklin Percival H (1995) Effects of ecotourism on distribution of waterbirds in a wildlife refuge. Conserv Biol 6:1454–1465
- Kosmos (2002) Die Kosmos Vogelstimmen Edition. Franckh-Kosmos, Stuttgart (compiled from >40 sound authors)
- Kroodsma DE (1989) Suggested experimental designs for playback experiments. Anim Behav 37:600–609
- Lima SL, Bednekoff PA (1999) Back to the basics of antipredatory vigilance: can nonvigilant animals detect attack? Anim Behav 58:537–543
- Lind J, Cresswell W (2005) Determining the fitness consequences of antipredation behavior. Behav Ecol Sociobiol 16:945–956
- Madsen J (1988) Experimental refuges for migratory waterfowl in Danish wetlands. I. Baseline assessment of the disturbance effects of recreational activities. J Appl Ecol 35:386–397
- Martin PR, Martin TE (2001) Behavioral interactions between coexisting species: song playback experiments with wood warblers. Ecology 82:207–218
- Miller SG, Knight RL, Miller CK (2001) Wildlife responses to pedestrians and dogs. Wildl Soc Bull 29:124–132
- Monclús R, Rödel HG, von Holst D, de Miguel J (2005) Behavioural and physiological responses of naive European rabbits to predator odour. Anim Behav 70:753–761
- Owen M, Wells RL, Black JM (1992) Energy budgets of wintering barnacle geese: the effects of declining food resources. Ornis Scand 23:451–458
- Pomerantz GA, Decker DJ, Goff GR, Purdy KG (1988) Assessing impact of recreation on wildlife: a classification scheme. Wildl Soc Bull 16:58–62
- Pöysä H (1987) Feeding-vigilance trade-off in the teal (*Anas crecca*): effects of feeding method and predation risk. Behaviour 103:108–122
- Randler C (2003) Reactions to human disturbances in an urban population of the swan goose *Anser cygnoides* in Heidelberg (SW Germany). Acta Ornithol 38:47–52
- Randler C (2004) Coot benefit from feeding in close proximity to geese. Waterbirds 27:240–244
- Randler C (2005a) Vigilance during preening in coots *Fulica atra*. Ethology 111:169–178
- Randler C (2005b) Coots *Fulica atra* reduce their vigilance under increased competition. Behav Processes 68:173–178
- Randler C (2006) Red squirrels (*Sciurus vulgaris*) respond to alarm calls of Eurasian jays (*Garrulus glandarius*). Ethology 112: 411–416
- Roberts G (1996) Why individual vigilance declines as group size increases. Anim Behav 51:1077–1086
- Roché JC (1995) Die Vogelstimmen Europas. Franckh-Kosmos, Stuttgart
- Rodgers JA, Smith HAT (1997) Buffer zone distances to protect foraging and loafing waterbirds from human disturbances in Florida. Wildl Soc Bull 25:139–145
- Schulze A (2003) Die Vogelstimmen Europas, Nordafrikas und Vorderasiens. Edition Ample, Germering
- Shriner WM (1998) Yellow-bellied marmot and golden-mantled ground squirrel responses to heterospecific alarm calls. Anim Behav 55:529–536
- Sime CA (1999) Domestic dogs in wildlife habitats. In: Joslin G, Youmans H (eds) Effects of recreation on Rocky Mountain wildlife: a review for Montana. Montana Chapter of the Wildlife Society, 307pp
- Skagen SK, Knight RL, Orians G (1991) Human disturbances of an avian scavenging guild. Ecol Appl 1:215–225
- Thomas K, Kvitek RG, Bretz C (2003) Effects of human activity on the foraging behaviour of sanderlings *Calidris alba*. Biol Conserv 109:67–71
- Treves A (2000) Theory and method in studies of vigilance and aggregation. Anim Behav 60:711–722
- van der Veen IT (2002) Seeing is believing: information about predators influences yellowhammer behavior. Behav Ecol Sociobiol 51:466–471
- Weisser M, Randler C (2005) Elterliches Investment und Jungenaufzucht bei städtischen Graugänsen. Ornithol Anz 44:1–8
- Welp T, Rushen J, Kramer DL, Festa-Bianchet M, de Pasillé AMB (2004) Vigilance as a measure of fear in dairy cattle. Appl Anim Behav Sci 87:1–13
- Yalden PE, Yalden D (1990) Recreational disturbance of breeding golden plovers *Pluvialis apricaria*. Biol Conserv 51:243–262
- Yasué M (2005) The effects of human presence, flock size and prey density on shorebird foraging rates. J Ethol 23:199–204
- Ydenberg RC, Dill LM (1986) The economics of fleeing from predators. Adv Study Behav 16:229–249