Human disturbance of grouse - why and when?

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Review article

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Disturbance caused by human outdoor recreation and tourism activities is increasingly viewed as a threat to wildlife. Particularly in areas where threatened populations of wildlife overlap with highly frequented tourist locations, managers are challenged with reducing impacts of human disturbance on wildlife. For grouse, Tetraonidae, most studies on the effects of human disturbance address individual responses, whereas for conservation, the most relevant question is whether human presence negatively impacts the abundance and viability of populations. I here summarise published studies on the responses of grouse to the presence of humans, review the conceptual foundations of predation-risk theory and the risk-disturbance hypothesis, and propose a framework for research to aid conservation of grouse. Because grouse are found in many environments they are excellent model species for testing the predictions of the risk-disturbance hypothesis.

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Associate Editor: R.J. Gutiérrez

World-wide, non-lethal human disturbance because of recreational and tourism activities (hereafter 'disturbance') has become recognised as a threat to wildlife. Disturbance can be defined as an animal's avoidance response to a stimulus resulting from the presence of humans in its habitat (Frid & Dill 2002). When disturbance negatively impacts the fitness of individuals and the viability of populations, it becomes a conservation concern.

Disturbance effects include short-term changes in behaviour, long-term shifts in habitat use, reduced reproductive success and declining populations (Ingold 2005). However, population-level effects are difficult to demonstrate so their importance remains unclear. Nevertheless, many conservationists tend to reduce the effects of outdoor activities simplistically to 'human presence = disturbance = negative effects on wildlife'. The public commonly views wildlife as being 'wild' by nature; that is, wild animals will avoid humans, and encounters with humans result in avoidance behaviour (Knight 2009). Wild animals that do not flee from humans are often perceived as 'unnatural' (Reynolds & Braithwaite 2001). For example, especially aggressive capercaillie *Tetrao urogallus* males that approach and attack humans are referred to as 'mad cocks' in European languages (Klaus et al. 1989, Höglund & Porkert 1992). However, there are many examples of wildlife living near human habitation, ranging from deer in North America (Rutberg 1997) to large carnivores in India (Athreya et al. 2013), that indicate that approaching rather than fleeing humans may simply be at one end of the spectrum of normal behaviour. From an evolutionary perspective, the question is 'why should animals be disturbed by humans?' When disturbance was first recognised as a conservation issue, such a question had not received much attention. Only recently has predation risk theory (Brown et al. 1999, Caro 2005) been advanced as a conceptual framework for disturbance studies (Frid & Dill 2002, Beale & Monaghan 2004). Predation risk theory has allowed the formulation of predictions and the

testing of hypotheses, which has contributed to more rigorous designs of research studies of human disturbance of wildlife.

Grouse, Tetraonidae, are important game species in both Eurasia and North America. However, several species of grouse are red-listed at regional, national and international levels (Storch 2007a). Conservation legislation requires wildlife managers to assess the impacts of human activities on threatened species. Hunting of threatened grouse populations has been banned in most places (Storch 2007a). In contrast, non-lethal human activities in grouse habitat are not usually banned, but may be a conservation concern. For example, infrastructure development (e.g. forestry roads, hiking trails, ski resorts, gas and oil prospecting and wind energy plants) requires evidence-based environmental impact assessments, which also consider the impacts of human disturbance. Grouse conservationists consider disturbance as a threat to population viability (e.g. Suchant & Braunisch 2008), but evidence for such threats is anecdotal. Therefore, a strong conceptual and empirical understanding of human disturbance effects on grouse would provide a more defensible basis for management decisions than mere pleas using the 'precautionary principle' (Cooney 2004).

I synthesise the current understanding of the effects of non-lethal disturbances on grouse resulting from recreational activities of humans from an evolutionary and behavioural perspective. I first introduce disturbance from outdoor recreation and tourism as a conservation concern and summarise existing disturbances studies on grouse. I then briefly review current theoretical foundations of research on human disturbance of wildlife. Finally, I propose a framework for research that should increase our understanding and improve our management of the effects of human disturbance to enhance coexistence of grouse and humans.

Material and methods

I derived my synthesis based on journal articles retrieved from the Web of Knowledge (last updated April 2013), and cited references in these papers. For publications on grouse responses to human recreational disturbance, my search criteria were: Title = (grouse OR ptarmigan OR prairie chicken OR capercaillie) AND Title = (disturb* OR touris* OR recreat*). I excluded publications which used 'disturbance' as a synonym for anthropogenic impacts on the habitat.

Recreational disturbance as a conservation concern

Around the globe, people are spending more time and money in pursuit of outdoor recreation and nature tourism than they have in the past. While the contributions of these activities to local economies and public health are considered important, it is a growing challenge to manage outdoor recreation sustainably (Cordell et al. 2004, Bell at al. 2007, Cordell et al. 2008). Disturbances by recreationists have negatively impacted wildlife, and have become a major concern. This is particularly true for threatened species and areas used intensively by humans for outdoor activities (Ingold 2005).

The IUCN Status Survey and Conservation Action Plans for grouse, based on questionnaires among grouse specialists, indicated that disturbance rose between successive surveys in perceived importance as an impact on grouse (Storch 2000b, Storch 2007b). In 2000, IUCN grouse specialists identified disturbance as a threat in 26% of countries and five species of grouse (Storch 2000a) and in 2007, this rose to 38% of countries and eight species of grouse (Storch 2007a). The questionnaires also revealed that human disturbance still was a predominantly European concern, and European grouse specialists named disturbance as a threat for one third (2000) and one half (2007) of all countries and species. However, American and Asian grouse specialists also reported disturbance as an issue. In general, concerns about disturbance as a threat to grouse were related to those areas where intensive outdoor recreation occurred. Typical examples were the European and Japanese Alps, which are surrounded by countries with high human population densities, great popularity of outdoor activities and affluent recreational users.

In Europe, conservation initiatives to reduce disturbance to grouse and other wildlife range from local measures to country-wide campaigns. In the Black Forest, Germany, tourism is a major component of a conservation plan for capercaillie (Suchant & Braunisch 2008). Most initiatives, however, focus on disturbance during winter because winter is perceived as an energetic bottleneck for grouse and, therefore, effects of disturbances are assumed to be particularly serious (Ingold 2005). In England, for

example, humans have been excluded legally from known winter feeding areas of black grouse *Tetrao tetrix* (Warren et al. 2009). In Germany, a cooperative project between state conservation authorities and the largest European association of outdoor users, the German Alpine Club (DAV), resulted in a survey of the entire Bavarian Alps to identify areas of potential impact to grouse from ski touring. Ski routes were redirected in areas considered as critical for grouse, and wildlife reserves that were closed for recreational use were marked on Alpine club maps. However, measures to reduce impacts of disturbance remained largely voluntary (Scheuermann 1999, Zeitler 1999, DAV 2013). Similar approaches to identify and mitigate disturbances by humans engaging in winter sport activities in capercaillie habitats have also been applied in parts of Switzerland (Rupf et al. 2011). Starting in Austria and extending into neighbouring countries, a media campaign addressed negative effects of winter sports on wildlife. The focus of this campaign has been on education, maps, guide books and signposting of routes (Erhart 2013). Numerous local- to regional-scale examples of efforts to reduce negative effects of disturbance on wildlife while promoting coexistence of wildlife and humans have been posted on the internet.

Grouse responses to disturbance: existing studies

Despite widespread concerns about the negative effects of disturbances on grouse (Miquet 1988, Zeitler 1995, Baydack 1998, Ménoni & Magnani 1998, Mollet 1998, Suchant & Roth 1998, Zeitler & Glänzer 1998, Cas 2010), the issue of disturbance has long played a minor role in grouse research (Moss et al. 2010). Only since about 2005 have disturbance studies on grouse become more numerous (Appendix I). Most of these studies have used two major approaches: 1) comparative studies assessed habitat use, relative abundance, or vital rates of grouse in relation to the presence of humans, and 2) experimental studies simulated encounters of grouse with humans and assessed behavioural and physiological responses of grouse. For conservation, the most relevant question is whether human presence negatively impacts the abundance and viability of populations. Because grouse population dynamics are influenced by numerous extrinsic and intrinsic factors, demonstrating disturbance impacts at the

population level is challenging. Therefore, most studies assess disturbance responses by grouse at the level of individuals. It is important to note, however, that individual responses are insufficient proof of disturbance effects at the population level.

Early experiments by Baydack & Hein (1987) revealed that female grouse are more susceptible to human presence on leks than are males. Female sharp-tailed grouse *Tympanuchus phasianellus* in Manitoba, Canada, avoided disturbed leks, while males returned to their lek soon after a disturbance had ceased. Experiments on black grouse in the North Pennines, UK (Baines & Richardson 2007), and capercaillie in the Pyrenees, France, and the Black Forest, Germany, (Thiel et al. 2007) used flight initiation distances as an indicator of disturbance effects. Birds that were disturbed more regularly, or that lived in areas with intensive tourism or hunting pressure, flushed at greater distances than those less exposed to disturbance. Telemetry studies in Scandinavia assessed whether grouse showed greater movements when disturbed by hunters (Olsson et al. 1996, Brøseth & Pedersen 2010). Contrary to hunters' beliefs, willow ptarmigan *Lagopus lagopus* exposed to hunting neither left the hunting grounds nor increased their movements. Rather, they made greater use of dense cover in response to hunting (Brøseth & Pedersen 2010). Similarly, radio-marked capercaillie in the Black Forest, Germany, did not leave their home ranges when disturbed by winter sport activities, but preferentially used less-disturbed parts of the forest (Thiel et al. 2008). Evidence of shifts in habitat use has also been found in Scotland, where capercaillie avoided habitat near tracks used by humans (Summers et al. 2007, Moss et al. in press). Likewise, lesser prairie chickens *Tympanuchus pallidicinctus* in Kansas, USA, nested farther from human infrastructure than would have been expected at random (Pitman et al. 2005).

In Switzerland, Patthey et al. (2008) reported that local abundance of displaying black grouse males was negatively correlated with the density of ski lifts. However, displaying black grouse have been shown to be flexible in their spatio-temporal behaviour (Chamberlain et al. 2012); they will use both stable communal leks and spatially more variable solitary display sites. While larger leks are usually found in open exposed locations, solitary males may display at less conspicuous sites, and may be easily overlooked. Observations in the German Alps suggest that black grouse in ski resorts tend to use variable display sites, either solitarily or in small groups of males, rather

than stable traditional leks (Zeitler 2000). Thus, it remains unclear whether disturbance from human activities associated with ski resorts results only in behavioural responses or also in reduced carrying capacity. Early telemetry studies in France found no differences in home-range use and reproductive success of black grouse occupying either an area surrounding a ski resort or undisturbed areas (Miquet 1988). However, collisions of grouse with cables caused high mortality and resulted in population decline in skiing areas (Miquet 1990).

These studies provide evidence that grouse may adjust their habitat use in response to human presence, yet continue to use tourist areas opportunistically despite the risk of disturbance (Miquet 1988, Zeitler 2000). Grouse exposed to humans may even show signs of habituation, such as suggested for black grouse in Alpine ski resorts (Miquet 1988, A. Zeitler, unpubl. data). However, rigorous demonstration of population-level effects of human disturbance is still lacking. Only three studies appear to have assessed reproductive rates and survival rates of grouse in relation to disturbance levels, and neither shows any effects (Pitman et al. 2005, Baines & Richardson 2007, Moss et al. in press). However, a long-term study on greater sage grouse *Centrocercus urophasianus* in Wyoming, USA, provides evidence that abandoned grouse leks were best explained by proximity to oil and gas wells (Hess & Beck 2012). However, it remained unclear if grouse abandoned these areas because of changes in the habitat or human presence *per se*.

Recent research involving corticosterone metabolites measured in faeces promises new insights into physiological stress levels. In the Swiss Alps and in the Black Forest, Germany, Thiel et al. (2008, 2011) found greater concentrations of stress hormone metabolites from capercaillie that were closer to locations having winter recreation activity than locations farther from recreational activity. However, this pattern was found only in spruce *Picea abies* forests and not in pine-dominated *Pinus* spp. habitats. A similar study in the Italian Alps confirmed higher stress hormone levels in black grouse in highly disturbed areas, but only in one of the two winters of study (Formenti et al. 2012). Preliminary research on capercaillie in Austria suggested an interaction between habitat structure and human disturbance in stress hormone levels during mid winter (K. Hirschenhauser & V. Grünschachner-Berger, unpubl. data). Capercaillie in the vicinity of a ski run had greater levels of excreted stress hormone metab-

olites than individuals farther away. However, social conditions added variation: males having close neighbours had higher stress hormone levels than males without close neighbours, regardless of the presence of humans (K. Hirschenhauser & V. Grünschachner-Berger, unpubl. data). Obviously, better understanding is needed of corticosterone metabolites as a composite response to multiple stressors, including not only humans, but also predators, conspecifics and habitat conditions (Tempel & Gutiérrez 2004). Further, it is not known how stress hormone metabolite levels translate into birds' performance at individual and population levels.

The conceptual foundation: the risk-disturbance hypothesis

The reason why species respond differently to other species is, based on current theory, the perceived risk of predation. Predation risk theory and the 'ecology of fear' (Ydenberg & Dill 1986, Brown et al. 1999, Stankowich & Blumstein 2005) have been developed into a conceptual framework for studies on human disturbance of wildlife (Frid & Dill 2002, Beale & Monaghan 2004). Within the risk-disturbance hypothesis (Frid & Dill 2002), human disturbance stimuli are viewed as analogous to predation risk, and wildlife responses to disturbance are explained as responses to perceived predation risk. The analogy is predicated on the observations that both predation risk and human disturbance divert time and energy from activities such as feeding, resting or parental care. Thus, animals exposed to disturbance stimuli balance trade-offs between investment in avoidance behaviour such as alertness, hiding or fleeing, and other activities (e.g. feeding) in the same way used by prey when encountering predators. The risk-disturbance hypothesis has received empirical support in studies on various taxa, including mammals (Frid & Dill 2002), birds (Fernández-Juricic et al. 2003, Peters & Otis 2005) and amphibians (Rodriguez-Prieto & Fernández-Juricic 2005).

A brief summary of anti-predator behaviour
Theory suggests that predator recognition and anti-predator behaviour are based on a combination of a heritable predisposition (i.e. a genetic foundation) and experience (i.e. learning; Maloney & McLean 1995, Blumstein et al. 2004). Besides responses to general threat stimuli (e.g. rapidly approaching objects; Frid & Dill 2002), prey have evolved

responses to specific predators if the risk is strong and the exposure long enough (Blumstein et al. 2004, Blumstein 2006). With a strong genetic basis, even specific anti-predator behaviours may persist long after isolation from the predator. There are several explanations for these observations. The 'ghost of predation past hypothesis' (Peckarsky & Penton 1988, Byers 1998) purports that a prey species will retain anti-predator behaviour after isolation from the predator unless it is too costly to do so (Neill 1990, Blumstein et al. 2004). The 'multipredator hypothesis' predicts persistence of anti-predator behaviour after isolation from some, but not all predators, because these behaviours may be linked genetically (Blumstein 2006). Even in cases of genetically-based anti-predator behaviour, variation in individual responsiveness is expected in every population (Blumstein et al. 2004).

The learned basis of anti-predator behaviour is highly flexible and adaptable (Maloney & McLean 1995, Frid & Dill 2002, Blumstein 2004). Experienced-based predator-avoidance skills may be highly sophisticated, differentiated not only among predator species but also among context-specific risks related to factors such as time (seasonal or diurnal variation in risk), location (availability of cover, distance from predators), number and behaviour of the predators and prey group size (Stankowich 2008). Experience-based behaviour may be lost quickly after isolation from a predator, but may also be quickly restored (Maloney & McLean 1995, Brown et al. 1999, Berger 2007). Likewise, animals may quickly learn new threats such as introduced predator species, or new ways of human hunting (e.g. from cars or aircrafts; Andersen et al. 1996). However, learned responses may be maintained by tradition across generations after isolation from the predator (Maloney & McLean 1995). In birds, social learning is expected to be common and there is evidence both for vertical (inter-generation) and horizontal (intra-population) transmission of behaviours, including predator avoidance (Griffin 2004, Slagsvold & Wiebe 2011).

Anti-predator behaviour and hunting

From the above, hunting may be hypothesised to be a key to understanding variation in the susceptibility of wildlife to human disturbance. If the perceived predation risk affects an animal's response in a human-wildlife encounter, then susceptibility to disturbance will be influenced by hunting. According to the risk-disturbance hypothesis (Frid & Dill 2002),

populations with a long history of human hunting and those with high recent hunting pressure are expected to be most sensitive to disturbance stimuli, whereas populations that have never been hunted tend to behave indifferently towards humans.

Stankovich (2008) reviewed ungulate responses to human disturbance and illustrated how human hunting may affect animal behaviour. Humans were at least as evocative of anti-predator behaviours in ungulates as were wolves *Canis lupus* or other canids. Humans on horseback, on bicycles or in cars, however, were apparently perceived as less threatening (Stankovich 2008). This matches common field experience that many animals can be closely approached by car, unless hunters shoot from vehicles (Andersen et al. 1996). Marked changes in home-range use and escape behaviours have been observed in many game species following the opening of the hunting season (Madsen & Fox 1995). Stankovich's (2008) review further suggested that ungulates in hunting areas show greater flight responses than those in protected areas, and that ungulate response may relax in areas with frequent contact with non-hunting humans, particularly if these occur in a predictable context, such as hikers on trails. This was confirmed in a recent study in Canada where elk *Cervus elaphus canadensis* were most vigilant on public lands with hunting and recreational activities, and least vigilant in a protected area; the authors concluded that "effects of human disturbance on elk behaviour exceed those of habitat and natural predators" (Ciuti et al. 2012:1). Similar findings have been reported for other vertebrate taxa (Caro 1999, Conner et al. 2001, Setsaas et al. 2007, Sasaki et al. 2008, Magige et al. 2009), including grouse (Brøseth & Pedersen 2010).

For some species, humans may not always be the greatest of perceived risks. Berger (2007) provides evidence that prey species may use human presence and their infrastructure as shields against their non-human predators; if predators avoid humans, then habitats frequented or inhabited by humans may be more attractive to prey species than areas without human presence. This suggests that responses of prey species to humans are also affected by interactions between humans and predators.

Animal responses to human hunting may result not only from individual (learning) and social (tradition) experience, but also may have a heritable basis, which evolved during a long history of human exploitation. Recently, population geneticists have reported evidence of rapid evolutionary change in

game populations due to human hunting (Coltman et al. 2003, Sasaki et al. 2008, Darimont et al. 2009, Mysterud & Bischof 2010). So far, these effects have been shown primarily for life-history and morphological traits such as antler characteristics. However, human hunting pressure is likely to have evolutionary consequences in behavioural traits as well. There are examples of European species that appear to be much more timid towards humans than their North American relatives. North American researchers catch grouse using hand-held noose poles (Zwickel & Bendell 1967), a technique that fails in Europe where even non-hunted grouse are intolerant of closely-approaching humans. Ungulate studies suggest that the explanation may be in the longer history and greater intensity of human hunting in Europe compared with North America (Sand et al. 2006). One may speculate that the long history of intensive human predation may not only have influenced ungulates, but also other European wildlife populations, including grouse, for a disposition towards stronger escape behaviours, and thus, greater susceptibility to disturbance.

Grouse responses to disturbance: a framework for research

Based on the conceptual basis outlined above, past and present human hunting provides a key to interpreting variation in the responses of wildlife to encounters with humans. However, an animal's risk allocation and behavioural responses towards humans will vary among species and will be confounded by factors such as habitat, predator community, and timing, location and context of the encounter. Due to methodical constraints, many field studies on the effects of human disturbance on wildlife have been restricted to individual species and/or study areas. Thus, general patterns and population-level effects remained unclear. Combining empirical studies with modelling is a recent, promising approach to overcome the challenges of predicting disturbance effects (Beale & Monaghan 2004, Bennett et al. 2011). In such an approach, empirical data that spans large environmental gradients and various human-wildlife relationships are needed for modelling. Therefore, grouse would make an excellent case for testing predictions of the risk-disturbance hypothesis because grouse inhabit such gradients and associations with humans.

Grouse are widely distributed in the temperate, boreal and Arctic zones of the Northern Hemisphere. Grouse species differ in their habitat associations (tundra, grassland and forests), body sizes ($< 0.5 - > 5$ kg), life-history traits, sociability (solitary to flocking) and mating systems (monogamous pairs to polygamous leks) (Johnsgard 1983). Grouse are exposed to numerous avian and mammalian predators, including humans. All species of grouse have been hunted, and grouse hunting has played a role in local human cultures and economies (Johnsgard 1983). Yet, there are places where grouse very rarely have been exposed to hunters; examples are grouse in remote areas in far northern latitudes and grouse protected from hunting by religious beliefs, such as in Japan (Nakamura 2010). Elsewhere, grouse hunting has been banned for conservation purposes only during the last few decades (Storch 2007b). Grouse responses to humans vary among species and even within the same species. Rock ptarmigan *Lagopus muta* in the European Alps are likely to hide or flush from a hiker (pers. obs.), whereas the same species in the Japanese Alps may tolerate humans at arm's length distance (Nakamura 2007, 2010). Ruffed grouse *Bonasa umbellus* at one location at Lake Superior, Minnesota, USA, allowed a photographer to follow them closely, whereas the species, even within this region, was viewed as particularly wary (Gullion 1989). Similar to Gullion's (1989) experience with ruffed grouse, field researchers report anecdotal evidence of variation in wariness among local populations of grouse, and some have known individuals that appeared to be particularly indifferent towards humans.

Predictions

In grouse, there are many examples of different kinds of past and present hunting practices and intensities (season of hunting, sex and age classes hunted, rifle/ shotgun shooting, stalking/drive hunt, with/without dogs, snaring and trapping). For heuristic reasons, when addressing the risk-disturbance hypothesis, it may be helpful to distinguish between hunted (regularly) and non-hunted (never or very rarely) populations, and consider four scenarios (past/present vs hunted/non-hunted). In the following scenarios 1-4, the risk grouse allocate to humans, and therefore the behavioural responses grouse show when encountering humans, are predicted to vary as follows:

1) Grouse in populations that have never been hunted behave indifferently to the presence of humans. Their response to humans is not different from that towards other larger non-predatory mam-

mals (e.g. ungulates). For example, a grouse would eventually step aside when directly approached by a human, but would not avoid areas regularly frequented by people.

These predictions are consistent with the ecology of the Japanese rock ptarmigan *L. m. japonica* (Nakamura 2007, 2010). With the exception of a short period in the late 19th century, this subspecies has never been hunted. The reason was cultural; according to Shugendo religious belief, the gods lived in the mountains and, by association, the rock ptarmigan was considered a holy species (Nakamura 2007, 2010). Thus, it was safe from hunting. Within the last century, the species has been protected by law. Other cases of grouse species that are relatively fearless of humans exist in parts of North America, and it would be worthwhile to review their history of hunting. Although the predictions from scenario 1) may appear trivial, their documentation would be valuable as a baseline reference for scenarios 2-4.

2) Grouse in populations exposed to intensive past and present human hunting avoid encounters with humans, and will hide or escape when approached by humans at a long distance. They have evolved an innate fear of humans, which is enforced by individual and/or social learning (Griffin 2004, Slagsvold & Wiebe 2011). Grouse in hunted populations are also more susceptible to disturbance from non-lethal recreational activities.

Grouse in North America and northern Europe may match this situation; in many places, they have been hunted intensively for centuries. Three studies explicitly assessed the effects of hunting on grouse responses to disturbances. They indicate grouse will take flight at longer distances and increase the use of dense cover in areas where they are hunted relative to protected areas (Olsson et al. 1996, Thiel at al. 2007, Brøseth & Pedersen 2010), and are thus in agreement with the above expectations. There is no indication, however, that grouse will disperse from areas with even intensive hunting (compare Appendix I); rather, the birds will adjust their investment in avoidance behaviour.

3) Grouse in areas that have been effectively protected from human hunting for at least several generations of grouse, but were exposed to intensive human hunting in the past, are predicted to be intermediate to situations 1) and 2) above. As in 2), one would expect that an innate fear of humans had evolved during the population's history of hunting, which may persist long after isolation from hunters. However, risk-avoidance behaviour is no longer enforced by experience. Thus, individuals with a less responsive disposition may show signs of reduced risk allocation, i.e. habituation, towards humans, which may, via social learning, extend to their social groups.

This situation may hold for grouse in protected areas where hunting is banned, such as National Parks in countries where grouse hunting otherwise is common, and for grouse species in most of Central Europe, where grouse hunting for food, sport and trophies has a long history, but is no longer permitted. For example, capercaillie in Switzerland and all grouse in Germany have been fully protected since the early 1970s (Storch 2000b). These populations no longer have individual experience with hunters, and some evidence of habituation has been suggested (Miquet 1988). However, even after > 40 years without hunting, grouse in most central European situations still retain wariness of humans (Zeitler 2000, Thiel et al. 2008).

4) Grouse in areas where hunting has no history, but has recently been introduced, will quickly learn humans are a threat. As hunters may inadvertently select the less wary individuals, they may exert selection pressure that shapes behavioural dispositions towards avoidance of humans. These predictions might be examined by studying birds in remote areas of the Eurasian or American North that have only recently been exploited by hunting.

A proposal for research

Available studies on human disturbance of grouse are in agreement with the conceptual framework provided by the risk-disturbance hypothesis (Appendix I). However, none of these studies have explicitly addressed the risk-disturbance hypothesis. To test its general predictions regarding the susceptibility of grouse to human disturbance, as sketched in the above scenarios, I propose a cooperative research project across multiple study sites, grouse species and hunting histories. Grouse responses to human presence could be assessed both empirically and experimentally, following standardised field protocols. Research designs should consider past and present hunting, effects of habitat associations, other predator species, life-history traits, social systems, systemic relationships and interactions among these factors.

Such factors can be used to explain variation in observed responses of grouse to humans. For example, susceptibility to disturbance may be affected by habitat quality (grouse in excellent habitat may take

greater risks and flush at shorter distances, as compared to grouse in poor habitat), and by inter-actions between humans and predators: where predators avoid humans, areas with human presence may become attractive habitats for prey species such as grouse (Berger 2007). Anecdotal observations, in tourist resorts in the Alps, suggest that lesser predation risk from golden eagles *Aquila chrysaetos* may partly explain black grouse's continued use of such areas despite disturbance from humans. Beyond the confounding effects of external factors such as habitat and predators, the ethological literature suggests that responses of grouse to humans should be variable among and within species. Individuals within a population are likely to differ in their predispositions for risk allocation and habituation because of individual experience and genetic variability, and likewise, one may expect that social groups (such as lek populations or winter flocks) and local populations develop distinct traditions of responsiveness (Griffin 2004, Slagsvold & Wiebe 2011). As a result, some individuals and some populations may habituate better than others. Also, the demographic history of a population should be taken in account, because individuals within small isolated populations may undergo behavioural and evolutionary change more rapidly than individuals within larger populations with extended distribution (e.g. Lande et al. 2003).

Urgent questions

Finally, I identify questions that are relevant to wildlife managers responsible for managing disturbance issues, and therefore ones I believe should receive priority for research. Disturbance is a management issue particularly in areas where three conditions cooccur: grouse are species of conservation concern, grouse hunting is, or has been in the past, local practice, and outdoor tourism and recreation occur and overlap significantly with grouse habitats.

Is the 'ghost of hunting past' affecting grouse behaviour?

Grouse managers in areas frequented by humans may put high hopes in habituation. With regard to the management of threatened species of grouse, the expected timeframe for habituation is relevant, and thus their susceptibility to disturbance from human outdoor activities. Experience-based behaviour may be lost quickly (i.e. after one or a few generations after isolation from hunting). In populations with a long history of intensive human hunting, however, genetically-based avoidance behaviours may persist long after protection from hunting. According to the 'ghost of predation past hypothesis' (Peckarsky & Penton 1988; see above), grouse formerly exposed to hunting may retain their fear of humans for a long time if there is no cost to maintaining it. Alternatively, the 'multipredator hypothesis' (Blumstein 2006) predicts that grouse exposed to other ground predators would be less likely to lose their fear of humans, as compared to grouse which are primarily subject to avian predation.

Will hunting prevent habituation to non-hunting recreationists?

There are red-listed populations of grouse which are legally hunted (and probably many more where illegal hunting occurs; compare Storch 2007b). However, it is unclear if, and under which circumstances (e.g. practices and intensity of hunting vs types and intensity of disturbances), grouse in hunted populations distinguish between hunters and other recreationists. The ratio of lethal (hunters) and non-lethal (recreationists) encounters between grouse and humans may play a role in the timeframe of habituation (see Stankovich 2008). It is also possible that harassment of grouse by tourists could reinforce adaptive traits of escape responses.

What are the population-level effects of disturbance?

Wildlife managers require guidance about the threshold levels of human disturbance before conservation goals are compromised. So far, there is no answer to this question. Individual responses to disturbance stimuli are insufficient proof of negative effects at the population level. Negative impacts of disturbance on the fitness of individuals and the viability of populations, however, are difficult to show, and have been addressed by only few disturbance studies on grouse (Appendix I). Future work should therefore emphasise comparing vital rates and viability of populations exposed to disturbances relative to undisturbed populations. In this context, it will be important to consider multiple spatial scales from disturbed locations (e.g. a grouse lek) to the annual ranges used by local populations.

anonymous reviewers, John Bissonette and R.J. Gutiérrez helped to improve the manuscript.

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Appendix I. Studies (chronological order) that assess various non-lethal effects of human disturbances on grouse. Disturbance stimuli considered were restricted to recreational activities, including hunting.

Study	Species, location	Disturbance type	Study approach	Response variables	Explanatory variables	Result/interpretation
Miquet 1986	Black grouse; Alps, France	Ski resort	Radio-telemetry, direct observation	Range use, reproductive success	Ski resort as compared to undisturbed areas	No differences in range use and reproductive success between ski resort and undisturbed areas
Baydack & Hein 1987	Sharp-tailed grouse; Manitoba, Canada	Human presence and activities at leks	Experimental disturbance, telemetry	Lek attendance, displacement	Disturbed vs undisturbed leks	Human presence displaced grouse from leks; females did not visit disturbed leks, while males returned to the lek upon cessation of disturbance
Olsson et al. 1996	Willow ptarmigan; Sweden	Hunting, experimental flushing	Telemetry	Movements	Presence or absence of hunting	No difference in movement rates and distances; no difference in timing of seasonal migration
Zeitler 2000	Black grouse; Alps, Germany	Ski resort	Direct observation	Presence, range use	Ski resort as compared to less disturbed areas	Continued presence of birds and opportunistic use of resources > 20 years after ski resort development; temporal separation of habitat use by grouse and humans
Pitman et al. 2005	Lesser prairie chicken; Kansas, USA	Human land use, roads, oil and gas development	Telemetry	Nest location, nest success	Distance from anthropogenic features	Nesting grouse kept distances between 80-1000 m from anthropogenic features; nest success was not related to distance from such features
Baines & Richardson 2007	Black grouse; North Pennines, UK	Encounters with/without flushing	Experimental disturbance, telemetry	Flight initiation distance	Intensity of disturbance	More regularly disturbed birds flush at longer distances
				Movements	Intensity of disturbance	No differences in home-range sizes and movements in relation to disturbance levels
				Demographic rates	Intensity of disturbance	No differences in reproductive success or survival rate in relation to disturbance levels

Appendix I. Continued

Study	Species, location	Disturbance type	Study approach	Response variables	Explanatory variables	Result/interpretation
Thiel et al. 2007	Capercaillie; Pyrenees, France	Simulated hiker	Visual observation	Flight initiation distance	Presence or absence of hunting	Birds in areas with hunting flush at longer distances
	Black Forest, Germany	Simulated hiker	Telemetry, direct observation	Flight initiation distance	Intensity of winter tourism	Birds in more disturbed areas flush at longer distances
Summers et al. 2007	Capercaillie; Scotland, UK	Human activities on woodland tracks	Indirect sign	Presence of droppings under trees	Distance from tracks	Avoidance of trees along tracks
Patthey at al. 2008	Black grouse; Alps, Switzerland	Winter sports	Direct observation	Abundance of displaying males	Density of ski lifts; hunting pressure	Abundance of displaying males negatively correlated with density of ski lifts; no difference in relation to hunting
Thiel et al. 2008	Capercaillie; Black Forest, Germany	Winter sports	Telemetry	Home range	Intensity of winter sport activities	No change in home-range location; preference for least-disturbed parts of home range
		Winter recreation	Faecal analysis	Corticosterone metabolite levels	Intensity of winter sport activities	Increased stress levels in birds in more disturbed areas
Brøseth & Pedersen 2010	Willow ptarmigan; Norway	Hunting	Telemetry	Movements	Presence or absence of hunting	No difference in home-range location and size and no difference in movement rates and distances in relation to hunting
				Habitat use	Presence or absence of hunting	Greater use of dense habitats in hunted areas
				Demographic rates	Intensity of disturbance	No differences in reproductive success in relation to disturbance level
Thiel et al. 2011	Capercaillie; Alps, Switzerland	Winter recreation	Faecal analysis	Corticosterone metabolite levels	Distance from winter recreation activities	In spruce forest, but not in pine forests, increased stress levels in birds closer to recreation activities

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Appendix I. Continued

Study	Species, location	Disturbance type	Study approach	Response variables	Explanatory variables	Result/interpretation
Formenti et al. 2012	Black grouse; Alps, Italy	Skiing	Faecal analysis	Corticosterone metabolite levels	Intensity of use by skiers	In one of two winters: higher stress levels in birds in highly disturbed areas and closer to ski lifts found
Hess & Beck 2012	Greater sage grouse; Wyoming, USA	Human land use, roads, oil and gas development	Lek abandonment	Lek occupancy	Landscape variables at various radii around leks	Oil and gas wells in 1-km radius was strongest predictor of lek occupancy; energy development increases lek abandonment
Moss et al., in press.	Capercaillie; Scotland, UK	Human activities on woodland tracks	Indirect sign	Frequency of droppings	Distance from tracks	Fewer droppings closer to tracks and track entrances; avoidance of habitat along tracks
K. Hirschenberger, V. Grünschachner-Berger, unpubl. data	Capercaillie; Alps, Austria	Winter tourism	Faeces	Corticosterone metabolite levels	Distance from ski route	Stress levels in male capercaillie explained by interactions between habitat structure, presence of other males, and distance from ski run