EFFECTS OF NON-CONSUMPTIVE LEISURE DISTURBANCE TO WILDLIFE

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RÉSUMÉ. — *Effet des activités de loisirs non consommatrices sur la faune sauvage.* — Les activités de loisirs sont de plus en plus variées et répandues, ce qui peut augmenter leurs effets en termes de dérangement de la faune sauvage. Dans cet article, nous présentons une synthèse des connaissances actuelles sur l'effet des activités de loisirs non consommatrices (ne prenant pas en compte la chasse et la pêche, dont les effets ont été largement étudiés par ailleurs) pour les espèces sauvages. L'objectif n'est pas de fournir une revue exhaustive de la littérature, mais plutôt de présenter une sélection des publications pertinentes sur les différents aspects du sujet. Nous présentons d'abord les différentes définitions de la notion de dérangement, listons les activités reconnues comme les plus dérangeantes et les espèces ou groupes taxinomiques considérés comme les plus sensibles. La définition du dérangement que nous retenons ici est « toute déviation du comportement normal en réponse à des événements inattendus à proximité d'un animal ». Une grande variété d'activités de loisirs peuvent entraîner un dérangement de la faune sauvage, en particulier celles employant des véhicules à moteur ou celles amenant un contact rapproché entre le pratiquant et la faune sauvage (que ce rapprochement soit recherché ou non). La littérature démontre que tous les groupes animaux peuvent potentiellement être affectés par les activités de loisirs, même si c'est chez les oiseaux et les mammifères que le phénomène a été le plus étudié. Suite à ces définitions et revues initiales, nous résumons les différents modes de mesure du dérangement, mettant en exergue le fait que le changement de comportement des animaux, même s'il est un critère souvent évident à mesurer, n'est pas forcément le meilleur indicateur du dérangement. Car les individus commencent généralement à ressentir ses effets avant de modifier leurs activités ou de quitter la zone dérangée. Nous présentons ensuite les différentes échelles auxquelles le dérangement a été étudié, du comportement individuel à la dynamique des populations, les effets sur les populations étant évidemment les plus difficiles à mesurer, mais aussi les plus cruciaux à long terme. Nous suggérons donc quelques perspectives de recherche, en particulier le besoin reconnu de travaux expérimentaux et sur les conséquences du dérangement à long terme pour la valeur sélective des individus, donc la dynamique des populations. C'est en effet à cette échelle que doivent être prises les mesures de gestion adéquates dans le futur.

SUMMARY. — Human leisure activities are becoming more and more various and widespread, which may increase their potential consequences for wildlife in terms of disturbance. This paper summarizes existing knowledge on the effect of non-consumptive (*i.e.* not hunting nor fishing) leisure activities on wildlife. The aim is not to provide an exhaustive literature review but through the selection of relevant literature to examine the various aspects of the subject. First, we present the different definitions of disturbance, list the types of activities most likely to affect wildlife, and the species or taxonomic groups generally considered as being the most susceptible. Then, we summarize the various means of measuring the effects of disturbance, highlighting the fact that, though generally most obvious, changes in animal behaviour are not necessarily the most appropriate index of disturbance. Then we present the various scales at which disturbance has been studied, from individual behaviour to population dynamics. Finally, we suggest further research priorities, especially the recognized need for more experi-

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mental studies and studies of long-term effects of disturbance on individual fitness, hence population dynamics, since it is at this scale that appropriate management measures of disturbance have to be taken in the future.

Current threats to global biodiversity have lead many scientists to study the consequences of human-induced disruption of wildlife. On the one hand, many wild animal species face habitat change and loss linked with human activities, and/or hunting or fishing uptakes. Consequently, these potential threats have already been well documented, and many conservation measures in protected areas aim at reducing their impact. On the other hand, disturbance induced by non-consumptive leisure activities has long been neglected. In the current context of a rapid increase in these activities, it seems essential to be able to quantify their effects on wildlife.

Here we consider the potential influences of leisure activities on wildlife. Many examples are related to waterbirds, which live in habitats where spatio-temporal competition with man can sometimes be acute (*e.g.* Boer & Longamane, 1996), and at the same time are often flagship species of wetland biodiversity (*e.g.*, Rodgers & Schwikert, 2002). Many studies dealing with leisure disturbance have been published, and we summarize them in this paper so as to propose a synthesis of current knowledge, show potential limits and gaps, and highlight management and conservation perspectives.

It is a fact that leisure activities lead to other perturbations than simply disturbance of individuals: for example, trekking people can directly disturb animals, but trekking can also be associated with local habitat change linked, for example, to foot trampling (*e.g.* simplification of the vegetation structure, soil erosion... Speight, 1973 in Boyle & Samson, 1985; Liddle, 1975). Leisure activities can also be associated with the building of dedicated infrastructures (Davidson & Rothwell, 1993a), or be the source of various pollutions (of air or water, through rubbish or sound production). Leisure activities can also lead to voluntary killing of animals (sport hunting and fishing). We will not consider here these so-called "consumptive" activities, since their effects have long been studied and earlier and recent reviews have already been published (*e.g.* Madsen & Fox, 1995; Madsen, 1998b; Tamisier *et al.*, 2003 for a review).

Disturbance therefore is only one aspect of perturbations associated with outdoor leisure activities. It is precisely because the effect of disturbance is more subtle and thus difficult to ascertain that further work on this question is needed. Our aim was not to produce an exhaustive review of all papers dealing with the subject, but rather to present a selection of pertinent studies highlighting the diversity of the influence of disturbance, and of the species potentially concerned.

We first define the essential terms linked with disturbance, then review the leisure activities most likely to disturb animals. We then consider the different consequences of disturbance on wildlife in general, and waterbirds in particular, and finally summarize management and conservation implications, as well as identified future research needs.

DEFINITIONS OF DISTURBANCE TERMS

Most of the definitions we present here are from authors working with birds, but they can often be generalized to all wildlife.

The notion of disturbance might be confusing, because disturbance is generally associated, and often confounded with the more general notion of perturbation. In ecology, perturbation is a very general term, describing discrete events in time that affect populations, ecosystems or landscapes by affecting their structure and functioning, as well as the physical environment (Dajoz, 2000). Therefore this encompasses unpredictable natural perturbations like climatic events, fire, flooding, drought, etc, but also human-induced perturbations. Disturbance is only one type of perturbation.

Boere's (1975) definition of disturbance is "any situation in which a bird (an animal) behaves differently from its preferred behaviour". Some authors only consider the human-induced part of disturbance, which is then defined as any situation in which human activities lead birds (animals) to behave differently than they would in the absence of these activities (Oranjewoud, 1982, in Smit & Visser, 1993). This definition therefore excludes "natural" disturbance, linked for example to predators' appearance, even if of course natural perturbation by predators is frequent, notably its disturbance part (Johnson & Rohwer, 1996 in Triplet *et al*., 2003; Quinn, 1997; Fritz *et al*., 2000). Following Cayford (1993) "Disturbance is a rather nebulous concept which loosely describes causal relationships between a wide range of (usually) anthropogenic stimuli and the responses they elicit in animals. Disturbance can be described operationally as any relatively discrete event in time that disrupts ecosystems, communities or populations, where disruption refers to a change in behaviour, physiology, numbers or survival. Disturbance varies in its magnitude, frequency, predictability, spatial distribution and duration".

The most general agreed definition of disturbance seems to be the one of the European Commission, cited by Harradine (1998): a disturbance is "any phenomenon that may cause a significant change in the dynamics of a population or the ecoethological characteristics of populations". The European Directive 92/43/CEE ("Habitats Directive") states (article 6, paragraph 2) that " Member States shall take appropriate steps to avoid, in the special areas of conservation, [...] disturbance of the species for which the areas have been designated, in so far as such disturbance could be significant in relation to the objectives of this Directive ". Significance in this case can be judged after several criteria, but a disturbance will be considered "significant" if the event "contributes to the long-term decline of the population of the species on the site", "contributes to the reduction or to the risk of reduction of the range of the species within the site" or "contributes to the reduction of the size of the habitat of the species within the site" (European Commission, 2000).

For some authors, only these patterns occurring at the scale of population dynamics should be used as indicators of disturbance, since the lack of behavioural reactions at the scale of individuals may simply be constrained by the absence of alternative behavioural options (*e.g.* Gill *et al*., 2001a). Of course, the above definition often remains theoretical, for it is difficult to evaluate if an individual's reaction to a disturbance event will significantly affect population dynamics, for example (Triplet *et al*., 2003). In practice, is considered as a disturbance "any deviation from normal behaviour in response to unexpected occurrences in the vicinity of a bird [an animal]" (Platteeuw & Henkens, 1997). This is the definition we will use in this review. The same term will be used to define the action and the effect of this action (Triplet *et al*., 2003), despite the pertinent remarks of some authors concerning the potential ambiguity of this semantic ambivalence (Nisbet, 2000). As underlined by Patonnier (2000), it is important to distinguish short-term direct effects (stopping of the current activity, vigilance, escape, death), from long-term direct effects (alteration of behaviour, of daily activity rhythm, of animal distribution, of demographic parameters) and from indirect effects (increase of predation rate, penetration of habitats by communication paths, hunting of sympatric species).

It has also been suggested to distinguish the "impact", and the "effect" of disturbance (Hill *et al*., 1997; Triplet *et al*., 2003). The effect is the reaction of the animal (which can be visible or not for the observer) following a disturbance. By potentially affecting survival or reproduction of individuals, these effects can reverberate at the higher population level. This repercussion at the population level will be called impact (either significant or not; Triplet *et al*., 2003). We will therefore consider that these two interdependent notions are associated with two distinct organization levels: "effects" on individuals and "impacts" on populations. This is different from some authors, who distinguish significant impacts and non-significant effects on populations (Triplet *et al*., 2003). However, because it is often difficult to determine in the field if a disturbance has a significant effect or not, we will distinguish impacts from effects on the basis of the organization level at which they occur.

Potentially disturbing activities

Outdoor leisure activities are numerous, and occur in all types of habitats, either aquatic (coasts, estuaries, marshes and lakes) or terrestrial (almost all of them). These activities mostly differ in terms of their nature, intensity (which can be measured in terms of frequency, *i.e.* number of events per unit of time, density, *i.e.* number of events per unit of space, or regularity, *i.e.* predictability), and periods of occurrence. These differences translate into contrasted importance of the effects and impacts of the disturbance they induce (Burger, 1981; Klein *et al.*, 1995; Rodgers & Smith, 1997; Rodgers & Schwikert, 2002). These activities can be divided in those practised with a motor vehicle (motocross, 4-wheel drive, quad, snow bike, planes, and boats) and those without. Among the latest, it is possible to distinguish visit activities, mainly associated with tourism and eco-tourism (walking with or without a dog, nature observation and photography, etc.), from more sportive activities like biking, climbing, trekking, skiing, as well as water activities like swimming, sailing or windsurfing... Among the vulnerable bird species potentially affected by tourism and leisure activities in France, 56.8% were affected by simple walkers (with or without dogs), while only 2.4% suffered regular disturbance from leisure motor vehicles (MATE/DNP, 2000).

All these leisure activities can potentially be sources of major income, and are therefore an essential element of local economy. In addition, some of them, like for example nature observation, can be the basis for public information related to environmental questions in general, and the protection of natural habitats and species in particular. However, the interference of outdoor leisure activities with wildlife also makes them potential sources of disturbance. Because they are practiced in natural, sometimes protected, habitats, the nuisance caused by these activities may even force animals to leave the area, while these species are precisely those one tries to protect and promote the interest for in the public (Carney & Sydeman,1999).

Are participants aware of the problem?

Some authors, like Klein (1993), raise the question of whether people practicing outdoor leisure activities are aware of the potential disturbance they cause. In some few activities, participants try to measure and mitigate their effects, or at least are conscious they can be sources of disturbance (*e.g.* scientific research, though this is generally not practiced as a hobby; Brown & Morris, 1995). However, most people practicing outdoor activities, and the broad public more generally, do not think their activity can affect wildlife (Taylor & Knight, 2003; Grossberg *et al.*, 2003), even if they see animals reacting (Cooper *et al.*, 1981). People generally do not feel responsible for causing trouble, as soon as they have followed the instructions they were potentially given (Klein, 1993; Taylor & Knight, 2003). Natural habitats managers themselves are not always conscious they can be sources of disturbance (Farell & Marion, 2001), while this has been demonstrated (Boyle & Sampson, 1985).

Which species are concerned?

To some degree, almost all animal species are sensitive to leisure activities practiced in the habitats they inhabit, and highly specialized species or species with the smallest geographical ranges should especially be so. Among vertebrates, birds, especially waterbirds, are the most studied group (see Dahlgren & Korschgen, 1992, for an annoted bibliography; Triplet *et al.*, 2003, for a general review), followed by mammals, while the herpetofauna is very rarely considered (Boyle & Samson, 1985). Of course, the difference between these groups only reflects the contrasted interest of researchers, not necessarily the intensity of threats they face. Among the 131 vulnerable species in France to which some human activities may have a significant negative impact on populations, 81 (61%) were potentially affected by tourism and non-consumptive leisure activities (MATE/DNP, 2000).

All wildlife species are not equally sensitive to disturbance (*e.g.* Burger & Gochfeld, 1998; Rodgers & Schwikert, 2002, for waterbirds; Fernandez-Juricic *et al.*, 2001, for urban birds). Estimating sensitivity is a difficult task, and results for the same species are sometimes contradictory, since they do not only depend on populations and individuals (genetic dispositions, physiological state, individual paradigm, habituation...), but also on the period of the year, the physical environment, the study place, etc. Some authors have tried to rank species after their level of susceptibility to disturbance which, in the case of waterbirds for example, provided sometimes opposite results: Platteeuw & Henkens (1997) ranked 7 species as follows, from less to more susceptible: Coot *Fulica atra*, Great Crested Grebe *Podiceps cristatus*, Mute Swan *Cygnus olor*, Great Cormorant *Phalacrocorax carbo*, Pochard *Aythya ferina*, Tufted Duck *Aythya fuligula*, Gadwall *Anas strepera*, Shoveler *Anas clypeata*. Considering only wildfowl species, Tuite *et al*. (1984) found the following ranking, from less to more susceptible: Pochard, Tufted Duck, Common Merganser *Mergus merganser*, Mute Swan, Mallard *Anas platyrhynchos*, Wigeon *Anas Penelope*, Teal *Anas crecca*, Shoveler, Goldeneye *Bucephala clangula*. While Shoveler was among the most susceptible species to disturbance in both cases, the differences between *Aythya* species and Mute Swan were opposite in the two cases.

In the same way, it is difficult to rate activities after their disturbance levels, for this depends very much on the way they are practiced, their intensity, frequency, as well as local specificities (*e.g.* topography, history of sites...). However, even if results are sometimes contrasted, general patterns nonetheless emerge.

Levels of disturbance

The relationships between wildlife and leisure activities show a great variety: in some activities, the contact with animals is more or less sought for (ecotourism, trekking to some extent), while this is less the case for most sports or riding/driving of vehicles, for example. However, most participants look for the "natural" character of the area where they practice their activity, which of course is important in terms of disturbance.

Disturbance seems to be more intense when activities are dispersed within the habitats, or not practiced on predictable paths. For example, boats outside the established channels elicited the strongest response by breeding Common Terns *Sterna hirundo* (Burger, 1998). In the same way, trekking people going off-track enlarge the perturbation area, therefore increasing the consequences of disturbance. This has been showed many times, like *e.g.* in Peak District National Park, UK, on Golden Plover *Pluvialis apricaria* (Finney *et al.*, 2005), in the Swiss Alps for Marmot *Marmota marmota* (Mainini *et al.*, 1993), in Colorado, USA, for American Robin *Turdus migratorius*, Mule Deer *Odocoileus hemionus*, Vesper Sparrow *Pooecetes gramineus* and Western Meadowlark *Surnella neglecta* (Miller *et al.*, 2001). In the same way, people looking for mushrooms or off-track skiers, because of their sinuous paths, are more likely to cause disturbance on large areas (Patonnier, 2000). Zegers (1973 in Smitt & Visser, 1993) showed that a single walking person on an estuary can lead to the departure of most Oystercatchers *Haematopus ostralegus*, Curlews *Numenius arquata* and Common Redshanks *Tringa totanus* from their favoured site, while only 9% of birds initially present remained. In most cases the canalization of perturbations to precise areas and paths has been recommended. It has been showed that people looking for direct and close contact with wildlife potentially cause more disturbance than people practicing activities where these contacts are not voluntary. It is likely that the frequent and longer confrontations in the first case, as opposed to occasional and furtive contacts in the second, are responsible for this difference in effects (Boyle & Samson, 1985). Some studies have found pedestrian activities to cause more disturbance than the circulation of vehicles (Freddy *et al.*, 1986; Klein, 1993; Taylor & Knight, 2003), probably because animals react more to the shape of a human body. However, because they are associated with greater speed and louder noise, some motor activities like motor boating have been found to be most disturbing, to wildfowl (*Anatidae*) for example (Matthews, 1982). Nevertheless, windsurfing or kayaking, even if they are more silent activities, may induce major disturbance, because of their penetration in otherwise "sanctuary" areas inaccessible to pedestrians: windsurfers and boats have for example been held responsible for the total desertion of a lake by all wildfowl species in the Netherlands (Tuite *et al.*, 1984).

Dogs accompanying walkers in natural areas are a major source of disturbance, especially if not kept on leash, which can easily be explained by the predatory (or predatory-like) behaviour of dogs. For example, it has been shown on Mediterranean Mouflon *Ovis gmelini musimon* x *Ovis* sp that the passage of a dog, even not barking, induced changes in the behaviour of the animals (Martinetto *et al.*, 1998). Dogs off leash were also one of the main sources of disturbance of Western Snowy Plover *Charadrius alexandrinus nivosus* (Lafferty, 2001). In addition, people walking dogs are more likely to leave designated paths, which we have seen is increasing disturbance (Martinetto *et al.*, 1998).

EFFECTS AND IMPACTS OF DISTURBANCE ON WILDILFE

Indices of disturbance occurrence

The main effect of disturbance, also the easiest to detect, is the change in the behaviour of the animals (vigilance), either associated with movement and escape or not. Many studies consider the distance between the source of disturbance and the animal showing a reaction as an estimator of animals'susceptibility to disturbance (*e.g.*, Rodgers & Smith, 1997). For birds, it is thus most generally the distance within which the individual takes flight (Beale & Monaghan, 2004b). However, it has to be kept in mind that the take-off distance of a bird is shorter (30% less on average, after Van der Meer, 1985 in Smit & Visser, 1993) than the distance inducing the first change in behaviour. For this reason, Fernandez-Juricic *et al.* (2001) recommend the use of alert distance ("the distance between an animal and an approaching human at which point the animal begins to exhibit alert behaviours to the human") instead of flight distance, because alert distance encompasses a buffer area in which birds may adapt their reaction to the behaviour of visitors. In most studies, the measure of this take-off distance is empirical, through the observation of disturbances and the reaction of animals to it (*e.g.*, Smitt & Visser, 1993). Some studies, however, have a more experimental approach, trying to standardize the disturbance event: for example, the same observer will walk towards flocks of individuals, measuring the distance at which the birds take flight in different circumstances (*e.g.*, Lord *et al.*, 2001). These distances of reaction allow establishing areas of animals susceptibility, in which any stimulus will lead to a change in the behaviour of individuals. This consequently corresponds to the undisturbed area necessary to these individuals (buffer zone distances, *sensu* Rodgers & Smith, 1997). For example, Taylor & Knight (2003) estimated that 70% of Bison *Bison bison*, Mule Deer and Pronghorn *Antilocapra americana* fled at a distance of 100 m. Another estimator of disturbance is the time necessary for individuals to return to their initial activity, which also provides information on the length of disturbance events (Madsen, 1998a).

These estimators of disturbance suffer from two main limitations: first, they are highly dependent on local conditions and the nature of the activity, and are therefore hardly transposable to other places and times, as is generally the case of studies dealing with disturbance (Davidson & Rothwell, 1993a). Secondly, sensitivity and vulnerability are complex questions, which are not always correlated with observed reactions of the individuals. It is therefore difficult to link observed effects and their potentially negative effects on the individual in the longer term (as also underlined by Burger & Gochfeld, 1998). Caution should thus always be taken when interpreting observed effects, especially when the aim is to subsequently study impacts at the higher organization level, or implement local policies for the management of disturbance. Gill *et al.* (2001a), for example, argue that in some conditions the species most susceptible to disturbance could be those not showing escape responses, if this lack of response is simply constrained by the absence of possible alternative strategies. Individuals from those species therefore would have to suffer the costs of disturbance, while individuals able to move away would simply have to pay the cost of moving away.

Consequences of disturbance

Studies of disturbance on wildlife often show negative, sometimes neutral but very rarely positive consequences (Boyle & Samson, 1985), though part of this may be linked to the reluctance of researchers to submit manuscripts showing counter-intuitive positive effects of human activities. In natural habitats, the effects of different perturbations are likely to be additive to each other (Davidson & Rothwell, 1993b), animals therefore being submitted to the different cumulative effects of natural and human-induced stresses (Duchesne *et al.*, 2000). This makes difficult the isolation of disturbance effects *per se*, especially if disturbance only affects animals indirectly through intensification of other selection pressures.

Effects on individuals

At the individual level, the perception of a disturbance stimulus will induce gradual fear reactions in animals, whose evolutionary significance is the protection of the individual towards danger. These reactions can be:

— Physiological: they can occur through an increase in the cardiac rhythm (Platteeuw & Henkens, 1997 for waterbirds, Weimerskirch *et al.*, 2002, in the Wandering Albatross *Diomedea exulans*), or in the level of circulating stress hormones (Romero & Romero, 2002, in birds). In some species, physiological responses have been demonstrated while no behavioural response was apparent (*e.g.*, Wilson *et al.*, 1991). In the longer term, it is known that such physiological stress can reduce breeding success (Silverin, 1986, for birds).

— Behavioural**:** in most cases increase in vigilance and/or escape. The individual tries to avoid perturbation, by moving to "refuge" less disturbed areas. These refuge areas are generally less profitable (lower food abundance, higher competition, higher predation risk, etc.; Tuite *et al.*, 1984).

Of course, following Oranjewoud (1982, in Smit & Visser, 1993) definition, vigilance and escape responses occur at the expense of the activities the individual would have if undisturbed. In most cases, disturbance induces a reduction in foraging or resting time, which has a double energy cost: a reduction in food intake linked to shorter foraging times and the use of poorer areas, and an increase in energy expenses through energy-costly reactions (*e.g.*, in Woodcock *Scolopax rusticola*, the energy cost of flight represents more than 17 times the basal metabolic rate of a resting individual, Duriez, 2003). To illustrate these phenomena, Don White *et al.* (1999) have quantified the effect of disturbance on Grizzly Bear *Ursus arctos horribilis* by alpinists in Montana, USA: this leisure activity lead to a 53% reduction in feeding time by the bears (energetic cost estimated at 12 kcal not ingested per minute), a 52% increase in movements and a 23% increase in aggressive behaviours. In the same way, Asian Rhinoceros *Rhinoceros unicornis* show a reduced foraging time and an increased vigilance activity due to tourist visits (Lott & Mc Coy, 1995).

Knock-off effects of disturbance on body condition have been demonstrated, for example in females Chamois (*Rupicapra rupicapra*) which, if living in an area frequently overflew by paragliders, show a lower body mass and fewer lipid reserves (Ingold *et al.*, 1996 in Patonnier, 2000; Schnidrig-Petrig, 1998). Mosbech & Glahder (1991) also suspected that massive helicopter traffic for oil exploration activities in Greenland may have prevented Pink-footed Geese *Anser brachyrhynchus* from fulfilling their daily energy requirements in summer.

In addition to foraging and resting activities, negative consequences of disturbance have also been recorded for maintenance and reproductive activities, like alteration of pairing displays, egg-brooding, caring of young, etc., which can negatively affect parent-offspring relationships (Klein, 1993).

At the upper level, the costs associated with disturbance can also translate into a lower breeding success, as documented in Adelie Penguin *Pygoscellis adeliae* by Giese (1996), in Oystercatcher by Verhulst *et al*. (2001), in Guillemot *Uria aalge* and Kittiwake *Rissa tridactyla* by Beale & Monaghan (2004b), and reviewed by Frid & Dill (2002).

Factors affecting individual response

The reaction of an animal to a potentially disturbing stimulus is the result of a complex trade-off between many factors acting at various levels, from the propagation or perception of the stimulus to its interpretation by the animal, and its choice to respond to it or not. Among these factors are the individual paradigm and characters, either genetic, behavioural (shy or not), physiological (body-condition, stress hormones), social (dominant or subordinate), historical (see habituation below) and secondly the environmental conditions (refuge availability, climatic conditions, etc.).

Beale & Monaghan (2004a) suggest that birds in the best body condition, perceiving their environment as being of good quality or having more refuge alternatives are the most likely to respond to human disturbance and are more vigilant. In this case, individuals responding the most would therefore be those less susceptible to suffer from consequences of perturbations in terms of fitness (while indexes used to measure the effects of disturbance generally assume the opposite). It has to be kept in mind, for example, that individuals foraging in poorer areas will be more likely to leave if disturbed (*e.g*., Frid & Dill, 2002), and that disturbed individuals will leave foraging patches earlier, *i.e*. have higher giving-up densities (Gill *et al*., 1996; 2001b).

Effects on spatial distribution

Because of the movements and potential departures it induces, disturbance linked with leisure activities may affect the spatial distribution of animals as well as, in consequence, their number at particular sites. For example, Killer Whale *Orcinus orca* are more likely to leave the Ecological Reserve of Robson Bay (Canada) when the number of whale-watching boats increases (Trites *et al*., 1995 in Williams *et al*., 2002), while Golden Plover distribution is affected by trekkers in some areas (Finney *et al*., 2005).

Generally speaking, most studies show that escape movements lead to local or regional redistribution of individuals towards their concentration in refuge areas (*e.g*., Tuite *et al*., 1984; Marsden, 2000), which can have profound consequences. Following the Ideal Free Distribution (Fretwell & Lucas, 1970), individuals select the most profitable foraging strategy from an energy point of view, selecting both the less costly foraging behaviour and the most profitable prey and foraging sites. Disturbance will affect the natural distribution of individuals, mainly through an increase in animal density in refuge areas. This will in most cases lead to higher food depletion rates and interference competition (Goss-Custard, 1980; Sutherland, 1996). Food access in refuge areas can therefore become the limiting factor of a population while more disturbed areas can remain under-exploited (Tamisier & Dehorter, 1999). It may then be the carrying capacity in refuge areas that limits population size (Patonnier, 2000). However, it has to be kept in mind that even if local redistributions of individuals are relatively easy to study, it is very difficult to assess regional redistribution, and the consequences of disturbance at this scale. In some studies, conversely, disturbance seems to have very limited effects on movement and distribution of animals (Boyle & Samson, 1985).

The effect of disturbance on spatial distribution may also profoundly differ between species: upon the approach of a boat, Mute Swan and Coot will more likely swim away for short distances, while Wigeon most frequently take flight directly to less disturbed areas, or leave the site completely (Madsen, 1998a).

Disturbance and gregariousness

The tendency of individuals to get in flock or not may influence the way they respond to disturbance, but studies dealing with this subject have provided contradictory results: for example, Manor & Saltz (2003) consider that Mountain Gazelle *Gazella gazella* in larger flocks spend less time vigilant (as found in other ungulates by Hunter & Skinner, 1998, but also as most gregarious animals generally do, Krebs & Davies, 1993)**.** They also suggest that this size effect tends to decrease if the intensity of disturbance increases, *i.e.* individuals in larger flocks would get fewer benefits in terms of reduction of vigilance. Other studies show that individuals in larger flocks generally react less to disturbance (Recarte *et al.*, 1998; Gutzwiller *et al.*, 1998), while some papers suggest, on the contrary, that sensitivity to human perturbation is higher in larger groups (*i.e.* larger groups showing higher escape distances), because the probability of encompassing a shy individual which will take-off and frighten its congeners is higher in larger groups (Taylor & Knight, 2003). Studying the relationships between disturbance and animals social structure is a complex task, due to the influence of both environmental (*e.g.*, opening of the land, Manor & Saltz, 2003) and intrinsic factors on these mechanisms.

Effects on habitats and communities

Leisure activities may reduce the overall carrying capacity of sites (*e.g.*, Tuite *et al.*, 1984, for wildfowl), and can therefore be comparable to habitat loss. Hill *et al.* (1997) underlined the fact that habitat loss linked with leisure activity disturbance is different from the one caused by other human perturbations like buildings, drainage, etc., since in the first case the loss of habitat is reversible. It is actually more a loss of habitat availability rather than a true loss of the habitat itself (the habitat still exists, but temporarily cannot be used by wildlife): once leisure activities decrease in intensity, animals can use the area again. Evans & Warrington's (1997) study illustrates these patterns: in the protected area close to London they monitored, the authors showed that during week-ends the bird community significantly differed from during the week. They also recorded a 19% increase in bird numbers, which can even reach 50% in some species (Pochard, Mallard and Goldeneye) and illustrates the desertion of surrounding, disturbed areas. In this case, Pochard apparently were less selective in the choice of their habitat, and additional individuals apparently were excluded from the best, more sheltered, resting areas.

Similarly, Camp & Knight (1998), studying three Californian sites with different disturbance (*i.e.* rock climbing) levels, showed that bird communities differed markedly. In particular, the more heavily disturbed sites were more favourable to species with a broad ecological niche, like American Robin, European Starling *Sturnus vulgaris*, Brown-headed Cowbird *Molothrus ater* and House Finch *Carpodacus mexicanus*.

Adaptation to disturbance

Animals can get used to disturbance under some conditions, through behaviours aiming at reducing or compensating its effects: these are the habituation and compensation phenomena.

Habituation

Habituation is the mechanism by which organisms minimize their reaction or stop reacting completely to a stimulus, therefore avoiding useless energy expenses (Boudreau, 1968). Habituation is frequent in animals, and Nisbet (2000) considers that most colonial waterbirds can become extremely tolerant to repeated human disturbances. He even suggests that the management of natural areas should promote this habituation whenever possible, so that this will make research, education and leisure activities easier. Of course, habituation can only appear when animals face repeated and predictable stimuli, which do not represent a true lethal threat (Conomy *et al*., 1998b). For example, Brilman (1989 in Smit & Visser, 1989) observed a whole Bewick Swan *Cygnus columbianus* population (1400-4300 individuals) deserting a lake after the building and one year of use of an Ultra Light Motorized track, while Lapwing *Vanellus vanellus*, Gulls (*Larus* spp.), and Starling are common birds in airports, where take-off and landing patterns are more predictable. On the other hand, Béchet *et al*. (2004) showed that animals do not habituate to activities like hunting, which do represent a threat. On the contrary, a "Facilitation" phenomenon will arise in this case (Platteeuw & Henkens, 1997), which is defined as the pattern by which animals get more and more likely to react to more intense, less predictable and potentially more dangerous disturbance as they get more experienced. All species therefore do not have the same capacity for habituation, leading many authors to consider habituation as a specific phenomenon (Bélanger & Bédard, 1990). Conomy *et al*. (1998b), for example, showed that Black Duck *Anas rubripes* were habituating more to planes than Wood Duck *Aix sponsa*. Overall, only 2% of Black Duck, American Wigeon *Anas americana*, Gadwall and Green-winged Teal *Anas crecca carolinensis* reacted to over-flying planes (Conomy *et al*., 1998a). Habituation does not only depend on individuals and species, but also on local conditions, especially the nature of the disturbing activity, its intensity and frequency of occurrence, as already stated. Habituation time therefore is highly variable: Boudreau (1968) suggests that small passerines like House Sparrow *Passer domesticus*, Red-winged Blackbird *Agelaius phoeniceus* or Brown-headed Cowbird can habituate to a disturbance source in short periods of time, from an hour to 5 days, while Conomy *et al*. (1998b) consider learning time to be 2-17 days for Black Duck in the field.

The question of the threshold intensity at which habituation occurs also divides researchers: some authors consider that habituation is more likely to occur at low densities, below a certain threshold, while others consider that higher levels of disturbance induce higher levels of tolerance (Smit & Visser, 1993). Again, this is very likely to depend on local conditions and on the nature of the disturbing activity.

It has to be reminded that, though the benefits of habituation in terms of energy savings are straightforward, the fact that habituated animals reduce their vigilance and instinctive fear reactions can make them more vulnerable to other risks, like natural predators, or to poaching (Singer, 1975 in Boyle & Samson, 1985). Habituation has been demonstrated for Chimpanzees *Pan troglodytes* in Uganda, where Johns (1995) showed that, after a period of opening of the area to the public, apes showed fewer charge reactions and more ignorance towards visitors. Johns also showed differences between age and sex classes in the likelihood to habituate, and that habituation was related with the number and the behaviour of visitors. In Marmot, Mainini *et al*. (1993) demonstrated some habituation to trekkers in highly frequented areas, if these people were staying on designated paths, therefore showing a highly predictable behaviour. Habituation has also been recorded in wild ungulates (*e.g.* Isard *Rupicapra rupicapra pyrenaica*, Lamerenx *et al*., 1991; Caribou *Rangifer tarandus* in Duchesne *et al*., 2000 and Johnson & Todd, 1977 therein). Conversely, Mountain Goats *Oreamnos americanus* apparently never got habituated to helicopters (Côté, 1996). After Patonnier (2000), wandering dogs are another example of a disturbance source to which wildlife can never habituate, even after decades. Mainini *et al*. (1993) too documented the fact that habituation of Marmot to wandering people with dogs was more limited than to simple walkers. Reviewing the literature, Frid & Dill (2002) argued that habituation to disturbance stimuli is often partial or negligible, because the fitness consequences of underestimating danger (*i.e.* immediate death) are too large.

Compensation

We have seen that the main consequences of disturbance are a change in the time-budget of individuals, notably through reduced feeding time, while energy expenses linked with escape movements may become very high. In order to limit these negative consequences, and in addition to habituation, some animals can try to compensate for energy losses (or lost feeding opportunities) by increasing food intake after disturbance events. There are two main non mutually exclusive ways by which individuals can compensate:

Firstly, temporal compensation, by which individuals increase their feeding time once disturbance is over. This additional feeding time will take place by lengthening the time spent at feeding spots, or will be taken on periods of minor activity (Urfi *et al.*, 1996). This is not always possible, since animals rarely can afford to have periods of minor activity, and access to feeding sites may be limited in time, by tidal cycles for example. For Brent Geese *Branta bernicla*, Riddington *et al.* (1996) showed that disturbance induced an average 10.8% increase of hourly energy expenditure, even reaching a maximum 38.5% in case of increased flight times. On the study site along the Norfolk coast, these birds could not compensate such a loss during daylight, especially during short winter days, because foraging was already maximal. The energy balance could therefore only be equilibrated by one hour of nocturnal foraging, which jeopardized the whole daily activity rhythm.

Secondly, individuals can try to compensate physiologically, via increased ingestion capacity, so as to acquire more food in the same amount of time (*e.g.*, Swennen *et al.*, 1989). Here again, such phenomenon is very unlikely to occur, since it is expected that individuals most often try to maximize their food intake and assimilation rates. Urfi *et al.* (1996) have studied in great details the effects of disturbance for Oystercatcher. They observed that oystercatchers are apparently able to habituate to human presence by reducing their take-off distances, so as to limit energy expenses. They could not detect any increase in food intake rate, that would indicate compensation (neither did Meire, 1996). On the other hand, birds remained longer in the feeding area or, in case of short (< 1 hour) disturbance events, had fewer periods of low activity, though these are already rare in winter. However, Swennen *et al.* (1989) showed that captive oystercatchers were able to increase their food intake rate, which lead Urfi *et al.* (1996) to suggest that compensation mechanisms are strongly dependent upon habitats and disturbance intensity (birds would increase their intake rate only in case of major disturbance, because the associated risks of bill damage and parasite ingestion would exceed benefits in case of medium to low disturbance). In Caribou, Duchesne *et al.* (2000) documented the fact that individuals apparently compensated for the effects of disturbance by increased resting times after visits by tourists.

Animals therefore seem to be able to compensate, in some cases and to some extent, for the negative effects of disturbance. However, the modalities of this adaptive response still need to be further studied, at larger scales of space and time, for a wide variety of strategies seems possible. Most compensatory mechanisms occur at short term, and allow reaching the expected, disturbance-free condition through higher investment (being either more energy, more time spent, etc.). However, the longer term consequences of these compensatory mechanisms for individual fitness and survival have seldom been considered.

Are there positive effects of disturbance?

In general, the consequences of disturbance are negative for wildlife or sometimes neutral, even if it is difficult to assess long-term effects. Some authors believe that there is a publication bias in this domain of research: Nisbet (2000) even considers that "published papers and reviews systematically overstate the adverse effects of human disturbance".

However, there are examples in which disturbance may have positive (though indirect) consequences for wildlife: Nevin & Gilbert (2005a,b) believe that ecotourism may have a positive impact on productivity of a Brown Bear population in British Columbia, Canada. In this area, bear watchers apparently do not disturb the fishing activity of females, while male bears do, excluding females and cubs from the best fishing spots. Because tourists disturb male bears, which tend to avoid them, visitors therefore create temporary refuges for females and cubs, which has been showed to increase the average population productivity. Under very specific conditions, disturbance associated with a human leisure activity therefore can benefit to a wildlife population. This however remains poorly studied, and apparently very anecdotic.

Impacts on populations

Disturbance affects vital properties of organisms like foraging, maintenance and reproductive behaviours, energy budgets and spatial distribution. It is therefore very likely that disturbance will also have repercussions at the upper level of population dynamics and distribution (see review in Frid & Dill, 2002). However, as stressed by these authors this often remains a hypothesis given the difficulty, in complex natural systems, to consider simultaneously all the factors that may have a significant effect on population, and isolate the role of each of them.

Like for effects at the individual level, impacts on populations will strongly depend on species and differ between populations themselves. Of course, the strength of impacts will change with the frequency, intensity and duration of disturbances, the availability of refuges in the environment, but also the social structure of populations. For example, grouping in colonies may increase the vulnerability of populations to disturbance, since one single disturbance event may affect the breeding success of very large numbers of pairs, sometimes even a whole population (an extreme example is given by the mass abandonment of breeding by Greater Flamingo *Phoenicopterus ruber roseus* in the only French colony in the Camargue, Southern France, after a single balloon was blown onto the breeding island, Cézilly *et al*., 1995). In many waterbirds, the negative consequences of disturbance for breeding success have been demonstrated, either directly through altered capacity of adults to provision young with food (*e.g*., African Black Oystercatcher *Haematopus moquini* in Lesenberg *et al*., 2000) or panic in seabird colonies (*e.g*., Beale & Monaghan, 2004b, for Guillemot and Kittiwake), or indirectly through, for example, increased predation rates on clutches (*e.g*., Velvet Scoter *Melanitta fusca* in Mikola *et al*., 1994).

Many birds show a high degree of gregarism, at least for a part of the year. Adélie Penguins, for example, form breeding colonies, where they are highly sensitive to human intrusion. Disturbance can induce nest abandon, leaving very large numbers of eggs and young unattended from predators, external conditions (*e.g*. temperature) and foot trampling (Boyle & Samson, 1985; Carney & Sydeman, 1999). Bat (*Chiroptera*) populations also are highly vulnerable to human disturbance, due to the concentration of individuals at few spots. Cave exploration can disturb whole colonies, which can have a dramatic impact during winter since the escape of individuals may completely jeopardize the energy-saving strategy of all individuals of the population. For this reason, disturbance is considered to be one of the main factors responsible for rarefaction or disappearance of bat populations (*e.g*., O'Shea & Vaughan, 1999). In the same way, wintering ducks (*Anatidae*) are highly sensitive to human disturbance when they flock on large day-roosts (Tamisier & Dehorter, 1999). In this case however, even if a single human disturbance can disturb thousands of individuals the broader long-term impact on populations remains less likely to be large, and anyway more difficult to ascertain.

PERSPECTIVES FOR RESEARCH AND MANAGEMENT

Research perspectives

This rapid overview of literature shows that despite studies on wildlife disturbance are numerous, they are still too few to fully understand the whole complexity of disturbance and its long term implications. In particular, the delayed impact of leisure disturbance on populations is almost unknown, while this knowledge will be absolutely necessary to firmly build up appropriate policies.

Hill *et al.* (1997) reviewed needs and gaps in bird disturbance studies, at three different scales: at the local population level, it is necessary to test the efficiency of attenuation measures, and comparative studies before and after disturbance, as well as between disturbed and undisturbed sites, are still needed. At the regional population level, monitoring the movement of disturbed individuals, and focus on periods of the year when individuals are the most likely to be sensitive to disturbance, to assess if regional compensation may occur, are still needed. At the flyway level, the variability of perturbation (especially disturbance) over space and time for models of population dynamics still has to be better taken into account.

Generally speaking, research on disturbance have mainly been conducted through very descriptive, observational and sometimes opportunistic studies. Only very occasionally was the response to disturbance considered while controlling for human activities and other factors of a given site (see however Madsen, 1998a,b). Developing such experimental studies seems to be the most crucially needed field of research in the domain of human disturbance for the coming years.

Management measures

Wildlife conservation needs to consider all potential perturbations. In the general context of habitat loss and degradation, coupled with increased human disturbance, the creation of protected areas is often regarded as the most efficient measure to save favourable habitats and limit perturbations. However, prevention of perturbation is sometimes limited to hunting activities only, while the above studies show that non-consumptive leisure activities should also be taken into account for a pertinent and sustainable management of wild populations. Indeed it seems necessary, in sites where leisure activities occur in contact with wildlife, to find the appropriate equilibrium trading-off between animals and human interests. Speight (1973 in Boyle & Samson, 1985) considered that 4 management alternatives are possible: i) minimizing of all effects of leisure activities (*i.e.* banning leisure activities), ii) finding ways of conserving the essential characters of ecosystems, despite the occurrence of leisure activities, iii) finding ways of replacing the essential characters of ecosystems by others, and iv) allow leisure activities without considering potential consequences at all. Management plans have to be written while combining these alternatives, for example an area can be sacrificed (alternative iv) to reduce the pressure of leisure activities to other adjacent areas managed after alternatives i or ii.

However, less drastically some simple measures can allow a strong reduction of the negative consequences of leisure activities (Finney *et al.*, 2005): first of all, get people respecting existing rules, in protected areas and beyond, like for example the laws linked with dog divagation or those limiting the circulation of motor vehicles in some natural areas. Then, let people become more aware of species protection in general, since potential restrictions will be more respected if well known and understood. Limiting the diffusion of human disturbance in natural habitats can be an efficient measure: trying to get people staying on delimited pathways, for example, seems to be an acceptable compromise quite easy to put in force if well explained. Providing hides well integrated in the habitat can also strongly reduce the negative effect of approaching ecotourists. Eventually, limiting or banning completely the most disturbing activities during periods of higher sensitivity (cold spells, hibernation, reproduction), in areas whose size should be delimited after the animal species requirements, may sometimes become necessary.

Most of the proposed management measures are relatively easy to take, especially in already protected areas. An efficient protection of wildlife against human disturbance may also require coordinated decisions at a broader geographical scale, *i.e.* region, country or flyways. For example, the creation of reserve networks along bird migration routes should provide an efficient shelter from the extension of human leisure disturbance. With very few noticeable exceptions (*e.g.*, Robinson & Pollitt, 2001), disturbance is mostly recorded at the site level. Estimations of disturbance levels at a broader geographic scale appear as a crucial need in the future.

CONCLUSION

Outdoor leisure activities, including non-consumptive ones, clearly lead to disturbance of wildlife in several ways, and the many studies cited in this paper clearly illustrate this pattern. Even if they generally do not lead to the death of animals directly, as opposed to hunting or fishing for example, outdoor leisure activities can, however, affect animals in their vital behaviours such as foraging and resting.

It has to be kept in mind, however, that leisure activities do not only have a punctual impact on the behaviour of individuals. Conversely, they may also more generally disrupt foraging strategies, prevent optimal spatial distribution patterns and also modify both intra and interspecific relationships. Although this is difficult to demonstrate, leisure activities can therefore have broader significant impacts on the dynamics of populations. The present overview therefore supports the idea that human leisure disturbance in general, not only consumptive activities, should wisely be considered in a more general and coordinated policy for sustainable wildlife management. This will require quantifying the effect of disturbance for populations in the longer term, and also being able to assess how adapted management may mitigate the effects of disturbance. Such objectives will probably require heavy experimental work, but these researches are crucially needed if we want to be able to combine legitimate human leisure activities and wildlife needs for quietness in the future.

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