Review

A unifying framework for the underlying mechanisms of avian avoidance of wind turbines

CrossMark

Roel F. May *

Norwegian Institute for Nature Research, P.O. Box 5685 Sluppen, NO-7485 Trondheim, Norway

A B S T R A C T

The construction and operation of wind-power plants may affect birds through collision mortality, reduced habitat utilization due to disturbance, barriers to movement and habitat modifications, with the nature and magnitude of those effects being site- and species-specific. Birds may however manage these effects through fleeing, activity shifts or changed habitat utilization; usually termed avoidance. Given the important role avoidance plays in estimating the impact wind-power development has on birds, there is a pressing need to formalizing the avoidance process. Crucial in this context is to identify the underlying mechanisms of behavioural responses by birds to wind-power plants and individual turbines. To provide a better basis for and improved understanding of the underlying mechanisms for avoidance a conceptual framework for wind-turbine avoidance is presented decomposing various forms of avoidance at different spatial scales. Avoidance behaviour includes displacement (macro-avoidance), anticipatory and impulsive evasion (meso-avoidance), and escape (micro-avoidance). For understanding why particular responses occur with regard to wind-turbine disturbance this concept is applied to predation risk theory. The risk-disturbance hypothesis elucidates possible trade-offs between avoiding perceived risk and fitness-enhancing activities. The four behavioural responses are related to, respectively, habitat selection, vigilance and fleeing (twice); from which specific predictions can be derived. Formalizing the different forms of avoidance facilitates design of effects studies, enhances comparisons among sites studied, and guide siting and mitigation strategies.

© 2015 Elsevier Ltd. All rights reserved.

Contents

* Tel.: +47 957 85 995.
   E-mail address: roel.may@nina.no

1. Introduction

The global potential for wind-power generation is enormous (Lu et al., 2009), and regarded by many as the most promising renewable energy source. All power generation, however, has environmental costs (IPCC, 2011). Bird mortality is generally perceived as a major conflict issue for wind-power development (Drewitt and Langston, 2006; Stewart et al., 2007). The construction and operation of wind-power plants may affect birds through collision mortality, reduced habitat utilization due to disturbance, barriers to movement and habitat modifications, with the nature and magnitude of those effects being site- and species-specific (Drewitt and Langston, 2006). Birds may however respond to these effects through fleeing, activity shifts or changed habitat utilization; usually termed avoidance. An increasing number of empirical studies have improved our understanding of avoidance, although significant knowledge gaps remain. However, comparison of studies are hampered by differences in definitions and methodology employed (cf. Furness et al., 2013); also the distinction between different forms of avoidance may in reality be challenging (Langston, 2013). Given the important role avoidance plays in estimating the effect wind-power development has on birds directly (risk of collision, energetic expenditure) or indirectly (e.g. reduced reproduction, resource exclusion), there is a pressing need to formalize the avoidance concept. Crucial in this context is to identify the underlying mechanisms of behavioural responses by birds to wind-power plants and individual turbines (Drewitt and Langston, 2008; Langston 2013). This may reveal species-, site- and state-specific factors enhancing avoidance (Chamberlain et al., 2006), improve impact estimates (Ferrer et al., 2012), and ultimately aid siting and mitigation strategies (Marques et al., 2014; May et al., 2014). Here I present a conceptual framework for wind-turbine avoidance and place this concept in the context of the movement ecology paradigm (Mueller and Fagan, 2008; Nathan et al., 2008) and the risk-disturbance hypothesis (Frid and Dill, 2002; Stankowich and Blumstein, 2005). The movement ecology paradigm facilitates understanding of the causes and mechanisms of avoidance responses and promotes hypothesis generation. Invoking the risk-disturbance hypothesis provides a better basis for predicting why particular avoidance responses may be expected to occur. This framework links behavioural and physiological theory to the reality of studying and interpreting avoidance by replacing often practical and intuitive definitions with a common playing field in terms of terminology and definitions to aid the study of bird avoidance of wind turbines.

2. Material and methods

I compiled studies, including both peer-reviewed articles, technical reports and conference proceedings relating to avian avoidance of wind turbines. Literature was collected through search engines (ISI Web of Knowledge and Google Scholar), databases (NREL's Wind-Wildlife Impacts Literature Database) as well as already compiled information derived from other reviews (e.g. Cook et al., 2014; Johnson et al., 2007; Marques et al., 2014; May et al., 2014). Information was searched for using the following key phrases: "avoid*", displace*" or "disturb*", coupled with "wind energy", "wind power" or "wind turbine". In addition, taking the reviews by Nathan et al. (2008), Mueller and Fagan (2008), Frid and Dill (2002) and Stankowich and Blumstein (2005) as a starting point, I further searched for peer-reviewed literature relating to the theoretical foundation for avoidance and predation risk. Appendix 1 summarizes the support for each formalized prediction for different forms of wind-turbine avoidance (Table A2), as derived from the original predictions of the risk-disturbance hypothesis (Table A1).

3. Decomposition of the avoidance process

In practise it may be difficult to tease apart different avoidance-related decisions as they may shift gradually into one another. To understand the mechanisms underlying specific avoidance-related decisions, however, require the decomposition of the concept of avoidance into distinct avoidance responses along this continuum. This distinction is important to be able to identify all factors influencing the proximate causes of avoidance responses. Avoidance may occur at varying intensities within multiple hierarchical spatial scales (Mueller and Fagan, 2008). Here three spatial scales may be distinguished: birds may avoid the wind-power plant area as a whole (i.e. 'forest'), turbine arrays or single wind turbines (i.e. 'trees') and last-second evasion of the rotor blades (i.e. 'branches'). (Cook et al., 2014) dubbed these scales 'macro-avoidance', 'meso-avoidance' and 'micro-avoidance' respectively. Although avoidance intuitively is defined based on the spatial scale it is likely to occur, this does not reveal specific behaviour causing avoidance responses. A behavioural response to the presence of a wind-power plant results in a reduced number of birds entering and possibly avoiding wind turbines (e.g. Desholm and Kahlert, 2005; Petersen et al., 2006). This apparent continuum means that wind turbine avoidance may for certain bird species involve a combination of reduced habitat utilization and consequent reduced flight activity close to wind turbines, hence reduced risk of collision (e.g. Dahl et al., 2012, 2013; Garvin et al., 2011; May et al., 2013; Pearce-Higgins et al., 2009). Alternatively, collision avoidance for birds commuting between areas of utilized habitat (e.g. foraging, resting, migration corridor) may depend only on active in-flight response to wind turbines intercepting their route (i.e. barrier effect) (e.g. Desholm and Kahlert, 2005; Larsen and Guillemette, 2007; Masden et al., 2009; Plonczkier and Simms, 2012). Birds may also reduce the risk of colliding with a wind turbine through changes in in-flight behaviour near turbines or last-second responses near the rotor blades (e.g. Krijgsveld et al., 2011). In-flight responses may also be influenced by external factors such as wind and topography (e.g. Barrios and Rodriguez, 2004; de Lucas et al., 2004; Farfán et al., 2009; Hull and Muir, 2013). These studied examples along that continuum may represent pronounced differences for some bird species, or more subtle distinctions for others, depending on a species' tolerance of disturbance and its behavioural plasticity in adapting to the perceived risk from wind turbines (Furness et al., 2013). To clarify the actual meaning of the term 'avoidance' in different circumstances, however, different terms for each form of avoidance should be reserved for the responses of birds to wind turbines at different spatial scales. The term 'avoidance' is here proposed to signify the entire conceptual process.

3.1. A movement framework for avoidance responses

To understand the concept of avoidance, we may place it in the context of the movement ecology paradigm (Nathan et al., 2008). This paradigm provides the framework facilitating the understanding of why, how and where animals move; and the ecological and evolutionary consequences of movement. The conceptual framework identifies four interacting mechanistic components central to movement: internal state (why move), motion (how to move) and navigation capacities (where to move), and external factors affecting movement. Navigation mechanisms may be further divided into (1) non-oriented (sensory stimuli), (2) oriented (perceptual cues) and (3) memory-based (cognitive maps) movements (Mueller and Fagan, 2008). The movement ecology paradigm unites fundamental paradigms central to movement of organisms (Fig. 1). With regard to avoidance, a bird's internal state (e.g. body
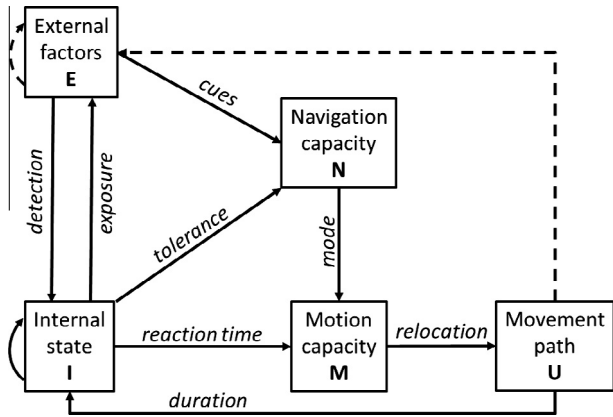
Fig. 1. The conceptual framework for the movement ecology paradigm (after: Nathan et al., 2008), composed of the four basic mechanistic components for movement. Relationships among these components represent the processes by which they affect each other. Each of these processes are identified according to the different stages of a disturbance response (cf. Blumstein et al., 2005).

condition, age, breeding status), motion capacity (e.g. body size, wing loading), navigation capacity (e.g. sensory faculties, spatial memory), and external factors (e.g. distribution of resources, lighting conditions) affects its ability to detect and respond to wind turbines and/or wind-power plants. Avoidance as a behavioural movement response to disturbance involves four stages linking the four mechanistic components (Fig. 1): (i) detection and exposure, (ii) cues and tolerance, (iii) mode and relocation, (iv) reaction time and duration (cf. Blumstein et al., 2005).

Perception of wind turbines as risk factors, and tolerance for such risks, will vary between individuals and species (Blumstein et al., 2005; Smallwood et al., 2009), depend on life history traits (Blumstein, 2006) and will be affected by birds' ability to discriminate such risks from those posed by other sources of disturbance (Frid and Dill, 2002; Stankowich and Blumstein, 2005), as well as the effects of other motivations on behavioural decisions (Stephens, 2008). Continuous exposure over time to the presence of wind turbines in an area may lead to learning by birds, either resulting in functional habitat loss or reduced risk perception (increased tolerance) and increased habituation (i.e. waning of responsiveness/wariness, Rankin et al., 2009) (e.g. Madsen and Boertmann, 2008). Birds may also use social learning to aid recognition of risks (Griffin, 2004), for instance by following cues of other birds in terms of their in-flight, but also non-aerial (e.g. walking, swimming), locomotion behaviour when approaching turbines. Dependent on the intensity of the perceived risk, coupled with a species' behavioural and cognitive traits, it may respond in several ways to the presence of wind turbines. Sensory cues (as a function of physiology but also e.g. visibility) and a species' tolerance for disturbance hereby affect the flight mode as well as the extent of the relocation, reaction time and duration of the response upon detection.

3.2. Displacement

The presence of turbines and associated infrastructure (access roads, buildings, power lines) alters the landscape through direct habitat loss and degradation (e.g. nesting sites, Dahl et al., 2012) as well as introducing raised structures in the airspace within the surrounding landscape. Although the physical encroachment may be limited, the wind-power plant footprint may affect bird abundance through functional habitat loss. Functional habitat loss may not only be the consequence of a redistribution due to

behavioural avoidance, but also be the population-level consequence of changes in habitat (location of nest/roost sites, vegetation composition and structure), prey base, competitor and predator densities (Gill et al., 2001). Dependent on a species' susceptibility for disturbance (Furness et al., 2013) coupled with species-specific traits (e.g. life history, body size, mobility) determine whether this will lead to partial or complete displacement from (parts of) the wind-power plant area. Displacement can be defined as the reduced density of birds occurring within or immediately adjacent to wind-power plants due to long-term disturbance leading to functional habitat loss (Drewitt and Langston, 2006; Furness et al., 2013). In specific cases also attraction may occur due to for instance increased food availability and perching structures (Lindeboom et al., 2011; Vanermen et al., 2013). Hence I will use the term displacement also to include possible attraction effects. While displacement relates to reduced habitat utilization and thereby reduced abundance of birds within the wind-power plant footprint (Madders and Whitfield, 2006), it is often confounded with avoidance indicating flight behaviour to avert a potential collision with a wind-turbine (Smales et al., 2013). Although these two terms may be the same semantically, the term 'avoidance' often remains ambiguous both with regard to the type of response studied (e.g. habitat utilization versus flight behaviour), its cause (direct versus indirect) and the spatial scale at which it is expected to occur. They therefore signify different behavioural responses to wind turbines. For instance, Garvin et al. (2011) estimated the change in raptor abundance at 47%, whereas only 4% of all recorded flights within 500 m from the turbines displayed small-scale avoidance (31% of all flights within 100 m from the turbines). The change in raptor abundance could therefore not be explained solely by in-flight avoidance. In practice, displacement is often related to macro-avoidance ('forest'), however displacement may also occur at the meso-scale ('trees') depending on a species' susceptibility versus wind-power plant design (e.g. Larsen and Madsen, 2000).

Displacement can be memory-based (cf. Mueller and Fagan, 2008) and relates to the effect exposure to external factors has on the internal state (Fig. 2). Displacement is the complex result of a hierarchy of, partly conflicting, decisions to optimize patch exploitation (Stephens, 2008); befitting the optimality paradigm. This paradigm explores strategies optimizing fitness (e.g. energy, survival, reproduction) in organisms.
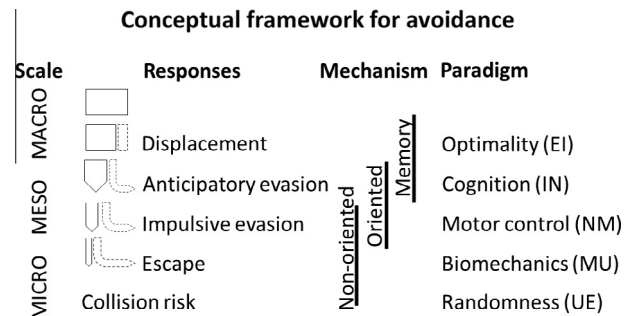
Fig. 2. Visual representation of the conceptual framework for the decomposition of wind turbine avoidance. The figure depicts the different avoidance Responses which may recursively occur at spatial scales ranging from wind-power plant (single), wind turbine (array) to the rotor swept zone. Scale relates to currently used avoidance distinctions. The thick vertical lines under Mechanism indicate which class of navigation (Mueller and Fagan, 2008) will act upon these responses. The Paradigms on the right-hand side relate to the paradigms identified by the movement ecology paradigm (Nathan et al., 2008) for each of the responses. Between brackets those movement ecology components (see Fig. 1) central to each of these responses are identified.

3.3. Evasion and escape

When a flying bird, upon detection, behaviourally evades a wind-power plant or single wind-turbines to avert perceived predation risk or potential collision risk this can be termed evasion. While detection depends on a bird's visual sensory perception (Martin, 2011) and perceptual range (Olden et al., 2004), the perceived risk – in the form of a wind turbine– can only then be evaded when its locomotive morphology (e.g. wing load, wing aspect) and aerodynamic capacities enables the bird to do so in due time (Bevanger, 1998; Pennycuick, 2008). Dependent on the timing of detection and their tolerance thresholds (e.g. flight initiation distance) this may either result in a direct and stress-related – impulsive – behavioural in-flight response, or in a more anticipatory response due to prior knowledge/experience on the location of such structures. While impulsive evasion implies an oriented in-flight response to perceptual cues (cf. Mueller and Fagan, 2008), anticipatory evasion results from early detection from a perceived safe distance or previous recollection of the turbine locations leading to a redistribution of birds within the wind-power plant footprint. To what degree birds may learn to evade wind turbines probably depends on their ability to include these structures perceptually in their cognitive spatial map (i.e. turbines as landmarks; Healy and Braithwaite, 2010). Anticipatory evasion can therefore be placed in-between displacement and impulsive evasion with regard to the abruptness of the response as well as the distance it is likely to occur. An example of anticipatory evasion is when a bird chooses to fly farther from turbines without changing its in-flight direction abruptly as with impulsive evasion (i.e. circumventing the physical turbine structure).

Both types of evasion may occur at the scale of the entire wind-power plant area (i.e. macro-avoidance ('forest'), Desholm and Kahlert, 2005; Krijgsveld et al., 2011; Masden et al., 2009; Plonczkier and Simms, 2012) and at the scale of (rows of) wind-turbines (i.e. meso-avoidance ('trees'), Desholm and Kahlert, 2005; Garvin et al., 2011; Hull and Muir, 2013; Krijgsveld et al., 2011). In close proximity to the rotor swept zone ('branches'), last-second evasion likely becomes more reflexive in nature (cf. non-oriented response from sensory stimuli at the current location, Mueller and Fagan, 2008). To differentiate from anticipatory and impulsive avoidance at larger spatial scales, I suggest terming this 'escape' (micro-avoidance).

Anticipatory evasion combines memory-based and oriented responses where navigation capacity and internal state (i.e. tolerance upon detection) determine the cognitive response (Fig. 2). The cognition paradigm studies the rules that govern movement-related decisions. Impulsive evasion represents an oriented in-flight response to perceptual cues, whereby navigation capacity and motion capacity result in relocation of the bird (Fig. 2). This process is central to the motor control paradigm. Motor control involves the awareness of the position of body parts in relation to each other while selectively attending to an external goal. Sensory information acquisition and processing determine, in turn, patterns of motor activation (Biewener and Daniel, 2010). Escape mainly depends on the motion capacity of a species, coupled with stochasticity affecting the capacity's efficacy (Fig. 2). Escape fits within the biomechanics paradigm focusing on the physical motion machineries, including physiology, energetics and aerodynamics.

4. Avoidance and the risk-disturbance hypothesis

To predict the extent of, and understand the underlying drivers for avoidance it might be useful to adopt the hypothesis that non-lethal disturbance stimuli caused by humans are analogous to predation risk (Frid and Dill, 2002; Stankowich and Blumstein, 2005). Evolutionarily, prey have evolved anti-predator responses to generalized threatening stimuli such as loud noise and rapidly approaching objects, and consequently, this approach might be especially useful since responses to predation risk and disturbance stimuli divert time and energy from other fitness-enhancing activities (e.g. feeding, parental care and courtship behaviour) (Frid and Dill, 2002). They define a disturbance stimulus as a human-related presence or object (or sound) that creates a deviation in an animal's behaviour from patterns occurring without human influences. Wind turbines may therefore be characterized as sources of disturbance stimuli, whereby their framework may also apply to the concept of avoidance. Avoidance as a form of evolved anti-predator strategy hereby enable birds to cope with the perceived risk of the presence of wind turbines. However contrary to the framework discussed by Frid and Dill (2002) the disturbance stimuli (i.e. wind turbines) are stationary, albeit with moving rotor blades, and the animal is approaching the stimuli instead of being approached.

The risk-disturbance hypothesis (Frid and Dill, 2002) distinguishes five areas of focus: energy trade-offs, mate acquisition, parental investment, population dynamics, and interactions at the community level. While the first will be most important for the scope of this paper with regard to risk-evaluating behaviour, the latter four definitely play a role in elucidating other indirect effects of wind-power plants on wildlife. The presence of a wind-power plant may result in reduced breeding success (e.g. Dahl et al., 2012) due to displacement effects (e.g. abandonment of nests) and/or loss of parents (through collisions). This in turn may affect population dynamics (Carrete et al., 2009), and ultimately result in changes at the community level (e.g. through increased scavenger presence). It may not always be clear whether the presence of wind turbines have significant population consequences (Dahl, 2014; de Lucas et al., 2008; Hunt et al., 1998; Madders and Whitfield, 2006), as this depends on the direct mortality, the fitness costs of disturbance and on the availability of alternative habitat (Gill et al., 2001). Indirect effects of wind-power development at higher organisational levels are relevant with respect to cumulative impacts (Dahl, 2014; Masden et al., 2010). Frid and Dill (2002) distinguish three different spatial responses with regard to energy trade-offs: fleeing, vigilance and habitat selection. Although also non-spatial responses to disturbance exist, such as group size, sociality, diet selection and diurnal patterns (Lima and Dill, 1990), these are not directly link to the avoidance process. The spatial responses will be presented in reverse order to follow the hierarchy in avoidance responses: (I) displacement, (II) anticipatory evasion, (III) impulsive evasion, and (IV) escape. Here it is important to note that this hierarchy not only is related to spatial scale, but also to the severity of the disturbance effect. For each of these responses they defined specific predictions (Table A1). These three different disturbance responses, and their associated predictions, are applied to the three different types of avoidance as described earlier including a non-exhaustive number of studies supporting or rejecting these (see also Table A2).

4.1. Habitat selection: predictions for displacement

Habitat selection is the result of decisions that balance the multiple trade-offs between predation risk and resource/patch quality to optimize net energy intake (Lima, 1998; Lima and Dill, 1990; Stephens, 2008). Consequently, birds would spend less time in places where resources are associated with greater danger and move to other habitats depending on the relative costs and benefits of leaving the current site (cf. Frid and Dill, 2002). However, if alternative habitats are unavailable or too distant, and/or habitat

quality within a wind-power plant is high (Smallwood and Thelander, 2004; Thelander et al., 2003) birds could be forced or tempted to stay in sites with increased collision risk. Ecological trap theory (Battin, 2004; Patten and Kelly, 2010; Robertson and Hutto, 2006) may help understand such maladaptive habitat selection with regard to wind energy development. Sudden environmental change may uncouple the cues that individuals use to assess habitat quality (yielding lower fitness) from the true quality of the environment (Robertson and Hutto, 2006). Ecological traps may occur when animals are falsely attracted to habitats with reduced survival and reproduction (Battin, 2004). Conversely, perceptual traps may occur when high-quality habitats are avoided when perceived to be less attractive (Patten and Kelly, 2010). There are many factors (e.g. species, body size, predator/prey-interactions, reproductive status, season etc.) that influence habitat choice, and decisions whether or not to stay at a disturbed site. Dependent on a species' sensitivity to disturbance (*D*) and vulnerability to collision mortality (*C*) (Furness et al., 2013), this may lead to either selection of risky habitat (i.e. ecological trap: *D < C*) or avoidance of good habitat (i.e. perceptual trap: *D > C*) within wind-power plants. While the first may occur when for instance novel perching structures become available (Lindeboom et al., 2011; Vanermen et al., 2013), the latter may occur when for instance birds are disturbed by ship traffic (Schwemmer et al., 2011). Although such decisions are constrained by limits to a species' sensory perception, memory, and locomotion (Olden et al., 2004), no direct behavioural change in the bird's trajectory is detected in displacement. The bird rather utilizes habitat away from turbines depending on the quality of the habitat versus the perceived risk. Conversely, increased – perceived – habitat quality may lead to enhanced utilization; attraction effects.

Displacement occurs when long-term, intense disturbance stimuli reduce access to resources (Prediction I.A) whereby the magnitude of displacement depends on the availability of alternative suitable habitat (Prediction I.B). A number of studies provide support for Prediction I.A (Dahl et al., 2012; Devereux et al., 2008; Larsen and Madsen, 2000; May et al., 2013; Pearce-Higgins et al., 2009), but this is less clear for Prediction I.B. While long-term studies indicate species-specific displacement effects (Garvin et al., 2011; Madsen and Boertmann, 2008; Petersen and Fox, 2007; Stewart et al., 2007), only two studies has related displacement to the intensity of disturbance (i.e. density, number and size of turbines, operating time and output, maintenance activity) (Pearce-Higgins et al., 2012; Winkelman, 1992c). Pearce-Higgins et al. (2012) found that the construction phase had greater impacts than operational phase. Breeding densities in upland birds were also largely unaffected by technical specifications (turbine height, number or total generating power).

4.2. Vigilance: predictions for anticipatory evasion

Prey is generally more vigilant when the perceived risk of predation is greater. While vigilance (or: awareness, alertness) reduces the probability of being injured or killed through collision, this will be at the cost of reduced foraging time or other activities. Many impulses that affect vigilance may act simultaneously upon the bird through its behaviour (e.g. foraging, courtship or territorial defence), and limit the detection and/or perception of wind turbines as potential dangers. Vigilance can here be related to anticipatory evasion where a turbine is detected from a perceived safe distance or is found at an expected location and activity is shifted consequently to reduce the perceived risk before any abrupt and stress-related (impulsive) evasive action is required. Such a transition from impulsive to anticipatory evasion depends on a species' life-history traits (Blumstein, 2006) and social learning (Griffin, 2004). Winkelman (1992b) noticed that local birds had habituated

to the turbines as was expressed by a larger proportion of gradual and calm shifts in trajectory and a smaller proportion of accelerated wing beats compared to migrating birds.

The probability of anticipatory evasion through increased awareness to the presence of the wind turbine(s) is affected by the relative location of the approaching animal relative to the wind turbine(s). A more direct approach is expected to increase the detection of predators in the form of wind turbines (Prediction II.A). Although this prediction is as yet untested, a study by Smallwood et al. (2009) indicated that Northern harriers (*Circus cyaneus*) switched to travelling flight when crossing turbine rows.

Alertness in birds will increase with decreasing distance towards wind-power plant and/or turbine (arrays) (Prediction II.B). Although no studies have directly measured alertness in birds, studies on consequent shifts in activity do support Prediction B, including redistribution of trajectories (Desholm and Kahlert, 2005; Larsen and Guillemette, 2007; Masden et al., 2009; Petersen et al., 2006; Skov et al., 2012) and decreased willingness to land (Larsen and Guillemette, 2007). In southern Spain, birds tended to fly along rather than across closer spaced turbine rows (Farfán et al., 2009). Also Hull and Muir (2013) indirectly support Prediction B by stating that eagles preferred to fly midway between turbine rows, likely anticipating the presence of turbines. (Pearce-Higgins et al., 2009), however, did not find evidence for altered flight height close to turbines in raptors. Vigilance and thereby anticipatory evasion will in addition increase sequentially from the outskirts of a wind-power plant inwards (Desholm and Kahlert, 2005; Krijgsveld et al., 2011; Petersen et al., 2006) due to increments in the perceived risk (Stankowich and Blumstein, 2005).

Wind-power plants with a greater number of turbines will enhance an anticipatory response (Prediction II.C). Although no comparative studies can yet support this prediction (Krijgsveld et al., 2011), noted that wind-power plant design seemed to affect avoidance behaviour at an offshore wind-power plant. A protruding single line of turbines and wider-spaced turbines were passed more often (i.e. evaded less).

Anticipatory evasion will further depend on factors affecting natural levels of awareness and risk perception (Prediction II.D), such as moving rotor blades (increased alertness; de Lucas et al., 2004), displaying behaviour (reduced alertness; Dahl et al., 2013; Smallwood et al., 2009), environmental conditions (either increased or reduced alertness; Barrios and Rodriguez, 2004; Carr and Lima, 2010; de Lucas et al., 2012; Desholm and Kahlert, 2005) and/or flock interactions (Croft et al., 2011).

4.3. Fleeing: predictions for impulsive evasion and escape

Fleeing from a perceived risk is the obvious way to avoid being injured or killed. Prey that detects an approaching predator have to make some (optimal) decisions that balance the benefits of reduced probability of being injured or killed against the costs of abandoning a patch of resources (food, mates, offspring), and the energy used on locomotion (Stephens, 2008). In the case where a wind-turbine is perceived as a risk equivalent to a predator, fleeing may represent impulsive evasion or escape upon detection to avert potential collision. While impulsive evasion relates to the response to the entire turbine structure, or meso-avoidance ('trees'), escape relates to the last-second response of the moving rotor blades (micro-avoidance or 'branches'). While escape is reflexive in nature, the abruptness of an impulsive evasion response is negatively related to the distance at which a turbine is detected.

4.3.1. Impulsive evasion

For impulsive evasion a bird's trajectory will change significantly and abruptly. Evasion probability and initiation distance,

but also its intensity (i.e. acceleration/deceleration, turning angle), is affected by the relative location of the approaching bird relative to the wind turbine(s). For aerial species both distance and the angle of approach is three-dimensional with both horizontal and vertical components (Frid and Dill, 2002). Any evasive action may therefore happen either by increasing the lateral distance or by shifting its flight altitude relative to a wind turbine (Cook et al., 2014; Furness et al., 2013). This becomes even more complex when incorporating the vertical dimension of landscapes (e.g. topography, trees).

A more direct approach angle towards wind-power plant or turbine is expected to increase detection probability and flight initiation distance (Prediction III.A). Although this prediction has not yet been tested, the high-resolution lateral visual field of birds – important to detection of conspecifics, foraging opportunities and predators including responses to novel stimuli – seems contradictory to this prediction but needs further testing (Martin, 2011; Martin et al., 2012). Still, visual perception (i.e. not expecting anything ahead, Martin, 2011) and geometric correlations (i.e. flight initiation distance can never be smaller than the minimal trajectory distance, Frid and Dill, 2002) could explain this deviation.

Faster flight should elicit stronger evasive responses (Prediction III.B). Faster flight (i.e. ground speed) relative to a species' aerodynamic capacities (e.g. wing loading, wing aspect ratio; Bevanger, 1998) should elicit stronger flight responses as less time is available for evasive action to avoid collision. The study by Larsen and Guillemette (2007) supports this prediction where the observed long-distance evasive response of common eiders was interpreted to be due to their high-speed and low-manoeuvrability flight within the vertical height range of the wind-turbines.

Larger and operational turbines will enhance detection probability and flight initiation distance upon detection (Prediction III.C). The increased "loom" rate of larger and operational ('moving') turbines is expected to increase impulsive evasion in approaching birds. Although so far no studies clearly differentiated between impulsive and anticipatory evasion, such effects seem to be supported by various studies showing higher rates of evasions when turbines were operational (de Lucas et al., 2004, 2008; Krijgsveld et al., 2011; Lindeboom et al., 2011; Winkelman, 1992b). Although most studies support this prediction (Larsen and Guillemette, 2007), found no effect of the movement and noise of rotor blades on flight behaviour in common eiders indicating species-specificity. Turbines with larger hub height and/or longer rotor blades should enhance the loom rate of the disturbance stimulus. This prediction is yet untested. However (Cook et al., 2014) found in their meta-analyses no effect of maximum tip height on avoidance rates in seabirds. (Larsen and Clausen, 2002) suggested that larger – but fewer – turbines would result in less disturbance. This clearly links turbine size to the number turbines required to reach the same output.

Impulsive evasion responses will increase when the distance from the wind-power plant edge inwards and inter-turbine (array) distance is smaller due to increased distance to refuge (Prediction III.D). Studies in Denmark showed that birds, upon entering an offshore wind-power plant, adjusted their flight orientation to fly equidistance between turbine rows and towards the nearest exit route, as well as reduced their flight altitude below rotor height (Petersen et al., 2006; Skov et al., 2012). Krijgsveld et al. (2011) observed that birds were hesitant to enter the (main body of the) offshore wind-power plant, and adjusted flight orientation to evade turbines.

Wind-power plants with a greater number of turbines will enhance an evasive response (Prediction III.E). No comparative studies can yet support this prediction. Still (Krijgsveld et al., 2011) noted at an offshore wind-power plant that a protruding single line of turbines and wider-spaced turbines were passed more often (i.e. evaded less).

Less favourable environmental conditions will lead to increased evasion probability and flight initiation distances (Prediction III.F). Although this seems contrary to the original prediction, adverse conditions that decrease detection and/or increase locomotion costs simultaneously lead to increased risk lowering resource quality and thereby fleeing cost (Frid and Dill, 2002). Reduced visibility (e.g. light levels, clouds/mist) (Blew et al., 2009; Desholm and Kahlert, 2005; Krijgsveld et al., 2011; Lindeboom et al., 2011; Petersen et al., 2006; Tulp et al., 1999; Winkelman, 1992a) and/or less favourable wind conditions (e.g. topography, wind speed) has been shown to result in higher impulsive evasion responses (Barrios and Rodriguez, 2004; de Lucas et al., 2008; Hull and Muir, 2013; Winkelman, 1992b). However, high wind speeds may also decrease the responsiveness of birds to potentially threatening moving stimuli such as turbines with revolving rotor blades (Carr and Lima, 2010).

4.3.2. Escape

Escape from the moving rotor blades is demonstrated as an involuntary (i.e. reflexive) and nearly instantaneous movement. Few studies have been conducted focusing especially on this type of avoidance response, not in the least because of the practical difficulties in recording such rare events. Escape responses depend on the aerodynamic capabilities of the approaching bird coupled with the structural properties of the moving rotor blades. To which extent rotor blades in motion are perceived by a bird depend on the distance from the hub (higher rotational speed) and rotor blade length (fewer rotations per minute). Although interlinked, these aspects are assessed as separate predictions as they relate to different escape mechanisms.

Escape – fleeing probability from moving rotor blades – is predicted to increase when the approach angle towards rotor disk is more direct (Prediction IV.A). The approach angle depends on the heading of flight relative to the wind direction adjusting the orientation of the rotor disk. Crosswind approaches, along the length of the turbine rotor blades, are expected to reduce detection due to the limited frontal visual field in birds relative to up- and downwind approaches when the entire rotor swept zone is visible (Martin, 2011). Although they did not differentiate between meso-and micro-avoidance (Krijgsveld et al., 2011), observed that most near-turbine passes (<50 m) were crosswind flights behind or in front of the rotor blades.

The probability of successful escape will decrease with increasing ground speed of the bird (Prediction IV.B). Winkelman (1992b) found that larger birds responded more strongly in tailwinds, while smaller birds responded more in headwinds. This difference may well be due to differences in wing morphology, limiting heavier birds with higher wing loading to avoid collision at higher wind speeds while smaller birds with high wing aspect ratios may lose balance (Bevanger, 1998).

Escape probability will increase with rotational speed of the rotor blades (Prediction IV.C). Operational turbines should, with increasing rotational speed, lead to a quicker approach of rotor blades towards the bird thereby enhancing an in-flight response. Winkelman (1992b) and Krijgsveld et al. (2011) indeed found that near-turbine responses were stronger when these were operational. However, with increasing rotational speed of the rotor blades, the moving rotor blades may also lose their visibility due to motion smear (Hodos, 2003), hampering detection and consequent escape probability. There are however no studies that can relate motion smear to increased collision risk. Again I would like to stress that the rotor blade speed increases towards its tip.

Escape probability should decrease with distance from the hub, both lateral and vertical, because the distance to refuge becomes

smaller (Prediction IV.D). Approaches at rotor height have been observed to elicit stronger responses (Winkelman, 1992b). Krijgsveld et al. (2011) noted that birds may in fact be at risk of collision beyond the reach of the rotor blades due to turbulence. They found that of all birds passing within 50 m of turbines, less than 7% were observed within the horizontal reach of the rotor blades (<45 m). Although so far few studies render direct support for this prediction, the theoretical collision risk model by (Tucker, 1996) indicates higher risk closer to the hub; necessitating stronger escape responses.

Longer or greater number of rotor blades (i.e. larger "group" size) should enhance escape responses (Prediction IV.E). Although longer blades result in larger rotor swept areas, this prediction is yet largely untested on modern turbines (but see: Howell, 1997). This is also the case for number of rotor blades, as no comparative studies exist including (similar) turbines with varying number of blades as most modern turbines consist of three blades.

Finally, escape responses are stronger in situations where environmental conditions impede the aerodynamic ability for escape, such as reduced visibility (e.g. low light levels, clouds/mist) and/or when wind conditions are less favourable (e.g. turbulence, wind gusts) (Prediction IV.F). Winkelman (1992b) found that escape responses were stronger during poor aerodynamic and visibility conditions. Barrios and Rodriguez (2004) observed that griffon vultures (*Gyps fulvus*), generally in good visibility and weak updrafts, adjusted their movements to avoid the revolving rotor blades.

5. Understanding avoidance mechanisms

Many studies so far have raised our understanding of avoidance responses from wind-power development (Cook et al., 2014; Langston, 2013). Most studies predominantly estimated evasion as a function of lateral or vertical distance to either wind-power plant or wind turbine, denoted as proportional changes in flight frequencies. However, more parameters may influence behavioural responses. Although harder to measure, the angle of approach (i.e. the angle between trajectory heading and bearing to disturbance stimuli) may also be expected to affect the behavioural response as a function of distance. Here, all things else being equal, greater distances correspond to smaller angles and more direct approaches. The (flight) speed with which distance and approach angle changes relative to a bird's aerodynamic skills influences the potential response (Larsen and Guillemette, 2007; Martin, 2011; Smallwood et al., 2009). How, when and from where wind turbines are perceived – and the consequent behavioural response – depends further on structure-specific (e.g. wind-power plant extent and openness, turbine dimensions, motion smear) and environmental (e.g. visibility, weather, habitat) parameters (e.g. Desholm and Kahlert, 2005; Garvin et al., 2011). Although proportional changes in flight trajectories as a function of distance can reveal possible evasive effects, it does not elucidate other, less intuitive mechanisms that may be equally important in explaining evasive responses. The avoidance framework ensures that the full scope of underlying mechanisms is considered a priori, associated predictions are tested and inconsistencies may stimulate further research.

This review has also made clear that we still lack knowledge in certain fields. Several of the predictions require comparative studies across wind-power plants, species and/or regions (e.g. Cook et al., 2014). This necessitates that avoidance responses are assessed using standardized and acknowledged methods. Displacement studies should preferably be able to capture long-term changes (e.g. habituation, demographic impacts) due to temporal variations in the intensity of the disturbance, and encompass a spatial scale larger than the species' home range to assess the effect of alternative habitat on the extent of displacement (Battin, 2004; Gill et al., 2001). This can be achieved by employing a gradient approach whereby abundance is recorded and compared across sites, classified by habitat and distance to nearest turbine (cf., Guillemette and Larsen, 2002). Preferably this is repeated a number of time to assess temporal effects (e.g. before–after construction, habituation over time). Further behavioural research studying vigilance, and related activity shifts, with respect to wind-turbine risk would be recommended as they so far are mostly lacking. While evasion and displacement may be studied *in situ* based on e.g. field observations, telemetry or radar, it may yet prove most difficult to obtain satisfactory data to study escape from rotor blades. This is due to the small spatial scale (i.e. rotor swept zone) and short time span at which escape occurs, coupled with the likely small number of birds traversing the rotor swept zone as most will already have avoided a wind turbine at an earlier stage. Possible techniques to obtain appropriate data for analysis may be field observations (albeit with possibility for observer bias), or automated systems based on radar or video (Collier et al., 2011; Desholm et al., 2006; Kunz et al., 2007).

In practise, however, it may prove to be difficult to tease apart the different avoidance mechanisms presented above as they may shift gradually in one another. For instance, when studying evasion behaviour one may observe flight trajectories at varying distances from wind turbines with varying degree of change in flight direction (anticipatory to impulsive evasion). Evasion may also gradually change from impulsive evasion towards escape in the vicinity of the rotor swept zone. The actual avoidance responses are very much species-specific, and may be modified by site-specific factors such as the extent and openness of the wind-power plant and environmental factors. Formalizing the different forms of avoidance facilitates design of avoidance studies and ensures that all associated predictions are considered à priori, which in turn helps minimizing modelling bias in collision risk models and enhances the possibilities to compare among sites studied. Estimates for different forms of avoidance enable deductions on cost-benefit effects of energy gain/loss separately (Frid and Dill, 2002; Gill et al., 2001; Masden et al., 2010). Last but not least, teasing apart the individual, structural and environmental factors affecting avoidance responses in birds towards wind turbines may guide siting and mitigation measures where they may be expected to be most effective for a given species and site (Marques et al., 2014; May et al., 2014).

Acknowledgements

Appendix A. Supplementary materials

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2015.06.004.

References

Barrios, L., Rodriguez, A., 2004. Behavioural and environmental correlates of soaring-bird mortality at on-shore wind turbines. J. Appl. Ecol. 41, 72–81.
Battin, J., 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conserv. Biol. 18, 1482–1491.

Bevanger, K., 1998. Biological and conservation aspects of bird mortality caused by electricity power lines: a review. Biol. Conserv. 86, 67–76.

Biewener, A., Daniel, T., 2010. A moving topic: control and dynamics of animal locomotion. Biol. Lett. 6, 387–388.

Blew, J., Hoffman, M., Nehls, G., Hennig, V., 2009. Investigations of the bird collision risk and the responses of harbour porpoises in the offshore windfarms Horns Rev, North Sea, and Nysted, Baltic Sea, in Denmark. Part I: Birds, Hamburg/ Husum, Germany, p. 133.

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

Blumstein, D.T., Fernández-Juricic, E., Zollner, P.A., Garity, S.C., 2005. Inter-specific variation in avian responses to human disturbance. J. Appl. Ecol. 42, 943–953.

Carr, J.M., Lima, S.L., 2010. High wind speeds decrease the responsiveness of birds to potentially threatening moving stimuli. Anim. Behav. 80, 215–220.

Carrete, M., Sánchez-Zapata, J.A., Benítez, J.R., Lobón, M., Donázar, J.A., 2009. Large scale risk-assessment of wind-farms on population viability of a globally endangered long-lived raptor. Biol. Conserv. 142, 2954–2961.

Chamberlain, D.E., Rehfisch, M.R., Fox, A.D., Desholm, M., Anthony, S.J., 2006. The effect of avoidance rates on bird mortality predictions made by wind turbine collision risk models. Ibis 148, 198–202.

Collier, M.P., Dirksen, S., Krijgsveld, K.L., 2011. A review of methods to monitor collisions or micro-avoidance of birds with offshore wind turbines. Strategic Ornithological Support Services Project SOSS-03A.

Cook, A.S.C.P., Humphreys, E.M., Masden, E.A., Burton, N.H.K., 2014. The avoidance rates of collision between birds and offshore turbines. British Trust for Ornithology, Thetford, UK.

Croft, S.A., Budgey, R., Pitchford, J.W., Wood, A.J., 2011. Group navigation and wind farm collision avoidance in flocks. In: May, R., Bevanger, K. (Eds.), Proceedings Conference on Wind energy and Wildlife impacts, 2–5 May 2011, Trondheim, Norway. Norwegian Institute for Nature Research, Trondheim, Norway, p. 79.

Dahl, E.L., 2014. Population Demographics in White-tailed Eagle at an On-shore Wind Farm Area in Coastal Norway. Department of Biology, Norwegian University of Science and Technology (NTNU), Trondheim, Norway.

Dahl, E.L., Bevanger, K., Nygård, T., Røskaft, E., Stokke, B.G., 2012. Reduced breeding success in white-tailed eagles at Smøla windfarm, western Norway, is caused by mortality and displacement. Biol. Conserv. 145, 79–85.

Dahl, E.L., May, R., Hoel, P.L., Bevanger, K., Pedersen, H.C., Røskaft, E., Stokke, B.G., 2013. White-tailed eagle (*Haliaeetus albicilla*) at the Smøla wind-power plant, central Norway, lack behavioral flight responses to wind turbines. Wildl. Soc. Bull. 37, 66–74.

de Lucas, M., Janss, G.F.E., Ferrer, M., 2004. The effects of a wind farm on birds in a migration point: the Strait of Gibraltar. Biodivers. Conserv. 13, 395–407.

de Lucas, M., Janss, G.F.E., Whitfield, D.P., Ferrer, M., 2008. Collision fatality of raptors in wind farms does not depend on raptor abundance. J. Appl. Ecol. 45, 1695–1703.

de Lucas, M., Ferrer, M., Janss, G.F.E., 2012. Using wind tunnels to predict bird mortality in wind farms: the case of griffon vultures. PLoS ONE 11, e48092.

Desholm, M., Kahlert, J., 2005. Avian collision risk at an offshore wind farm. Biol. Lett. 1, 296–298.

Desholm, M., Fox, A.D., Beasley, P.D.L., Kahlert, J., 2006. Remote techniques for counting and estimating the number of bird-wind turbine collisions at sea: a review. Ibis 148 (Suppl. 1), 76–89.

Devereux, C.L., Denny, M.J.H., Whittingham, M.J., 2008. Minimal effects of wind turbines on the distribution of wintering farmland birds. J. Appl. Ecol. 45, 1689–1694.

Drewitt, A.L., Langston, R.H.W., 2006. Assessing the impacts of wind farms on birds. Ibis 148 (Suppl. 1), 29–42.

Drewitt, A.L., Langston, R.H.W., 2008. Collision effects of wind-power generators and other obstacles on birds. Ann. N. Y. Acad. Sci. 1134, 233–266.

Farfán, M.A., Vargas, J.M., Duarte, J., Real, R., 2009. What is the impact of wind farms on birds? A case study from southern Spain. Biodivers. Conserv. 18, 3743–3758.

Ferrer, M., De Lucas, M., Janss, G.F.E., Casado, E., Muñoz, A.R., Bechard, M.J., Calabuig, C.P., 2012. Weak relationship between risk assessment studies and recorded mortality in wind farms. J. Appl. Ecol. 49, 38–46.

Frid, A., Dill, L., 2002. Human-caused disturbance stimuli as a form of predation risk. Conserv. Ecol. 6, 11.

Furness, R.W., Wade, H.M., Masden, E.A., 2013. Assessing vulnerability of marine bird populations to offshore wind farms. J. Environ. Manage. 119, 56–66.

Garvin, J.C., Jennelle, C.S., Drake, D., Grodsky, S.M., 2011. Response of raptors to a windfarm. J. Appl. Ecol. 48, 199–209.

Gill, J.A., Norris, K., Sutherland, W.J., 2001. Why behavioural responses may not reflect the population consequences of human disturbance. Biol. Conserv. 97, 265–268.

Griffin, A.S., 2004. Social learning about predators: a review and prospectus. Anim. Learn. Behav. 32, 131–140.

Guillemette, M., Larsen, J.K., 2002. Postdevelopment experiments to detect anthropogenic disturbances: the case of sea ducks and wind parks. J. Appl. Ecol. 12, 868–877.

Healy, S.D., Braithwaite, V.A., 2010. The role of landmarks in small- and large-scale navigation. In: Dolins, F.L., Mitchell, R.W. (Eds.), Spatial Cognition, Spatial perception: Mapping the Self and Space. Cambridge University Press, New York, NY, pp. 152–179.

Hodos, W., 2003. Minimization of Motion Smear: Reducing Avian Collisions with Wind Turbines. Period of performance: July 12, 1999–August 31, 2002. National Renewable Energy Laboratory, Golden, Colorado, 35pp.

Howell, J.A., 1997. Bird mortality at rotor swept area equivalents, Altamont Pass and Montezuma Hills, California. Trans. West. Section Wildl. Soc. 33, 24–29.

Hull, C.L., Muir, S.C., 2013. Behavior and turbine avoidance rates of eagles at two wind farms in Tasmania, Australia. Wildl. Soc. Bull. 37, 49–58.

Hunt, W.G., Jackman, R.E., Hunt, T.L., Driscoll, D.E., Culp, L., 1998. A population study of golden eagles in the Altamont Pass Wind Resource Area: population trend analysis 1997. Report to National Renewable Energy Laboratory, Subcontract XAT-6-16459-01. Predatory Bird Research Group, University of California, Santa Cruz.

IPCC, 2011. IPCC Special Report on Renewable Energy Sources and Climate Change Mitigation, Cambridge, New York.

Johnson, G.D., Strickland, M.D., Erickson, W.P., Young Jr., D.P., 2007. Use of data to develop mitigation measures for wind power development impacts to birds. In: de Lucas, M., Janss, G.F.E., Ferrer, M. (Eds.), Birds and Wind Farms. Risk Assessment and Mitigation. Servicios Informativos Ambientales, Quercus, Madrid, pp. 241–257.

Krijgsveld, K.L., Fijn, R.C., Japink, M., van Horssen, P.W., Heunks, C., Collier, M.P., Poot, M.J.M., Beuker, D., Dirksen, S., 2011. Effect Studies Offshore Wind Farm Egmond aan Zee. Final report on fluxes, flight altitudes and behaviour of flying bird, Culemborg, the Netherlands.

Kunz, T.H., Arnett, E.B., Cooper, B.M., Erickson, W.P., Larkin, R.P., Mabee, T., Morrison, M.L., Strickland, M.D., Szewczak, J.M., 2007. Assessing impacts of wind-energy development on nocturnally active birds and bats: a guidance document. J. Wildl. Manage. 71, 2449–2486.

Langston, R.H.W., 2013. Birds and wind projects across the pond: a UK perspective. Wildl. Soc. Bull. 37, 5–18.

Larsen, J.K., Clausen, P., 2002. Potential wind park impacts on Whooper Swans in winter: the risk of collision. Waterbirds 25 (Suppl. 1), 327–330.

Larsen, J.K., Guillemette, M., 2007. Effects of wind turbines on flight behaviour of wintering common eiders: implications for habitat use and collision risk. J. Appl. Ecol. 44, 516–522.

Larsen, J.K., Madsen, J., 2000. Effects of wind turbines and other physical elements on field utilization by pink-footed geese (*Anser brachyrhyncus*): a landscape perspective. Landscape Ecol. 15, 755–764.

Lima, S.L., 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Adv. Study Behav. 27, 215–290.

Lima, S.L., Dill, L.M., 1990. Behavioural decisions made under the risk of predation. Can. J. Zool. 68, 619–640.

Lindeboom, H.J., Kouwenhoven, H.J., Bergman, M.J.N., Bouma, S., Brasseur, S., Daan, R., Fijn, R.C., de Haan, D., Dirksen, S., van Hal, R., Hille Ris Lambers, R., ter Hofstede, R., Krijgsveld, K.L., Leopold, M., Scheidat, M., 2011. Short-term ecological effects of an offshore wind farm in the Dutch coastal zone; a compilation. Environ. Res. Lett. 6, 035101.

Lu, X., McElroy, M.B., Kiviluoma, J., 2009. Global potential for wind-generated electricity. Proc. Natl. Acad. Sci. 106, 10933–10938.

Madders, M., Whitfield, D.P., 2006. Upland raptors and the assessment of wind farm impacts. Ibis 148, 43–56.

Madsen, J., Boertmann, D., 2008. Animal behavioral adaptation to changing landscapes: spring-staging geese habituate to wind farms. Landscape Ecol. 23, 1007–1011.

Marques, A.T., Batalha, H., Rodrigues, S., Costa, H., Pereira, M.J.R., Fonseca, C., Mascarenhas, M., Bernardino, J., 2014. Understanding bird collisions at wind farms: an updated review on the causes and possible mitigation strategies. Biol. Conserv. 179, 40–52.

Martin, G.R., 2011. Understanding bird collisions with man-made objects: a sensory ecology approach. Ibis, 154.

Martin, G.R., Portugal, S.J., Murn, C.P., 2012. Visual fields, foraging and collision vulnerability in Gyps vultures. Ibis 154, 626–631.

Masden, E.A., Haydon, D.T., Fox, A.D., Furness, R.W., Bullman, R., Desholm, M., 2009. Barriers to movement: impacts of wind farms on migrating birds. ICES J. Mar. Sci. 66, 746–753.

Masden, E.A., Haydon, D.T., Fox, A.D., Furness, R.W., 2010. Barriers to movement: modelling energetic costs of avoiding marine wind farms amongst breeding seabirds. Mar. Pollut. Bull. 60, 1085–1091.

May, R., Nygård, T., Dahl, E.L., Bevanger, K., 2013. Habitat utilization in white-tailed eagles (*Haliaeetus albicilla*) and the displacement impact of the Smøla wind-power plant. Wildl. Soc. Bull. 37, 75–83.

May, R., Reitan, O., Bevanger, K., Lorentsen, S.-H., Nygård, T., 2014. Mitigating wind-turbine induced avian mortality: sensory, aerodynamic and cognitive constraints and options. Renew. Sustain. Energy Rev. 42, 170–181.

Mueller, T., Fagan, W.F., 2008. Search and navigation in dynamic environments – from individual behaviors to population distributions. Oikos 177, 654–664.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., Smouse, P.E., 2008. A movement ecology paradigm for unifying organismal movement research. Proc. Natl. Acad. Sci. 105, 19052–19059.

Olden, J.D., Schooley, R.L., Monroe, J.B., Poff, N.L., 2004. Context-dependent perceptual ranges and their relevance to animal movements in landscapes. J. Anim. Ecol. 73, 1190–1194.

Patten, M.A., Kelly, J.F., 2010. Habitat selection and the perceptual trap. Ecol. Appl. 20, 2148–2156.

Pearce-Higgins, J.W., Stephen, L., Langston, R.H.W., Bainbridge, I.P., Bullman, R., 2009. The distribution of breeding birds around upland wind farms. J. Appl. Ecol. 46, 1323–1331.

Pearce-Higgins, J.W., Stephen, L., Douse, A., Langston, R.H.W., 2012. Greater impacts of wind farms on bird populations during construction than subsequent

operation: results of a multi-site and multi-species analysis. J. Appl. Ecol. 49, 386–394.

Pennycuick, C.J., 2008. Modelling the Flying Bird. Elsevier, London, U.K..

Petersen, I.K., Fox, A.D., 2007. Changes in bird habitat utilisation around the Horns Rev 1 offshore wind farm, with particular emphasis on Common Scoter, Denmark.

Petersen, I.K., Christensen, T.K., Kahlert, J., Desholm, M., Fox, A.D., 2006. Final results of bird studies at the offshore wind farms at Nysted and Horns Rev, Denmark. Report commissioned by DONG energy and Vattenfall A/S, Denmark.

Plonczkier, P., Simms, I.C., 2012. Radar monitoring of migrating pink-footed geese: behavioural responses to offshore wind farm development. J. Appl. Ecol. 49, 1187–1194.

Rankin, C.H., Abrams, T., Barry, R.J., Bhatnagar, S., Clayton, D., Colombo, J., Coppola, G., Geyer, M.A., Glanzman, D.L., Marsland, S., McSweeney, F., Wilson, D.A., Wu, C.-F., Thompson, R.F., 2009. Habituation revisited: an updated and revised description of the behavioural characteristics of habituation. Neurobiol. Learn. Mem. 92, 135–138.

Robertson, B.A., Hutto, R.L., 2006. A framework for understanding ecological traps and an evaluation of existing evidence. Ecology 87, 1075–1085.

Schwemmer, P., Mendel, B., Sonntag, N., Dierschke, V., Garthe, S., 2011. Effects of ship traffic on seabirds in offshore waters: implications for marine conservation and spatial planning. Ecol. Appl. 21, 1851–1860.

Skov, H., Leonhard, S.B., Heinänen, S., Zydelis, R., Jensen, N.E., Durinck, J., Johansen, T.W., Jensen, B.P., Hansen, B.L., Piper, W., Grøn, P.N., 2012. Horns Rev 2 Monitoring 2010–2012. Migrating Birds. Orbicon, DHI, Marine Observers and Biola. Report commissioned by DONG Energy, p. 134, Fredericia, Denmark.

Smales, I., Muir, S., Meredith, C., Baird, R., 2013. A description of the biosis model to assess risk of Bird collisions with wind turbines. Wildl. Soc. Bull. 37, 59–65.

Smallwood, K.S., Thelander, C.G., 2004. Developing methods to reduce mortality in the Altamont Pass Wind Resource Area. Final report, In Final report by BioResource Consultants to the California Energy Commission, Public Interest Energy Research-Environmental Area, Contract no. 500-01-019. BioResource Consultants to the California Energy Commission, Public Interest Energy Research-Environmental Area, California, USA, p. 333 + appendices

Smallwood, K.S., Rugge, L., Morrison, M.L., 2009. Influence of behavior on bird mortality in wind energy developments. J. Wildl. Manage. 73, 1082–1098.

Stankowich, T., Blumstein, D.T., 2005. Fear in animals: a meta-analysis and review of risk assessment. Proc. R. Soc. B: Biol. Sci. 272, 2627–2634.

Stephens, D.W., 2008. Decision ecology: foraging and the ecology of animal decision making. Cognit. Affect. Behav. Neurosci. 8, 475–484.

Stewart, G.B., Pullin, A.S., Coles, C.F., 2007. Poor evidence-base for assessment of windfarm impacts on birds. Environ. Conserv. 34, 1–11.

Thelander, C.G., Smallwood, K.S., Rugge, L., 2003. Bird risk behaviors and fatalities at the Altamont Pass Wind Resource Area. Period of performance: March 1998 to December 2000. Report to National Renewable Energy Laboratory, Golden, Colorado. Work performed by BioResource Consultants, Ojai, California, pp. 1–86.

Tucker, V.A., 1996. A mathematical model of bird collisions with wind turbine rotors. J. Sol. Energy Eng. 118, 253–269.

Tulp, I., Schekkerman, H., Larsen, J.K., Winden, J., van der Haterd, R.J.W., van Horssen, P., Dirksen, S., Spaans, A.L., 1999. Nocturnal Flight Activity of Sea Ducks near the Windfarm Tuno Knøb in the Kattegat, Culemborg, the Netherlands.

Vanermen, N., Stienen, E., Courtens, W., Van der walle, M., Verstraete, H., 2013. Attraction of seabirds. In: Degraer, S., Brabant, R., Rumes, B. (Eds.), Environmental impacts of offshore wind farms in the Belgian part of the North Sea: Learning from the past to optimise future monitoring programmes. Royal Belgian Institute of Natural Sciences, Operational Directorate Natural Environment, Marine Ecology and Management Section, Brussels, Belgium, pp. 163–165.

Winkelman, J.E., 1992a. The impact of the Sep wind park near Oosterbierum (Fr.), the Netherlands, on birds, 2: nocturnal collision risks. DLO-Instituut voor Bos-en Natuuronderzoek.

Winkelman, J.E., 1992b. The impact of the Sep wind park near Oosterbierum (Fr.), the Netherlands, on birds, 3: flight behavior during daylight. DLO-Instituut voor Bos-en Natuuronderzoek.

Winkelman, J.E., 1992c. The impact of the Sep wind park near Oosterbierum (Fr.), the Netherlands, on birds, 4: disturbance. DLO-Instituut voor Bos- en Natuuronderzoek.