

Context-dependent perceptual ranges and their relevance to animal movements in landscapes

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Summary

1. An animal's perceptual range defines the spatial extent of the landscape for which information is available to make movement decisions. Ecologists studying and modelling animal dispersal have commonly assumed that individual movements arise from a predefined set of local decision rules operating within a static isotropic (i.e. circular) perceptual range.

2. We discuss how this assumption fails to recognize the potential for plasticity in perceptual ranges and present a conceptual model that illustrates how anisotropic perceptual ranges can arise from animal orientation to environmental stimuli.

3. Using model simulations we show how perceptual distance (i.e. greatest Euclidean distance at which habitat patches can be perceived), horizon (i.e. panoramic view or angular degrees of the landscape perceived) and breadth (i.e. areal extent of the landscape perceived), change as a function of increased strength of a hypothetical stimuli.

4. Our results show that anisotropic perceptual ranges can differ substantially from traditional, isotropic perceptual ranges in all three aspects depending on the strength of the stimuli and nature in which it interacts with other elements of the landscape.

5. We highlight the implications of these findings for modelling animal movements in ecological landscapes with the hope that context-dependent perceptual ranges are considered in future studies.

Key-words: anisotropic, behaviour, connectivity, isotropic, orientation, patch context.

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Introduction

Understanding how landscape structure mediates animal movements has been the focus of considerable theoretical and empirical research in ecology. Animal behaviour plays an important role by shaping fine-scale decision-making processes, such as habitat patch choice, which define animal movements and ultimately influence biological processes at broader spatial scales and higher levels of organization (Wiens *et al.* 1993; With & Crist 1996; Roitberg & Mangel 1997; Russell, Swihart & Feng 2003). The concept of landscape or functional connectivity has been advanced to describe

the degree to which the landscape facilitates or impedes animal movement among habitat patches (Taylor, Fahrig & Merriam 1993; Tischendorf & Fahrig 2000), and has received increased attention recently (e.g. Brooks 2003; Goodwin & Fahrig 2003). Although rarely considered, an animal's perceptual range plays an important role in landscape connectivity by defining the informational window onto the greater landscape that all movement decisions are predicated (Lima & Zollner 1996). An animal's realized perceptual range is not entirely 'perception' *per se*, but refers to the fraction of the landscape that is both detectable and accessible via movement, and therefore it defines the spatial scale at which an individual interacts with the landscape. An animal's perceptual range influences many processes, including its movement behaviour, choice of search strategy, probability of reaching a new patch and ability to respond to habitat disturbance and fragmentation

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(e.g. Lima & Zollner 1996; With & Crist 1996; Zollner & Lima 1999a).

Ecologists have traditionally viewed an animal's perceptual range as being fixed in the landscape. As such, few studies have investigated the importance of changing perceptual ranges on animal movement, even though such plasticity can be substantial (e.g. Zollner & Lima 1997, 1999a; Kawata & Agawa 1999; Schooley & Wiens 2003). An animal's perceptual range may vary among individuals and change in response to features of the environment. For example, perceptual range is related to particular life-history characteristics, such as individual body size (Mech & Zollner 2002), and is therefore expected to differ among species (Zollner 2000). Perhaps more importantly, we have also failed to recognize the importance of animal orientation, a phenomenon that is among the earliest studied aspects of behaviour (Loeb 1918; Fraenkel & Gunn 1940) in shaping perceptual ranges. Extrinsic environmental stimuli, such as physical currents like water flow and wind (see Jander 1975 and Schöne 1984 for comprehensive treatments of important environment stimuli), can potentially modify an animal's perceptual range by influencing its orientation behaviour and ability to assess different features of the landscape when making movement decisions.

Given the potentially dynamic nature of an animal's perceptual range, it is unfortunate that models of animal dispersal have commonly assumed that individual movements arise from a predefined set of local decision rules operating within a fixed isotropic perceptual range (e.g. Pulliam, Dunning & Liu 1992; Gustafson & Gardner 1996; Zollner & Lima 1999a). Such models therefore predict an individual's movement pathway as a function of only those patches in some finite 'detection circle' surrounding its location on the landscape. However, if environmental stimuli modify an animal's perceptual ranges and thus can be considered context-dependent in the landscape (Schooley & Wiens 2003), then it is imperative that we broaden our current static view of perceptual ranges to model animal movements more accurately in ecological landscapes. We consider this an important, yet unexplored, research area in ecology that deserves both theoretical and empirical investigation. Here, we illustrate the context-dependence of the perceptual range and discuss its relevance for understanding and modelling animal movements. We hope that this paper stimulates further theoretical modelling and empirical research that investigates the importance of dynamical perceptual ranges for animal movements.

Influence of environmental stimuli on components of perceptual range

We use a simple conceptual model (Fig. 1) that considers how an animal's orientation response to an environmental stimulus can alter three different aspects of its perceptual range – the distance, horizon and breadth.

Perceptual distance refers to the greatest Euclidean or straight-line distance at which habitat patches can be perceived, i.e. greater distances enable an animal to gain information from more distant patches (although not necessarily in all directions). *Perceptual horizon* refers to the panoramic view or angular degrees of the landscape that can be perceived, and therefore influences the ability of an animal to survey the landscape in different directions. *Perceptual breadth* is a function of distance and horizon and refers to the areal extent of the landscape that is perceived, and represents the total amount of the landscape from which information regarding movement decisions can be obtained. We are the first to partition the perceptual range into these components, and think this conceptual refinement is important given that different aspects of the perceptual range may differentially influence an animal's movement behaviour and may change differentially in response to an environmental stimulus. Previous studies have used the term 'perceptual range' to refer solely to perceptual distance (see Goodwin *et al.* 1998 and Zollner & Lima 1999c for discussion of ways to quantify perceptual distance), while perceptual breadth and horizon have yet to be considered explicitly.

Traditionally, ecologists have assumed that animals exhibit fixed isotropic perceptual ranges that are specific to the species and are independent of any environmental stimuli (hereafter called the traditional perceptual range). This approach simply defines the perceptual range as a static detection circle surrounding an animal's location on the landscape (Fig. 1a). Our conceptual model explores three scenarios in which an environmental stimulus (of varying strength) can alter the distance, horizon and breadth of an animal's perceptual range, and therefore define the realized perceptual range and modify the information available for individuals to make movement decisions. Below, we discuss each of these scenarios and, using simple geometry, we examine how increasing strength of an environmental stimulus may influence perceptual breadth, distance and horizon according to each scenario, and compare these values to the traditional perceptual range (see Fig. 1 legend for methodological details).

In our first scenario (Fig. 1b), we depict a situation where an environmental stimulus influences the detection of landscape features in all directions from the animal, which we call a context-dependent isotropic perceptual range. Differences in the intensity of landscape illumination associated with time of day provide a good example of this scenario. Zollner & Lima (1999b) found that the perceptual distance of the white-footed mouse (*Peromyscus leucopus*) in relation to distant forested habitat increased along an illumination gradient, from nights with complete darkness to full moonlight evenings to twilight levels at dusk. In another interesting example, Yeomans (1995) found that under clear sky conditions yellow-bellied pond slider turtles (*Trachemys scripta*) exhibit orientation behaviour toward distant waterbodies reflecting polarized light, whereas

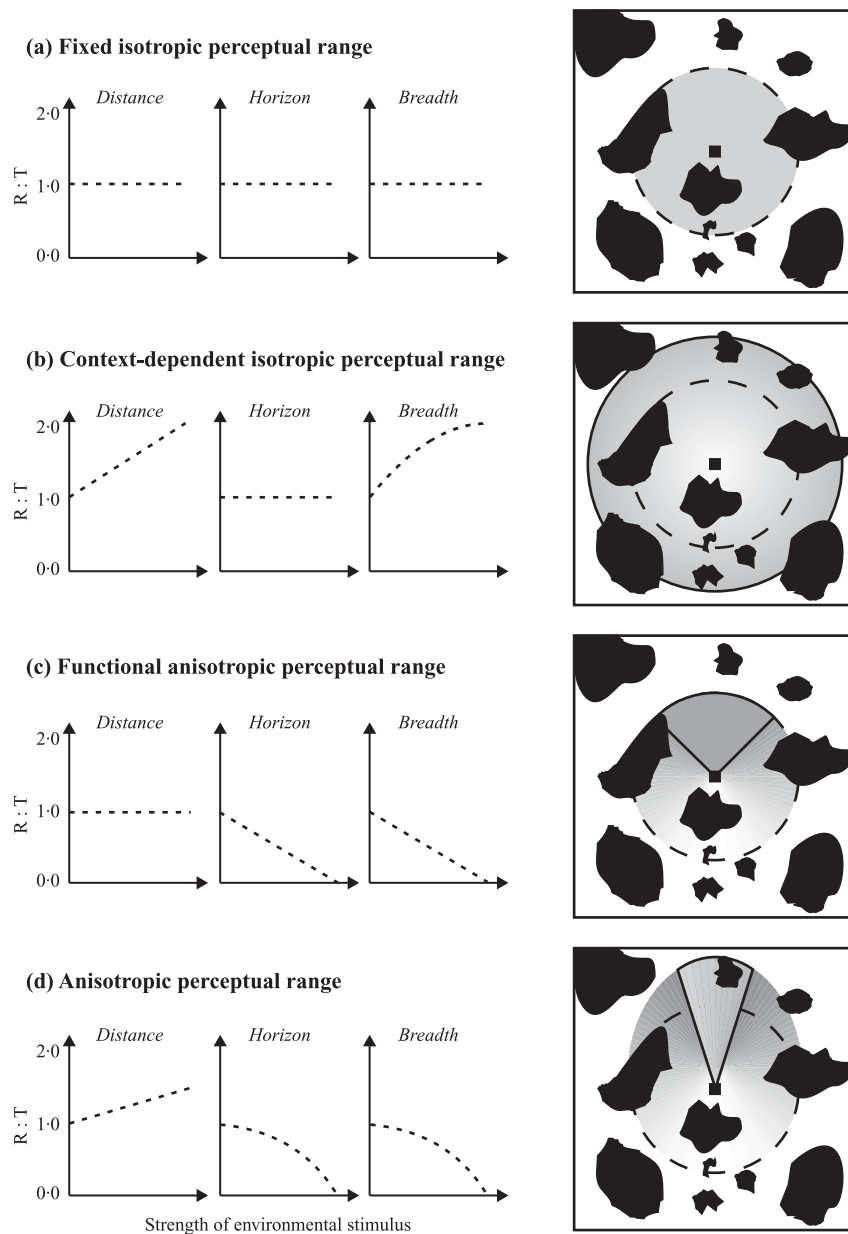


Fig. 1. A conceptual model illustrating how orientation behaviour to an environmental stimulus can influence the three components of an animal's perceptual range. The four panels represent: (a) the traditional view of a fixed isotropic perceptual range that is independent of any environmental stimuli and (b–d) changing perceptual ranges according to three scenarios under an environmental stimulus of varying strength. The right column shows a hypothetical landscape (square arena with black habitat patches) with the location of an animal (square symbol) and its perceptual range, and the left column illustrates how the perceptual distance, horizon and breadth change under increasing strength of an environmental stimulus. Change is calculated using simple geometry* and is expressed as the ratio of the realized perceptual range (depicted in panels b–d): traditional perceptual range (fixed isotropic perceptual range depicted in panel (a) and is represented as R : T. Stimulus originates at the top of the page for panels (c) and (d). The fixed isotropic perceptual range is depicted by a circular detection area (dashed lines) in all panels and represents the traditional perceptual range. The solid lines in panels (b–d) represent perceptual ranges modified by responses to environmental stimuli. Greyscale shading (from white to black) represents increasing strength of the environmental stimulus.

*Perceptual distance was calculated as the radius of the circle for (a–c) (r) and the length of the semi-major axis of the ellipse for (d) (a). Perceptual horizon was constant for (a) and (b) ($2\pi r$), and was calculated as the arc length of a circle for (c) ($\theta(\pi/180r)$) and the arc length of an ellipse for (d) ($\theta \left(2\pi \sqrt{(a^2 + b^2)/2} \right)$). Perceptual breadth was calculated as the area of the circle for (a) and

(b) (πr^2), area of a circle sector for (c) ($\theta/360\pi r^2$) and area of an ellipse sector for (d) ($\theta/360\pi ab$). Variables in the above equations are $\pi = 3.141592 \dots$, r = radius of the circle, θ = central angle, a = semi-major axis of the ellipse, b = semiminor axis of the ellipse. Model simulations involved using the above formulas and systematically varying the values of the variables across their ranges to explore changes in perceptual distance, horizon and breadth as a function of increasing strength of the environmental stimulus. Variables exhibited the following ranges: $r = 1-500$; $\theta = 0-360^\circ$; $a = 500-750$; and $b = 500$. The following protocol was executed to mimic increasing strength of the stimulus. In scenario (b) we incrementally increased r for distance and breadth, and horizon remained unchanged. In scenario (c) we incrementally decreased θ for horizon and breadth (r remained constant), and distance remained unchanged. In scenario (d) we incrementally increased a for distance, and incrementally increased a and decreased θ for horizon and breadth (b remained constant).

under cloudy sky conditions orientation toward these same waterbodies did not occur. Under this scenario, the context-dependent isotropic perceptual range resulting from increased intensity of an environmental stimulus (i.e. increased illumination of the landscape in the case of white-footed mice) is expected to increase perceptual breadth and distance and have no effect on perceptual horizon, relative to a traditional perceptual range (Fig. 1b). This results in a larger realized perceptual range when compared to the traditional view of a fixed isotropic perceptual range in Fig. 1a.

In our second scenario (Fig. 1c), we show how a functional anisotropic perceptual range can result from animal orientation toward the direction of a particular stimulus (e.g. wind or water current) in the absence of additional cues that interact with the stimulus, such as wind-borne chemical plumes used for finding resource patches (Bell 1991). We find evidence of this scenario in our research on stream-bed landscapes where increased current velocity resulted in increased upstream orientation behaviour of a caddisfly larvae (*Agapetus boulderensis*: Poff & Ward 1992) and a pleurocerid snail (*Leptoxis carinata*: Poff & Nelson-Baker 1997), a behaviour believed to reduce the probability of individuals being dislodged downstream. According to this scenario, increased intensity of an environmental stimulus (i.e. current velocity) is not expected to affect distance, but to decrease horizon and breadth of the anisotropic perceptual range relative to a fixed isotropic perceptual range. Here, the realized perceptual range is smaller compared to the traditional perceptual range due to the directed orientation of the animals.

In our third scenario (Fig. 1d), we show how animal orientation toward the direction of a particular stimulus (e.g. wind or water current) in the presence of an additional interacting cue (e.g. odours from a food source) can result in a truly anisotropic perceptual range. Ample evidence exists for this scenario, including animals that use chemical cues for detecting food resources, conspecifics and potential mates (Schöne 1984). In a recent example, Schooley & Wiens (2003) found that cactus bugs (*Chelinidea vittiger*) were more likely to orientate toward *Opuntia* cactus patches located upwind than to those located crosswind or downwind, suggesting that perceptual distance is dependent on how chemical cues from resource patches (in this case cacti) interact with prevailing winds directions. In another example, Morrow *et al.* (1989) illustrate how the perceptual range of goldenrod leaf bugs (*Trirhabda canadensis*) changes from isotropic to anisotropic under different environmental conditions. Individuals chose resource patches from all directions under low wind speeds, but chose only from upwind patches under high wind speeds. Under this scenario, perceptual horizon is expected to decrease but distance will actually increase in response to increased intensity of an environmental stimulus, relative to a traditional isotropic perceptual range. The resulting realized perceptual breadth could either increase or decrease

depending on the rates of change in horizon and distance; the direction and magnitude in which will depend on the particular study system. In our hypothetical example, we depict a situation where the decreased horizon outweighs the increased distance and therefore results in decreased perceptual breadth. Therefore, if horizon were reduced from 360 to 270 degrees then distance would have to increase by 133% in order to maintain the same perceptual breadth.

Prospectus

The importance of animal orientation behaviour in landscape ecology continues to be understated, and those modelling animal dispersal through landscapes seldom incorporate information on how an animal's orientation to changing environmental conditions may alter its realized perceptual range. This is an unfortunate disconnect because this phenomenon may be important in shaping animal movements by altering the characteristics of the landscape that an animal perceives and evaluates when making movement decisions. If perceptual ranges of animals are context-dependent (Zollner & Lima 1997) and sometimes anisotropic (Poff & Ward 1992; Schooley & Wiens 2003), then we expect the perceptual abilities of individual animals to differ with respect to environmental stimuli that vary across the landscape. As such, the three components of an animal's perceptual range – distance, horizon and breadth – should not be treated as a fixed, isotropic trait as is frequently performed when modelling animal movements through ecological landscapes. Importantly, the results from our study shed the first qualitative insight into these topics using simple geometry. Future studies that conduct quantitative simulations and explore the linkages between context-dependent perceptual range, landscape connectivity and animal movement are needed.

A comprehensive treatment of the analytical approaches that could be used to incorporate the influence of anisotropic perceptual ranges into animal movement models is beyond the scope of this paper. Again, it is our hope that this paper stimulates future work in this field. However, one example of how individual-based models could account for directed orientation (i.e. Fig. 1c,d) is by weighting patch colonization probabilities by the inverse of the absolute difference in central angle between each patch and the source of the stimulus with respect to present location of the focal animal (see Poff & Nelson-Baker 1997 for an example of using discrete angles). These probabilities could be coupled with distance-based probabilities (i.e. the Euclidean distance to each patch) to derive relative patch colonization probabilities for simulating animal movement through the landscape. Recently, Yamamura, Moriya & Tanaka (2003) developed a discrete random walk model for ragweed beetles (*Ophraella communa*) that incorporated directional movement caused by environmental factors such as wind.

In conclusion, landscape connectivity is an important property that results from the interaction between animal movement behaviour and landscape structure, and it is influenced directly by the animal's perceptual range. The fact that environmental stimuli may, through numerous mechanisms, elicit directional orientation and thus redefine perceptual ranges of animals while interacting with landscape structure is of strong consequence to ecology. We cite a need for (1) developing robust methodologies for quantifying the different components of an animal's perceptual range; (2) understanding how environmental stimuli modify perceptual ranges; (3) incorporating context-dependent perceptual ranges into models of animal movement and conducting spatially explicit dispersal simulations to explore their effects on model predictions; and (4) determining how environmental stimuli and landscape structure interact to modify individual movement behaviour. Progress in these areas will increase our understanding of animal dispersal, distribution and population dynamics in heterogeneous landscapes. We emphasize further that this exploration requires the increased integration of behavioural and ecological knowledge, as well as combination of ethological and landscape approaches.

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