

The role of animal sensory perception in behavior-based management

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6.1 INTRODUCTION

At the core of the conservation behavior framework is behavior-based management, which takes into consideration animal behavior in making conservation decisions (Chapter 1). Often, behavior-based management requires manipulation of the behavior of a species in order to accomplish specific conservation or management goals (Sutherland 1998) or avoiding actions producing stimuli that may elicit unwanted behavioral responses. Manipulating behavior may involve repelling an invasive nest parasite from a breeding site, attracting a species to a restored habitat, or sensitizing newly re-introduced individuals to predators. Obviously, the specific means of manipulating behavior will be a function of the biology of the species.

One strategy to modify the behavior of animals is to develop stimuli (visual, auditory, olfactory, etc.) intended to grab their attention and generate a specific type of response. For instance, songs of conspecifics have been used successfully to attract individuals of the endangered Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*) to suitable breeding areas in the Florida Everglades (Virzi *et al.* 2012). But, some situations can be more challenging. For example, in trying to cause aversive responses in rabbits close to agricultural fields, Wilson and McKillop (1986) tested the effectiveness of a commercially available scaring device that would broadcast sounds at high frequencies (9–15 kHz). They found that the device effect was limited to only 3 m and only while it was playing back the sounds, but most importantly animals habituated after just a few days. Despite the different characteristics of the acoustic stimuli and the different taxa, these opposite results suggest that some species may perceive our stimuli, but that perception alone does not guarantee a response. Is there any strategy

to increase the success of stimuli developed for conservation or wildlife management purposes?

The first limitation we should acknowledge is that there may be a discrepancy between the perceptual world of the biologists and that of the target species (Lim *et al.* 2008, Blumstein & Fernández-Juricic 2010). To illustrate this, let us think of the following hypothetical example. Imagine that in a large exhibition tank in an aquarium, we need to attract spotted wobbegong sharks (*Orectolobus maculatus*) to one part of the tank to feed them and avoid interactions with other species. So, we decide to use yellow LED lights to attract wobbegongs to the feeding portion of the tank, and blue LED lights to discourage them from going to other parts of the tank. The expectation is that individuals would go for the yellow lights as this color matches their body coloration (i.e. reducing their saliency to potential prey and predators). After several days, we realize that wobbegongs choose at random between colors. To us, these colors are easy to discriminate, so what could be the problem? One likely reason is the way they visually perceive these patches. Color vision is associated with the presence of more than one type of visual pigment in the cone photoreceptors (Land & Nilsson 2012). Humans have three types of visual pigments in their cone photoreceptors; however, spotted wobbegongs have recently been found to have a single type of cone visual pigment (Theiss *et al.* 2012), and are essentially color blind! This means that wobbegongs see their world in a very different way from us as they only rely on achromatic visual cues to make decisions.

The point of this example is that many times we try to develop novel stimuli using a trial-and-error approach motivated by our own human sensory system. Using stimuli outside of the perceptual world of the target species can (a) reduce the chances of observing the intended behavioral responses, (b) miss the limited time and opportunities we have to steer a change at the individual, population or community levels, and (c) waste the generally limited financial/logistical resources available to conservation/management projects (Lim *et al.* 2008). The magnitude of this problem can be substantial considering the diversity of the animal sensory systems beyond our sensory reach, including ultraviolet and polarized vision, echolocation, electroreception and magnetoreception (Dusenbery 1992, Stevens 2013).

The goal of this chapter is to illustrate conceptually how to tackle the problem of designing stimuli that are tuned to an animal's sensory system and to discuss some scenarios where this approach can be applied. For the

sake of space, the focus of the chapter is on vision and birds, although some examples from other sensory modalities and taxa are provided.

Considering the perceptual world of non-human species is not necessarily a new idea (Endler 1997, Lim *et al.* 2008, Fernández-Juricic *et al.* 2010, Martin 2011, Van Dyck 2012). However, there is relatively little guidance in the literature as to how to go about doing this. The key is for conservation scientists and managers to embrace sensory ecology and physiology. Such a task should be feasible given the inherent multi disciplinary nature of conservation biology (Chapter 1).

There are two elements that sensory ecologists study that are particularly relevant from an applied perspective: (1) what information animals gather from their environment, and (2) how that information is gathered. The first point defines the properties of the physical environment that a species makes use of (e.g. ultraviolet, infrasound, etc.); whereas the second establishes the configuration of the sensory organs and consequently the degree of spatial and temporal sensitivity (i.e. distance and rate at which signals can be gathered). Understanding these two components is essential to narrow down the range of sensory stimuli that can trigger changes in behavior.

6.2 SENSORY SYSTEMS

Sensory systems are not cheap! Devoting tissue to the peripheral sensory system as well as to the sensory centers in the brain is generally associated with solving specialized tasks under specific environmental conditions. For instance, star-nosed moles (*Condylura cristata*) have more than twenty appendages around their nostrils covered with somatosensory organs that are highly represented in the neocortex (Catania 2011). These sensory organs allow moles to detect food by touch with high precision and speed under low light conditions. Furthermore, processing sensory information in the brain is also costly due to the high energy needed to maintain neurons not only during signaling but also at rest (Niven & Laughlin 2008). For example, energetic consumption of the rat olfactory glomerulus can increase 400% in a single sniff with an increase of two orders of magnitude in odor concentration in the environment (Nawroth *et al.* 2007). Given these constraints, the null expectation should be that our study species may share some sensory capacities with us but also differ in many others depending on the ecological conditions it lives in. This precautionary approach toward the perceptual world of a species can help us consider more carefully sensory criteria in the early stages of any kind of

management strategy. Sorting out the sensory *modalities* (e.g. vision, audition, olfaction) in order of relevance for a given species will allow us to gain an initial understanding of the general and specialized tasks that its sensory system can accomplish.

However, we should keep in mind that even *within* a given sensory *modality* there are different *dimensions* (i.e. components that code for different features of a signal). For instance, the avian auditory system can process changes in the frequency as well as the temporal structure of a vocalization. Morphological constraints at the basilar membrane lead to a trade-off in the ability to process these two components of a signal: individuals with high frequency resolution cannot also have high temporal resolution. House sparrows (*Passer domesticus*) have higher temporal auditory resolution than Carolina chickadees (*Poecile carolinensis*), possibly to more efficiently process different components of conspecific vocalizations (Henry *et al.* 2011). The implication is that the different dimensions within a sensory modality may have different representation in the perceptual world of a species, and the relative relevance of these dimensions is likely to vary substantially between species.

Understanding the basic configuration of the sensory organs of our study species is a crucial step in providing an indication of the spatial and temporal ranges of its sensory systems. In this chapter, the focus will be on the visual system due to space constraints, but similar arguments can be made with any other sensory modality.

For example, let's compare human with avian vision. Humans have frontally placed and relatively large eyes that provide a wide binocular field, a single almost centrally placed center of acute vision in the retina (i.e. fovea with high density of cone photoreceptors) that projects into the binocular field, a large degree of eye movement and, as mentioned earlier in this section, three types of visual pigments. Birds have some similarities, but also many differences.

Birds have, generally, laterally placed eyes. Therefore, each eye projects a monocular field toward the sides of the head (Figure 6.1). Both monocular fields encompass the visual field, which is volume around the head from which the animal can see. There is an area in front of the head where the two monocular fields overlap giving rise to the binocular field (Figure 6.1). The areas covered by the visual field of each eye excluding the binocular field are the lateral fields (Figure 6.1). Finally, the area at the rear of the head that is not covered by either monocular field is the blind area (Figure 6.1). Because the specific location of the orbits and the degree of eye movement varies considerably between bird species, so does the

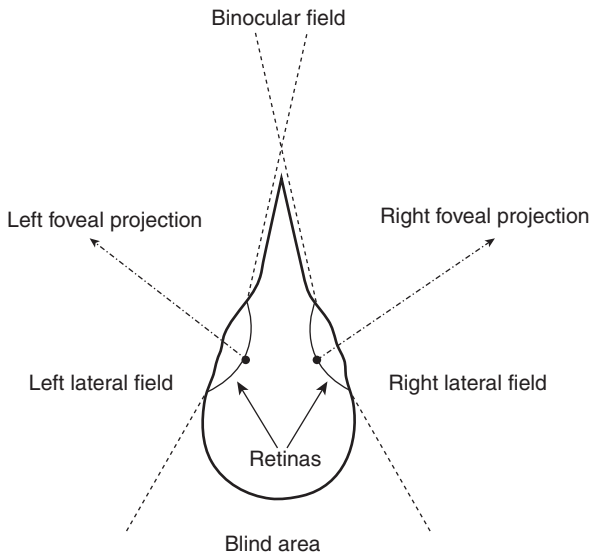


Figure 6.1: Schematic representation of the different components of the avian visual field, which is the projection of the margins of the retinas into visual space (not to scale). The binocular field is the overlap of the two lateral fields in front of the head, whereas the blind area at the rear of the head does not receive any visual input. Also shown is the relative position of the center of acute vision (fovea) in retina and its projection. The fovea has a high density of cone photoreceptors, which provide high visual resolution (chromatic and achromatic).

size of the binocular, lateral and blind areas (e.g. Martin 2007, O'Rourke *et al.* 2010, Fernández-Juricic *et al.* 2011, Moore *et al.* 2013), and consequently so does the amount and types of visual information available for a given bird species around its head. The configuration of the visual field can certainly affect the behavior of animals (i.e. species with wider blind areas tend to spend more time scanning head-up; Guilleman *et al.* 2002). Actually, Martin and Shaw (2010) argued that some collisions between birds and power lines may be caused by the limited visual coverage of some bird species, particularly above their heads (i.e. vertical extent of the binocular field). The goal, therefore, is to design stimuli with higher chances of detection based on the degree of visual coverage of the target species.

However, visual performance is not homogenous across the visual field. This is due to the configuration of the retina. The retina is a multi-layered tissue with different types of cells (Figure 6.2). The cells responsible for

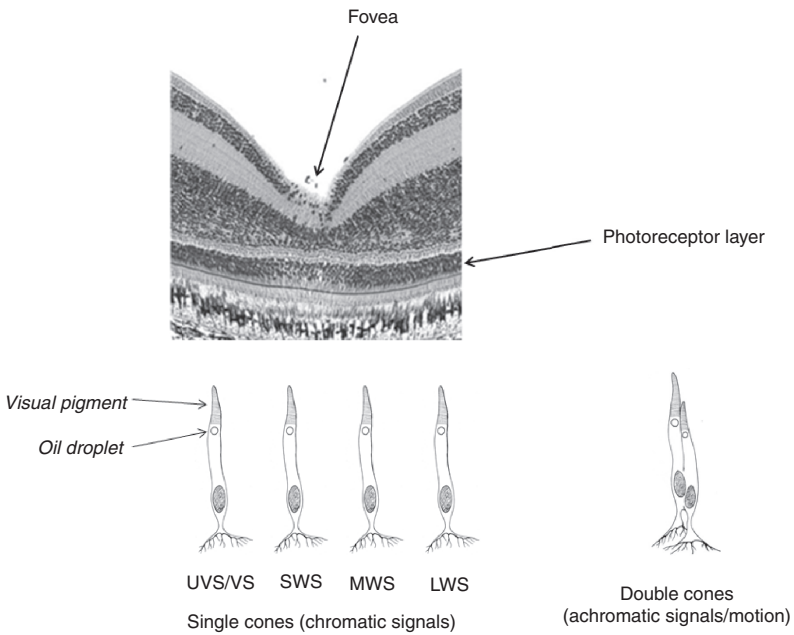


Figure 6.2: Cross section of the fovea (i.e. invagination of the retinal tissue) of the brown-headed cowbird showing the position of the photoreceptor layer, which has cone (involved in diurnal vision) and rod (involved in nocturnal vision) cells. There are two types of cones: single (involved in chromatic vision) and double (thought to be involved in achromatic and motion vision). Within the single cones, there are four kinds, depending on the sensitivity of the visual pigment: ultraviolet or violet sensitive (UVS/VS), short-wavelength sensitive (SWS), medium-wavelength sensitive (MWS) and long-wavelength sensitive (LWS). Each type of single cone also has an associated type of oil droplet, which is an organelle that filters light before it reaches the visual pigment.

phototransduction (i.e. conversion of light into electric signals) are rods (for low light conditions) and cones (for day light conditions). Birds (but not humans) have two types of cones that differ morphologically: double cones and single cones (Figure 6.2). Double cones appear to be involved in achromatic vision and motion detection, whereas single cones are responsible for color vision (Hart & Hunt 2007).

Birds have a single type of double cone, with a principal and an accessory member (Figure 6.2). The density of double cones tends to be higher than that of single cones (Hart & Hunt 2007). Birds have four types of single cones, each with a visual pigment sensitive to different parts of the spectrum (Hart & Hunt 2007): (1) ultraviolet- or violet-sensitive cone (UVS/VS) depending on the species, (2) short-wavelength sensitive (SWS),

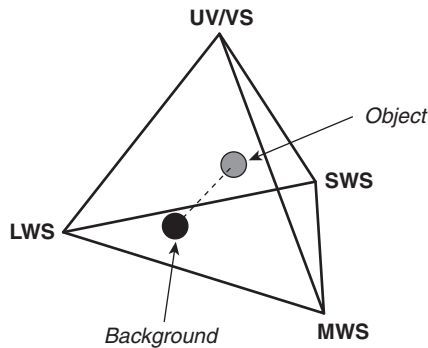


Figure 6.3: Schematic representation of the avian color space, which is limited by the visual pigment types present in the four types of single cones (Figure 6.2). Perceptual models estimate the relative distance in color space between the object and the visual background. The larger the distance, the higher the ability of the visual system to detect the object.

(3) medium wavelength sensitive (MWS) and (4) long-wavelength sensitive (LWS). Other retinal cells (e.g. ganglion cells) compare the levels of stimulation of the four different single cones when stimulated by light, which eventually leads to perception of color in the brain (Land & Nilsson 2012). The avian color space can be represented by a tetrahedron (Figure 6.3), which is bounded by four vertices, each corresponding to one of the four types of single cones (Goldsmith 1990, Neumeyer 1992, Cuthill 2006). To put things into perspective, the human color space is only bounded by three types of single cones, and hence it can be represented by the single triangular side at the bottom of the avian color space (Figure 6.3). Consequently, the avian color space is much wider than that of humans, which means that birds can perceive colors that humans cannot even imagine.

Furthermore, birds have within their cone photoreceptors organelles filled with carotenoids called oil droplets (Figure 6.2) that filter the light before it reaches the visual pigments. Because oil droplets act as wavelength-specific filters, they constrain the range of wavelengths that stimulate the visual pigments. This makes it easier to compare the degree of stimulation of different cones in response to light, thereby enhancing the ability to tell different colors apart (Cuthill 2006). Humans do not have oil droplets, and thus color discrimination may not be as refined.

Single and double cones are not homogeneously distributed, which means that visual performance varies across the retina. Recent studies mapping the density of both single and double cones have shown that

their highest densities are around the fovea (Fernández-Juricic *et al.* 2013, Baumhardt *et al.* 2014). The implication is that the fovea is not only the center of chromatic but also achromatic/motion vision. Still, birds can detect stimuli with the periphery of their retina (i.e. outside of the foveal area). However, after detection, they align the fovea with the stimulus of interest by moving their eyes or heads in order to inspect it visually with the high acuity provided by the high density of cone photoreceptors.

Another very important visual dimension to consider is visual resolution, which has spatial and temporal components. Spatial visual resolution can be thought of as the ability of an individual to resolve two objects from a distance: the higher the spatial resolution, the farther away these two objects can be differentiated. Spatial visual resolution is estimated in cycles per degree, which generally represent the number of different objects (e.g. black bars) that can be distinguished from the background in 1° of angular distance in the retina. For instance, humans have a spatial visual resolution of about 30 cycles/degree (Hodos 2012). By knowing the spatial visual resolution of a species and the size of a stimulus, we can calculate the threshold distance at which an object can be resolved from the visual background under optimal ambient light conditions. Beyond that threshold distance, the animal would have some difficulty telling that the object is there (i.e. it would blend with the background).

Spatial visual resolution has important implications for developing targeted stimuli. For instance, Blackwell *et al.* (2009) estimated that brown-headed cowbirds (*Molothrus ater*), with a spatial visual resolution of about 5 cycles/degree, would be able to resolve an object 2 m high (e.g. large vehicle approaching) from about 1000 m. Spatial visual resolution depends upon the size of the eye and the density of cone photoreceptors (along with ganglion cells). Consequently, spatial visual resolution varies considerably between species. Some bird species, such as raptors (e.g. brown falcon *Falco beribora*, 73 cycles/degree; Raymond 1987), have higher spatial visual resolution than humans, whereas other birds have much lower resolution, such as Passeriformes (e.g. European starlings *Sturnus vulgaris*, 6.3 cycles/degree; Dolan & Fernández-Juricic 2010).

There is also a temporal component of visual resolution, which estimates how fast the retina can process visual stimuli (i.e. number of snapshots it can get from the environment per unit time). Temporal visual resolution is measured as the ability to detect flicker in a pulsing light source, which varies with the intensity of light (Hodos 2012). The maximum flicker frequency that a retina can detect is called the critical flicker frequency (CFF) and is measured in Hz. Species exposed to pulsing lights at

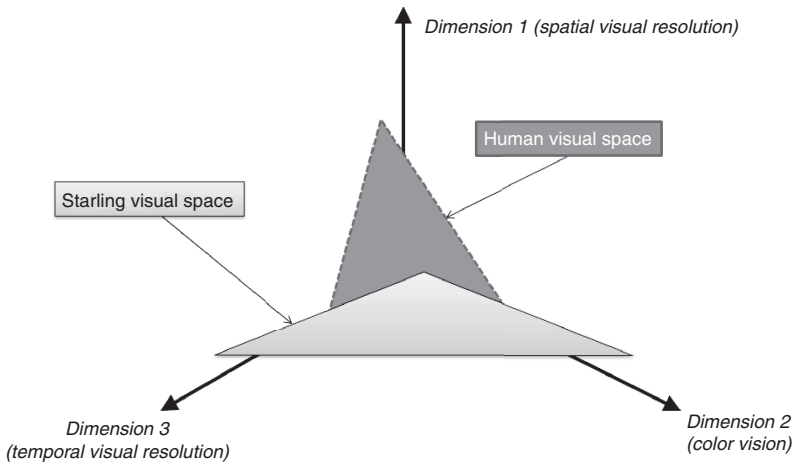


Figure 6.4: Schematic representation of the visual space of humans and European starlings, taking into consideration three visual dimensions: spatial visual resolution, temporal visual resolution and color vision.

frequencies higher than their critical flicker frequency would only be able to perceive it as a steady light. Imagine, for example, a ceiling fan working at high speeds. With our temporal visual resolution (~58 Hz; Hodos 2012), we would only see a blurred image of the blades rather than the individual blades rotating. However, European starlings, with much higher temporal visual resolution (~100 Hz; Greenwood *et al.* 2004), would likely see the individual blades rotating. In general, smaller-sized species that have higher metabolic rates tend to have higher temporal visual resolution (Healy *et al.* 2013). We can expect that a species with higher temporal resolution would be able to sample the approach of an object (e.g. predator) at a faster rate, perceive the looming more smoothly, and thus more accurately estimate the time to avoid danger.

Overall, there are some relevant points to make from an applied perspective (without taking into account ultimate explanations):

First, birds see their world in fundamentally different ways from humans. This is not just restricted to their ultraviolet vision, as emphasized in the literature (Cuthill 2006); but to multiple other visual dimensions (see earlier in this section).

Second, one of the implications of these taxon-specific visual traits is that if we plot the visual space (defined by different visual dimensions) of different species, there will be some degree of overlap as well as segregation (Figure 6.4). An area of sensory space occupied only by species A would be

“blind” to species B. However, visual space plots only show the visual sensory boundaries of each species, but not their visual sweet-spots. From an operational perspective, a visual sweet-spot can be defined as an area within the visual space where a visual stimulus increases the degree of activation of the neurons in the visual centers of the brain, leading to enhanced perception. For instance, research in humans has shed light into the optimal flicker rate that enhances the brightness perception of light bulbs (Rieiro *et al.* 2012), the viewing distance and resolution of mobile devices compared to TVs (Knoche & Sasse 2008), and ways of reducing visual distortions when looking through optical instruments (Merlitz 2010). It is important to keep in mind that visual sweet-spots may be context dependent (Gamberale-Stille *et al.* 2007) or even change with experience (Schmidt & Schaefer 2004). Experiments to determine the visual sweet-spot in humans are relatively easier as we can ask subjects their assessment of the perceptual experience. Obviously, this becomes much more challenging in non-human systems.

Third, there is considerable between-species variation in birds in terms of the visual dimensions discussed (Martin 2007, Gaffney & Hodos 2003, Hart & Hunt 2007, Fernández-Juricic 2012). This variability suggests that different bird species may have different visual sweet-spots. One question that needs to be addressed in the future is the degree of overlap in the sweet-spots of different species. This can be particularly relevant when targeted stimuli are intended to modify the behavior of multiple species at the same time rather than a single one. Furthermore, the between-species variation in the relative position of the sweet-spot in visual sensory space is important when we want to manipulate simultaneously the behavior of one species in one direction (i.e. attract) and another species in a different direction (i.e. repel). If the sweet-spots are in the very same position, it could be more challenging than if they are in different positions.

6.3 HOW TO GO ABOUT DEVELOPING TARGETED STIMULI TAKING THE SENSORY APPROACH

Determining how animals perceive a stimulus based purely on their behavioral response is a challenging task. Even if the stimulus is within their sensory space, they may perceive it but it may be so far outside of their sensory sweet-spot that they may not show any behavioral response (either positive or negative). Similarly, animals may not react if the stimulus is not associated with any particular risk or motivation (e.g. food). For instance, think of a group of people having a picnic in the woods and watching how a

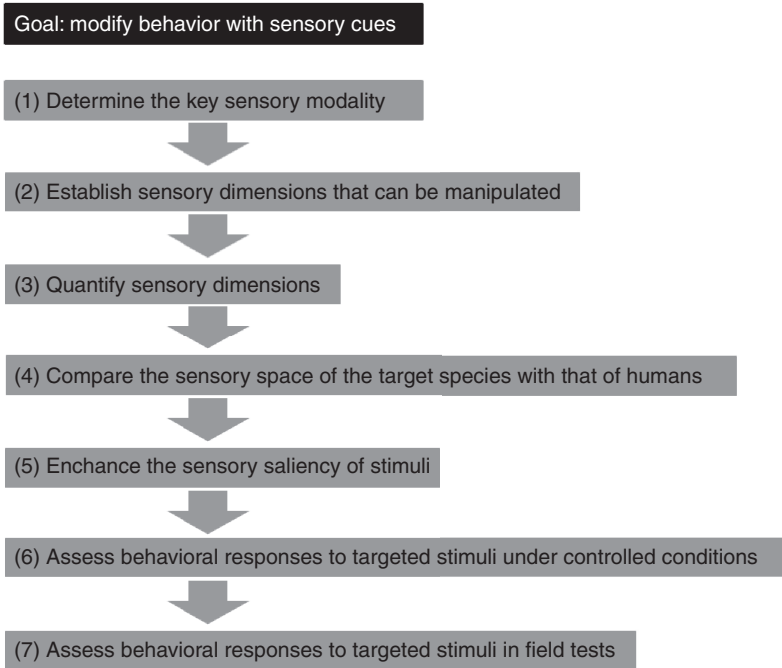


Figure 6.5: Suggested steps to develop targeted sensory cues to modify the behavior of animals. See text for details.

light breeze moves the leaves of trees. They can certainly detect such movements, but they are not likely to react, particularly if their attention is focused on maintaining a conversation. Given the difficulty in assessing animals' perception, what can managers and conservation biologists do?

Blackwell and Fernández-Juricic (2013) provided some suggestions, which I expand on here to formalize a seven-step approach to address this problem. The basic idea is to narrow down candidate stimuli based on the sensory configuration of the target species, possibly developing stimuli close to the sensory sweet-spot, expose animals to these stimuli and measure their behavioral responses. This approach encourages the development of sensory-based hypotheses that can make predictions about the degree of saliency, and the associated behavioral responses. The seven steps are summarized in Figure 6.5.

(1) Taking into consideration the type of behavior that we would like to modify (e.g. foraging, anti-predator, territory establishment), *determine the sensory modality that most likely could trigger the intended behavioral response*

depending on the species biology. This requires some natural history knowledge along with expert opinion. Even for taxa characterized as relying mostly on a single sensory modality, there may be species that may depart from the mainstream sensory pattern. For instance, birds are visually-oriented organisms, but kiwis (*Apteryx sp.*) rely mostly on chemical and tactile cues, with a reduction in the eye and visual centers in the brain (Martin *et al.* 2007). This is mostly due to the kiwis nocturnal habits.

(2) Within the sensory modality identified in (1), *establish the sensory dimensions that can be manipulated with the logistical resources available.* This step is essential as some ideas for targeted stimuli are biologically sound but technically not feasible. For instance, we can try to attract honey bees (*Apis mellifera*) to patches with nectar-rich flowers by showing them a rapid sequence of enlarged flower pictures with an iPad®. However interesting this idea may be, iPads® cannot playback in the ultraviolet, which is one of the visual channels that honey bees use to gather foraging information (e.g. Arnold *et al.* 2010). Besides creativity, this step sometimes calls for collaborations with engineers to adjust existing or develop new technology.

(3) *Quantify the sensory dimensions* identified in (2). Given that animals tend to use multiple sensory dimensions within a sensory modality, the more dimensions that can be manipulated, the higher the number of potential sensory channels we will have available to attempt behavioral manipulations. This step may benefit from establishing collaborations with sensory physiologists, obtaining the information from the literature, or estimating the sensory dimensions from life-history traits. Sensory physiologists may be willing to develop collaborations as their basic work can take an applied spin, potentially leading to new funding avenues. Nevertheless, it may be possible that many of these dimensions have already been characterized for the target species or species that are taxonomically very close. For example, with regards to the avian visual system, there are already multiple resources that provide information on the visual field configuration (Martin 2007), the type of center of acute vision (along with the density of photoreceptors and ganglion cells) (Collin 2008), the sensitivity of visual pigments and oil droplets (Hart & Hunt 2007), and so on, of several species. In cases where there is no possibility of studying a species using physiological techniques due to ethical reasons and/or availability (e.g. endangered or threatened species), we might be able to get some of this information behaviorally in the field. But, if we cannot even get the behavioral information, we can estimate certain parameters based on life-history associations found in some taxa. For instance, studies reported significant relationships between avian spatial visual resolution and body

mass (Kiltie 2000) as well as temporal visual resolution and body mass (Healy *et al.* 2013). The linear equations available can certainly be used to estimate values for these visual dimensions based on the body mass of the target species.

(4) *Compare the sensory space of the target species with that of humans to establish where the targeted stimuli will be played back.* If there are some portions of the sensory space of both species without overlap, we may need to address the question of whether humans should also perceive the stimuli or not. For instance, if the stimulus is meant to cause discomfort to repel the animal, it may be better to hide it sensorially from us (e.g. using ultraviolet, infrasound, etc.). There may also be some strict regulations. For instance, the Federal Aviation Administration does not allow white lights at airports to pulse at frequencies higher than 3 Hz (Rash 2004). In some situations, it might also be advisable to plot the sensory space of some non-target species of conservation concern that inhabit the same habitat to assess the potential indirect effects of the stimulus at the community level.

(5) *Within a sensory dimension, estimate stimuli that are more salient for the sensory system of the target species* (i.e. stimuli closer to its sensory sweet-spot). This can be done experimentally or through modeling approaches. Experimentally, it often involves using physiological approaches. For instance, in the case of the visual system, we can use electroretinograms to estimate the threshold frequency of flickering that a species can process as such at different wavelengths. Rubene *et al.* (2010) found that critical flicker frequencies of chickens (*Gallus gallus*) were higher (i.e. higher temporal visual resolution) for lights that included white plus UV components than only white, only yellow or only UV lights. Similarly, we can use auditory evoked potentials to different acoustic stimuli, which reflect the ability of the neurons in the peripheral auditory system to process sounds with different frequency, intensity and temporal characteristics, to determine the saliency of those signals. For example, Carolina chickadees (*Poecile carolinensis*) have good frequency resolution to vocal signals with relatively higher frequencies (4 kHz) compared to other bird species, whose peak frequency resolution ranges from 2 to 3 kHz (Henry & Lucas 2010). These physiological procedures yield information about the specific portions of the sensory space where targeted stimuli can be processed more finely, and thus their perceptual saliency can be enhanced.

There are some sensory dimensions in which the estimation of stimulus saliency is more complex. Modeling approaches may be necessary in these cases. One of the best examples is how to determine the saliency of a visual cue for a species where the number and the sensitivity of the visual

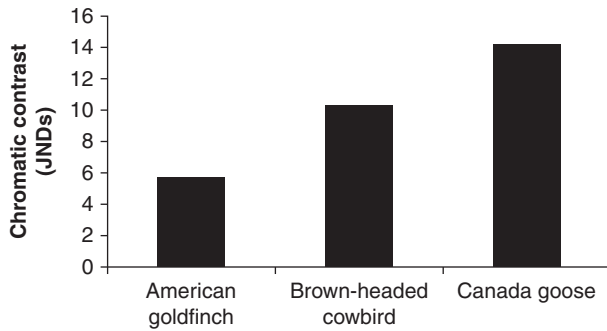


Figure 6.6: Chromatic contrast (in Just Noticeable Differences) of a rice panicle (object) against its leaves (visual background) from the perspective of the visual system of three species: American goldfinch, brown-headed cowbird and Canada goose. Calculations were done with the photon catch and receptor noise perceptual model (Vorobyev & Osorio 1998) using published physiological data from each species (Moore *et al.* 2012, Fernández-Juricic *et al.* 2013, Baumhardt *et al.* 2014).

pigments are quite different from those of humans (e.g. birds and bees). One of the solutions is to use perceptual modeling, which are mathematical algorithms that make predictions about the degree of visual contrast of a visual cue from the visual background for a specific visual system under specific ambient light conditions (Montgomerie 2006). Visual contrast can be estimated for chromatic and achromatic cues.

There are different types of perceptual models (e.g. Vorobyev & Osorio 1998, Endler & Mielke 2005, Stoddard & Prum 2008). For example, the photon catch and receptor noise perceptual model (Vorobyev & Osorio 1998) uses several visual physiological parameters of the study species, allowing us to make species-specific predictions about the saliency of visual cues. This is important because of the large between-species variability in the visual traits involved in chromatic and achromatic vision (i.e. density of cone photoreceptors, sensitivity of visual pigments and oil droplets; Hart & Hunt 2007, Moore *et al.* 2012, Fernández-Juricic *et al.* 2013, Baumhardt *et al.* 2014). For instance, using perceptual modeling, we can see the large degree of between-species variation (~130%) in chromatic contrast of the same branch of rice flowers for brown-headed cowbirds, American goldfinches, *Carduelis tristis*, and Canada geese, *Branta canadenses* (Figure 6.6). Even though we do not understand very well how these differences in modeled perception translate into behavior, perceptual models are a good starting point to establish the relative saliency of visual stimuli under different ecological conditions.

The photon catch and receptor noise model uses various parameters to calculate visual contrast (Vorobyev & Osorio 1998). Here is a summary of the three main parameters. First, we need information on some visual traits: the sensitivity of the visual pigments (and oil droplets if our target species is a bird, turtle, lizard or some fish) and the relative density of cone photoreceptors. Second, we need measurements of the reflectance of the stimulus and its background (i.e. how much light is reflected across different wavelengths). Third, we need measurements of the spectral properties of the ambient light (i.e. irradiance) upon which the animals will be modeled to be perceiving the stimulus. With all this information, the model calculates the relative distance between the stimulus and the background (i.e. degree of visual saliency) under specific ambient light conditions and within the color space of the target species (Figure 6.3), yielding values of chromatic and achromatic contrast. The units are called just noticeable differences (JNDs). At least theoretically (although this could be species-specific), JNDs < 1 indicate that the stimulus cannot be discriminated from the background, JNDs from 1 to 4 indicate that discrimination is possible but challenging, and JNDs > 4 indicate that visual discrimination is highly likely (Siddiqi *et al.* 2004). Based on the results presented in Figure 6.6, we can conclude that the rice panicle can be discriminated by all three species, but it would be easier to resolve from the background for Canada geese.

(6) *Expose animals to stimuli tuned to their sensory system under controlled conditions.* This step is aimed at testing different stimuli to identify those with higher chances of causing the expected behavioral responses (e.g. attraction, repulsion). This is an iterative process that may require going back to step (5) to establish the saliency of variations in the stimuli based on the results obtained in the behavioral assays. The value of using controlled experiments (lab, outdoor enclosures, etc.) is that several confounding factors can be minimized (e.g. identity effect, food availability, social interactions) or manipulated (e.g. ambient light conditions, noise levels). This will lead to a better understanding of the cause–effect relationships between the stimuli and the behavioral responses as well as the environmental conditions where the responses are enhanced (e.g. temperature, light intensity); however, it may not have a large degree of generality.

(7) *Expose animals in the wild to stimuli tuned to their sensory systems to generalize the responses.* The natural conditions may introduce factors that were not considered in the previous step (e.g. animals in a group modify their decision-making in relation to solitary conditions). Therefore, tweaking the stimuli in these experiments may require revisiting

steps (5) and (6). Additionally, if the stimulus is intended to replace an old one, the metrics to compare the performance of both would need to be established in advance.

This seven-step approach makes an important implicit assumption: stimuli close to the sensory sweet-spot would trigger an enhanced behavioral response, either in terms of attraction or repulsion. Unfortunately, there is a dearth of literature testing this key assumption and this is an area of future research that can provide much needed insights. Yet, the overall approach is still valid as we could tweak the stimulus in different directions from the sensory sweet-spot to assess at which point the behavioral response changes in type and strength.

To illustrate some of these steps let's consider a couple of hypothetical examples. First, imagine we are trying to develop stimuli to minimize the damage that European starlings cause on crops. Given how visually driven starlings are (Martin 1986), we decide to develop a visual stimulus in the form of a pulsing light, which is known to cause discomfort at high pulsing frequencies, at least to humans (Stone 1990). We choose three visual dimensions that have been characterized in starlings (Hart *et al.* 1998, Dolan & Fernández-Juricic 2010, Feinkohl & Klump 2011) to address this problem: (1) spatial visual resolution because it can provide information on the distance at which the lights would be detected, (2) temporal visual resolution because it would allow us to enhance the discomfort effect by increasing the pulsing frequency and (3) color vision because it would allow us to explore light colors that may be more noticeable to starlings. In mapping these dimensions for both starlings and humans (Figure 6.4), we find that starlings have higher temporal visual resolution and a wider color space, but their spatial visual resolution is lower than that of humans. A stimulus in the shared portions of the sensory space may also negatively affect humans. Therefore, we decide to hide the stimulus as much as possible from the human visual system by developing a light that pulses in the ultraviolet portion of the spectrum (360 nm) at high pulsing frequencies (90 Hz) for only starlings to detect. We deploy the lights in small boxes (10 x 10 x 10 cm) held by a 1-m-high dowel rod. Based on the starling visual acuity (6.3 cycles/degree), we estimate that under perfect light conditions individuals would be able to detect the light from 72 m. To increase the surprise factor (and save battery life) we install a motion detector system that would turn the lights on at 70 m from any object moving within that range. This simple system can be tweaked to enhance the behavioral response, for instance, by increasing the pulsing frequency of the lights as the starlings move closer to the lights.

A second hypothetical example involves the development of bird feeders that are more visually enticing to the real consumers, the birds themselves, as opposed to humans given the between-species differences in their visual systems. To get started, we can determine if some bird feeder colors available in the market stand out visually from the avian perspective. We can choose a feeder consisting of a semicircular dome from which three socks filled with seeds are suspended. The dome is available in three colors: red, yellow and green. We target the American goldfinch, a sexually dimorphic bird (males are brightly colored during the breeding season whereas females have a duller coloration), as this species generally visits bird feeders year round and the basic properties of its visual system have recently been characterized (Baumhardt *et al.* 2014). We address the basic question of which bird feeder, provided the seeds available are the same, would be more visually salient from the goldfinch perspective using perceptual modeling. This tool also allows us to explore the saliency of the feeders in different seasons as light intensity (affecting irradiance) as well as vegetation structure (affecting the reflectance of the visual background) change from the breeding to the non-breeding seasons. Additionally, goldfinches make use of both closed and open habitats, where the spectral properties of the ambient light vary substantially (Lythgoe 1979). Considering all these factors, we can model the chromatic contrast of these three feeders using the goldfinch visual traits (Figure 6.7). The results show that the yellow and red feeders are much more salient than the green feeder in open and closed habitats during the breeding season and in closed evergreen habitats during the non-breeding season. However, these differences in chromatic contrast are minimized in open and closed deciduous habitats during the non-breeding seasons. One implication is that for the bird feeders to have a similar level of visual saliency throughout the year, other color combinations would need to be explored during the non-breeding season. Another factor that could play a role is a potential seasonal difference in the visual system, as found in other taxa (e.g. Whitmore & Bowmaker 1989). Overall, these results open up interesting opportunities for novel bird feeder designs.

6.4 HOW TO IMPLEMENT THE APPLIED SENSORY ECOLOGY APPROACH INTO BEHAVIOR-BASED MANAGEMENT

6.4.1 Implementing the applied sensory ecology approach into conservation planning

Understanding the sensory system of the species in question can help improve reserve design to protect species, plan a corridor to facilitate the

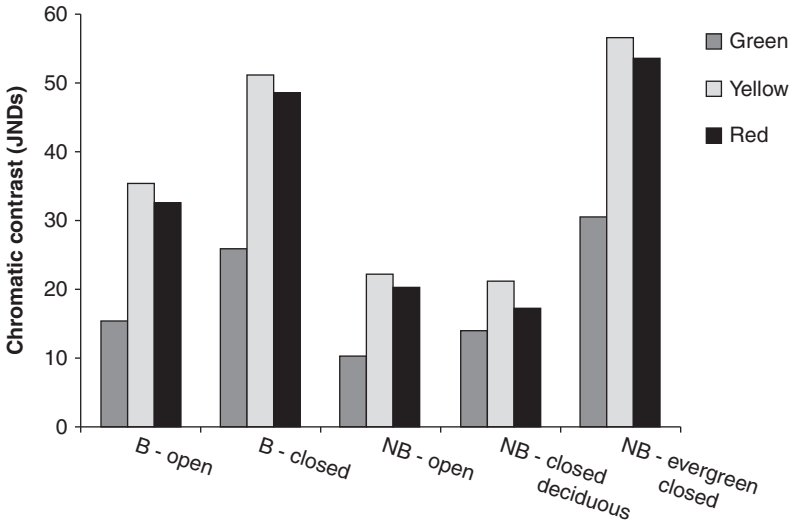


Figure 6.7: Chromatic contrast (in Just Noticeable Differences) of bird feeders of different colors (green, yellow, red) in the breeding (B) and non-breeding (NB) seasons and different habitat types and thus visual backgrounds (open, closed deciduous, closed evergreen), from the perspective of American goldfinches. Calculations were done with the photon catch and receptor noise perceptual model (Vorobyev & Osorio 1998) using published physiological data for goldfinches (Baumhardt *et al.* 2014).

movement of species or prepare the translocation of a species. Species interact with different components of the landscape (e.g. habitat structure), conspecifics and heterospecifics (e.g. prey, predators) through their sensory systems to make decisions (Chapter 7). Conservation measures that change the spatial and temporal distribution of these elements will likely change how the environment of a species is perceived and potentially its behavior. A couple of examples are described in this section.

Evolutionary traps occur when animals show stronger or similar preference to resources (e.g. foraging resources, shelter, breeding habitat) that provide lower fitness compared to other naturally available resources of the same type (Schlaepfer *et al.* 2002, Chapter 4). For example, water surfaces reflect polarized light, a cue that many insects use to locate areas where they lay their eggs (Schwind 1991). However, asphalt can also generate similar or even higher levels of polarized reflected sunlight, leading mayflies to lay their eggs in areas that have no reproductive value (Kriska *et al.* 1998), which can have negative population consequences (Horváth *et al.* 2009). A similar phenomenon takes place

with insects and glass buildings, which urban birds take advantage of for foraging purposes due to the higher availability of food (Robertson *et al.* 2010). The aforementioned applied sensory ecology approach can be used to reduce the incidence of this sensory pollution problem. For instance, Horváth *et al.* (2010) found that the degree of polarization was smaller in solar panels with white borders and grates, leading to lower preference for egg-laying by different flying insects. A better understanding of the key components of polarized light perception in these insects could allow us to find novel strategies to reduce their levels of preference. Alternatively, the same sensory principle can be used to attract some insects to polarizing traps (Egri *et al.* 2013).

Another potential application of the sensory approach corresponds to buffer areas, which are used by conservation biologists to exclude human visitation from areas in order to increase the nesting success of some species (Blumstein & Fernández-Juricic 2010). Buffer areas are generally calculated using information on escape behavior: a human approaches an individual at a steady pace and records the distance at which the animal flushes (e.g. flight initiation distance). This distance is then taken as the radius of a circle to estimate the buffer area (reviewed in Fernández-Juricic *et al.* 2005). The rationale is that by preventing humans from encroaching into this buffer area, we could prevent a species from leaving their nesting grounds.

However, there are many sensory problems with the way buffer areas are estimated (Fernández-Juricic *et al.* 2005). First, the distance at which an individual escapes is not necessarily the same as the one it detects the approach (see earlier in this section). Actually, it is likely that individuals detect the approach very early but refrain from leaving the patch until the risk is considered too high (i.e. humans are much closer). There is evidence using heart rate telemetry, for instance, that penguins that are visited by tourists at close distances do not necessarily flee but have high pulse rate levels that are sustained as long as the exposure lasts (Ellenberg *et al.* 2013). High pulse rate levels have been associated with higher levels of stress hormones and lower reproductive output (Ellenberg *et al.* 2007). Second, the buffer area approach does not consider the temporal component of the interactions between recreationists and wildlife. In other words, a species with higher temporal visual resolution could potentially gain information about the human exposure at a quicker rate (and thus make decisions faster) than one with lower temporal visual resolution (Healy *et al.* 2013), leading to the idea of species-specific differences in the temporal perception of disturbance and, potentially, stress.

Consequently, how long and from how far away should an animal be exposed to recreationists? Knowledge on the sensory physiology of the target species can help. If we consider a visually oriented organism, we can make some recommendations based on its spatial and temporal resolving power. Spatial visual resolution can give us estimates of the distance at which the target species would not be able to resolve recreationists visually. Using these distance values to calculate buffer areas would certainly reduce stress levels. This option could particularly work with species that have lower spatial resolution than humans. Those with higher spatial resolution than humans would require having blinds whose coloration/patterning make them difficult to visually resolve from the visual background. Temporal visual resolution could provide estimates of the optimal exposure time to minimize stress levels. There is evidence in humans that the perception of time may be associated with the temporal visual resolution (Hagura *et al.* 2012). We can then speculate that species with higher temporal visual resolution might perceive a “short” human visit as actually a long one; while the opposite effect might occur in species with lower temporal resolution. Taking this temporal perception into account could provide new ways of managing the rate of visitation to protected areas.

6.4.2 Manipulating behavior

The seven-step approach to develop stimuli tuned to the sensory system of a target species (see above) can be applied to different contexts relative to the manipulation of a species’ behavior. A couple of examples are described in this section.

Collisions between aircraft and birds (bird-strikes) have become a large problem despite successful management efforts to reduce the incidence of different bird species *within* airport property (Dolbeer *et al.* 2012). The reason is that the frequency of damaging strikes *outside* of the airport property has been increasing in the last few years (Dolbeer 2011). Commercial aircraft themselves do not currently have any specific means to minimize the chances of collisions with large species or small species flying in groups, which can damage critical mechanical elements of an aircraft (e.g. engine). This is what happened in January 2009 when a flock of migrating geese struck both engines of a flight departing from La Guardia Airport in New York City, causing the powerless aircraft to crash-land in the Hudson River (Marra *et al.* 2009). There have been efforts to develop lighting systems for aircraft tuned to the avian visual system that can be used to trigger early avoidance behavior on birds (Blackwell & Fernández-Juricic 2013). The rationale is simple. A recent study showed that

birds involved in collisions had tried to avoid aircraft unsuccessfully, possibly due to a lack of time to respond due to high aircraft speeds (Bernhardt *et al.* 2010). Lights that enhance avian perception may provide slightly extra time for birds to engage in successful avoidance maneuvers (Blackwell & Fernández-Juricic 2013). For instance, Blackwell *et al.* (2012) estimated that the chromatic contrast of a radio-controlled (RC) aircraft with lights on was substantially higher than the same aircraft with lights off from the visual perspective of Canada geese. Additionally, they showed that geese became alert to the approaching RC aircraft about 4 s earlier with the lights on than off (Blackwell *et al.* 2012). At the fast speeds at which these collisions occur, this is a considerable amount of time. Interestingly, the type of light (pulsing, steady) that enhances alert behavior depends on the ambient light conditions (sunny, cloudy; Blackwell *et al.* 2009), suggesting the possibility of an automatic system that adjusts the light regime depending upon weather. However, the ability of birds to assess the position of approaching vehicles gets reduced at higher speeds, increasing the chances of collision (Farmer & Brooks 2012). A recent study actually found that lights tuned closer to the avian visual sweet-spot can minimize this negative speed effect, probably by improving the tracking of the object at high speeds (Doppler *et al.* 2015).

Attracting animals to specific spots is another problem that this sensory approach can tackle. Animals move around for multiple reasons: foraging, roosting, nesting, migrating and so on. However, the high degree of human disturbance and resulting habitat modification has made the arrangement of landscapes much more complex: (a) regularly visited habitat patches may be gone or may still be present with high levels of disturbance (e.g. recreationists); (b) remaining undisturbed habitat patches may have a higher density of conspecifics, leading to direct and indirect intra-specific competition; (c) remaining undisturbed habitat patches may still be available but the landscape matrix surrounding them may have changed, and with it the cues used to get to them; and (d) never-used but new habitat patches may be available as a result of restoration efforts. The issue is how to help individuals go from point A to point B providing cues that are tuned to their sensory systems. Two examples are worth mentioning. First, Coleen St. Clair and collaborators have championed several studies to understand the behavioral mechanisms small forest passerine birds use to cross forest gaps using (a) homing experiments (i.e. translocating birds relatively short to medium distances from their territories and measuring their ability to return to the point of capture; Bélisle & St. Clair 2001), and (b) acoustic cues (mobbing calls) to measure the degree of willingness of an individual to cross different habitat arrangements (undisturbed forest, corridor, forest

gap; St. Clair *et al.* 1998). These types of studies have been relevant to understanding the differential responses of forest specialists and habitat generalists to changes due to habitat fragmentation and the value of stepping-stones in facilitating movements across different types of landscapes (e.g. Gillies & St. Clair 2010). The second example revolves around how larval fish in the pelagic phase find their way through the ocean to make it to the benthic juvenile phase. There is evidence that coral reef fish larvae can distinguish chemical cues from different habitat types (e.g. coral reef vs. open ocean odors; Atema *et al.* 2002). A recent study used an unmanned chamber in the open ocean to track the swimming behavior of larval fish and found that they swim toward the coral reef odor (Paris *et al.* 2013). These results open up the possibility of remotely cueing in larvae with chemical stimuli to enhance the possibility of a successful settlement process in areas with high levels of ocean pollution.

6.5 CONCLUSIONS

For decades, conservation biologists and wildlife managers have been generally developing stimuli to manipulate the behavior of target species using a trial-and-error approach, which assumes that the sensory system of the target species is the same as that of humans. If this sensory system overlaps to a large degree with the human one, the trial-and-error approach may be sufficient. But, when there are substantial differences in sensory perception between humans and the target species, the applied sensory ecology approach presented in this chapter can be a complement to open up novel strategies to manipulate the behavior of animals. A seven-step process is conceived as iterative to fine-tune the relationship between sensory input and behavioral output. This process considers sensory hypotheses (e.g., perceptual modeling) that can generate specific predictions regarding the degree of sensory saliency of the targeted stimulus to the study species. Overall, trying to perceive the world through animal senses (instead of our limited sensory experience) can improve the allocation of limited resources to management and conservation efforts.

There are many contexts to which the sensory ecology approach could be applied. Yet, one key component that future research should address is how any kind of short-term behavioral responses caused by targeted stimuli can be sustained in time. In other words, would the changes in behavior as a result of using sensory cues lead to habituation or sensitization (see Chapter 3)? Although the answer to this question is bound to be species- and context-specific, it can also provide some general understanding of the role of sensory

systems in the behavioral responses of animals to human-induced environmental change.

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REFERENCES

- Arnold, S.E.J., Faruq, S., Savolainen, V., McOwan, P.W. and Chittka, L. 2010. FReD: the floral reflectance database – a web portal for analyses of flower colour. *PLoS ONE*, **5**(12):e14287.
- Atema, J., Kingsford, M.J. and Gerlach, G. 2002. Larval reef fish could use odour for detection, retention and orientation to reefs. *Marine Ecology Progress Series*, **241**:151–160.
- Baumhardt, P.E., Moore, B.A., Doppler, M. and Fernández-Juricic, E. 2014. Do American goldfinches see their world like passive prey foragers? A study on visual fields, retinal topography, and sensitivity of photoreceptors. *Brain, Behavior and Evolution*, **83**:181–198.
- Bélisle, M. and St. Clair, C.C. 2001. Cumulative effects of barriers on the movement of forest birds. *Conservation Ecology*, **5**(2):9.
- Bernhardt, G.E., Blackwell, B.F., DeVault, T.L. and Kutschbach-Brohl, L. 2010. Fatal injuries to birds from collisions with aircraft reveal anti-predator behaviours. *Ibis*, **152**:830–834.
- Blackwell, B.F., Fernández-Juricic, E., Seamans, T.W. and Dolan, T. 2009. Avian visual system configuration and behavioural response to object approach. *Animal Behaviour*, **77**:673–684.
- Blackwell, B.F. and Fernández-Juricic, E. 2013. Visual deterrents at airports. In DeVault, T.L., Blackwell, B.F. and Belant, J.L. (eds.), *Wildlife Management in Airport Environments*, pp. 11–22. Baltimore, MD: The Johns Hopkins University Press.
- Blackwell, B.F., DeVault, T.L., Seamans, T.W., Lima, S.L., Baumhardt P. and Fernández-Juricic, E. 2012. Exploiting avian vision with aircraft lighting to reduce bird strikes. *Journal of Applied Ecology*, **49**:758–766.
- Catania, K.C. 2011. The sense of touch in the star-nosed mole: from mechanoreceptors to the brain. *Philosophical Transactions of the Royal Society*, **366**:3016–3025.
- Collin, S.P. 2008. A web-based archive for topographic maps of retinal cell distribution in vertebrates. *Australian Journal of Optometry*, **91**:85–95.

- Dolan, T. and Fernández-Juricic, E. 2010. Retinal ganglion cell topography of five species of ground foraging birds. *Brain, Behavior and Evolution*, 75:111–121.
- Dolbeer, R.A., Wright, S.E., Weller, J. and Begier, M.J. 2012. *Wildlife strikes to civil aircraft in the United States, 1990–2011*. U.S. Department of Transportation, Federal Aviation Administration, Office of Airport Safety and Standards, Serial Report No. 18, Washington, DC, USA
- Dolbeer, R.A. 2011. Increasing trend of damaging bird strikes with aircraft outside the airport boundary: implications for mitigation measures. *Human–Wildlife Interactions*, 5:235–248.
- Doppler, M., Blackwell, B.F., DeVault, T.L. and Fernández-Juricic, E. 2015. Cowbird responses to aircraft with lights tuned to the avian visual system: implications for bird-aircraft collisions. *The Condor* 117:165–177.
- Dusenbery, D.B. 1992. *Sensory Ecology: How Organisms Acquire and Respond to Information*. New York: W.H. Freeman.
- Egri, A., Blaho, M., Szaz, D., Kriska, G., Majer, J., Herczeg, T., Gyurkovszky, M., Farkas, R. and Horvath, G. 2013. A horizontally polarizing liquid trap enhances the tabanid-capturing efficiency of the classic canopy trap. *Bulleting of Entomological Research* 103:665–674.
- Ellenberg, U., Setiawan, A.N., Cree, A., Houston, D.M. and Seddon, P.J. 2007. Elevated hormonal stress response and reduced reproductive output in yellow-eyed penguins exposed to unregulated tourism. *General and Comparative Endocrinology*, 152:54–63.
- Ellenberg, U., Mattern, T. and Seddon, P.J. 2013. Heart rate responses provide an objective evaluation of human disturbance stimuli in breeding birds. *Conservation Physiology*, 1: coto13.
- Endler, J.A. 1997. Light, behavior and conservation of forest-dwelling organisms. In Clemmons, J.R. and Buchholz (eds.), *Behavioral Approaches to Conservation in the Wild*, pp. 330–356. Cambridge (UK): Cambridge University Press.
- Endler, J.A. and Mielke, P.W. 2005. Comparing entire colour patterns as birds see them. *Biological Journal of the Linnaean Society*, 86:405–431.
- Farmer, R.G. and Brooks, R.J. 2012. Integrated risk factors for vertebrate roadkill in Southern Ontario. *Journal of Wildlife Management*, 76:1215–1224.
- Feinkohl, A. and G. Klump. 2011. Processing of transient signals in the visual system of the European starling (*Sturnus vulgaris*) and humans. *Vision Research*, 51:21–25.
- Fernández-Juricic, E., Moore B.A., Doppler, M., Freeman, J., Blackwell, B.F., Lima, S.L. and DeVault, T.L. 2011. Testing the terrain hypothesis: Canada geese see their world laterally and obliquely. *Brain, Behavior & Evolution*, 77:147–158.
- Gaffney, M.F. and Hodos, W. 2003. The visual acuity and refractive state of the American kestrel (*Falco sparverius*). *Vision Research*, 43:2053–2059.
- Gamberale-Stille, G., Hall, K.S.S. and Tullberg, B.S. 2007. Signals of profitability? Food colour preferences in migrating juvenile blackcaps differ for fruits and insects. *Evolutionary Ecology*, 21:99–108.
- Gillies, C.S. and St Clair, C.C. 2010. Functional responses in habitat selection by tropical birds moving through fragmented forest. *Journal of Applied Ecology*, 47:182–190.

- Goldsmith, T.H. 1990. Optimization, constraint, and history in the evolution of eyes. *Quarterly Review of Biology*, **65**:281–322.
- Guilleman, M., Martin, G.R. and Fritz, H. 2002. Feeding methods, visual fields and vigilance in dabbling ducks (*Anatidae*). *Functional Ecology*, **16**: 522–529.
- Greenwood, V.J., Smith, E.L., Goldsmith, A.R., Cuthill, I.C., Crisp, L.H., Walter-Swan, M.B. and Bennett, A.T.D. 2004. Does the flicker frequency of fluorescent lighting affect the welfare of captive European starlings? *Applied Animal Behaviour Science*, **86**:145–159.
- Hagura, N., Kanai, R., Orgs, G. and Haggard, P. 2012. Ready steady slow: action preparation slows the subjective passage of time. *Proceedings of the Royal Society B*, **279**:4399–4406.
- Hart, N.S. and Hunt, D.M. 2007. Avian visual pigments: characteristics, spectral tuning, and evolution. *American Naturalist*, **169**:S7–S26.
- Hart, N.S., Partridge, J.C. and Cuthill, I.C. 1998. Visual pigments, oil droplets and cone photoreceptor distribution in the European starling (*Sturnus vulgaris*). *Journal of Experimental Biology*, **201**:1433–1446.
- Healy, K., McNally, L., Ruxton, G.D., Cooper, N. and Jackson, A.L. 2013. Metabolic rate and body size are linked with perception of temporal information. *Animal Behaviour*, **86**:685–696.
- Knoche, H.O. and Sasse, M.A. 2008. The sweet spot: how people trade off size and definition on mobile devices. *MM '08 Proceedings of the 16th ACM international conference on Multimedia* 21–30.
- Henry, K.S. and Lucas, J.R. 2010. Auditory sensitivity and the frequency selectivity of auditory filters in the Carolina chickadee, *Poecile carolinensis*. *Animal Behaviour*, **80**:497–507.
- Hodos, W. 2012. What birds see and what they don't. In Lazareva, O.F., Shimizu, T. and Wasserman, E.A. (eds.), *How Animals See The World: Comparative Behavior, Biology, and Evolution of Vision*, pp. 5–24. Oxford: Oxford University Press.
- Horváth, G., Blahó, M., Egri, A. Kriska, G., Seres, I. and Robertson, B.A. 2010. Reducing the maladaptive attractiveness of solar panels to insects. *Conservation Biology*, **24**:1644–1653.
- Horváth, G., Kriska, G., Malik, P. and Robertson, B.A. 2009. Polarized light pollution: a new kind of ecological photopollution. *Frontiers in Ecology and the Environment*, **7**:317–325.
- Kiltie, R.A. 2000. Scaling of *visual acuity* with body size in mammals and birds. *Functional Ecology*, **14**:226–234.
- Kriska, G., Horvath, G. and Andrikovics, S. 1998. Why do mayflies lay their eggs en masse on dry asphalt roads? Water-imitating polarized light reflected from asphalt attracts Ephemeroptera. *Journal of Experimental Biology*, **201**:2273–2286.
- Land, M.F. and Nilsson, D.-E. 2012. *Animal Eyes*. Oxford: Oxford University Press.
- Marra, P.P., Dove, C.J., Dolbeer, R., Faridah Dahlan, N., Heacker, M., Whatton, J.F., Diggs, N.E., France, C. and Henkes, G.A. 2009. Migratory Canada geese cause crash of US Airways Flight 1549. *Frontiers in Ecology and the Environment*, **7**:297–301.
- Martin, G.R. and Shaw, J.M. 2010. Bird collisions with power lines: failing to see the way ahead? *Biological Conservation*, **143**:2695–2702.

- Martin, G.R. 1986. The eye of a Passeriform bird, the European starling (*Sturnus vulgaris*) – eye-movement amplitude, visual fields and schematic optics. *Journal of Comparative Physiology A*, **159**:545–557.
- Martin, G.R. 2007. Visual fields and their functions in birds. *Journal of Ornithology*, **148**:S547–S562.
- Martin, G.R. 2011. Understanding bird collisions with man-made objects: a sensory ecology approach. *Ibis*, **153**:239–254.
- Martin, G.R., Wilson, K.J., Wild, J.M., Parsons, S., Kubke, M.F. and Corfield, J. 2007. Kiwi forego vision in the guidance of their nocturnal activities. *PLoS ONE*, **2**(2):e198.
- Montgomerie, R. 2006. Analyzing colors. In Hill, G.E. and McGraw, K.J. (eds.), *Bird Coloration: Mechanisms and Measurements* (Vol 1), pp. 90–147. Cambridge: Harvard University Press.
- Moore, B.A, Doppler, M., Young, J.E. and Fernández-Juricic, E. 2013. Interspecific differences in the visual system and scanning behavior of three forest passerines that form heterospecific flocks. *Journal of Comparative Physiology A*, **199**:263–277.
- Nawroth, J.C., Greer, C.A., Chen, W.R., Laughlin, S.B. and Shepherd, G.M. 2007. An energy budget for the olfactory glomerulus. *Journal of Neuroscience*, **27**:9790–9800.
- Neumeyer, C. 1992. Tetrachromatic color vision in goldfinch: evidence from color mixture experiments. *Journal of Comparative Physiology A*, **171**:639–649.
- Niven, J.E. and Laughlin, S.B. 2008. Energy limitation as a selective pressure on the evolution of sensory systems. *Journal of Experimental Biology*, **211**:1792–1804.
- O'Rourke, C.T., Hall, M.I., Pitlik, T. and Fernández-Juricic, E. 2010. Hawk eyes I: diurnal raptors differ in visual fields and degree of eye movement. *PLoS ONE*, **5**(9):e12802.
- Paris, C.B., Atema, J., Irisson, J.-O., Kingsford, M., Gerlach, G. and Guigand, C.M. (2013) Reef odor: a wake up call for navigation in reef fish larvae. *PLoS ONE*, **8**(8):e72808.
- Rash, C.E. 2004. Awareness and causes and symptoms of flicker vertigo can limit ill effects. *Human Factors & Aviation Medicine*, **51**(2):1–6.
- Reymond L. 1987. Spatial visual acuity of the falcon, *Falco berigora*: a behavioural, optical and anatomical investigation. *Vision Research*, **27**:1859–1874.
- Robertson, B.A., Kriska, G., Horváth, V. and Horváth, G. 2010. Glass buildings as bird feeders: urban birds exploit an ecological trap. *Acta Zoologica Academiae Scientiarum Hungaricae*, **56**:283–293.
- Rubene, D., Håstad, O., Tauson, R., Wall, H. and A. Ödeen. 2010. The presence of UV wavelengths improves the temporal resolution of the avian visual system. *Journal of Experimental Biology*, **213**:3357–3363.
- Schlaepfer, M.A., Runge, M.C. and Sherman, P.W. 2002. Ecological and evolutionary traps. *Trends in Ecology & Evolution*, **17**:474–480.
- Schmidt, V. and Schaefer, H.M. 2004. Unlearned preference for red may facilitate recognition of palatable food in young omnivorous birds. *Evolutionary Ecology*, **6**:919–925.
- Schwind, R. 1991. Polarization vision in water insects and insects living on a moist substrate. *Journal of Comparative Physiology A*, **169**:531–540.

- Siddiqi, A., Cronin, T.W., Loew, E.R., Vorobyev, M. and Summers, K. 2004. Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*. *Journal of Experimental Biology*, 207:2471–2485.
- St. Clair, C.C., Bélisle, M., Desrochers, A. and Hannon, S.J. 1998. Winter responses of forest birds to habitat corridors and gaps. *Conservation Ecology*, 2(2):13.
- Stevens, M. 2013. *Sensory Ecology, Behaviour, & Evolution*. Oxford: Oxford University Press.
- Stoddard, M.C. and Prum, R.O. 2008. Evolution of avian plumage color in a tetrahedral color space: a phylogenetic analysis of New World buntings. *American Naturalist*, 171:755–776.
- Stone, P.T. 1990. Fluorescent lighting and health. *Lighting Research and Technology*, 24:55–61.
- Sutherland, W.L. 1998. The importance of behavioural studies in conservation biology. *Animal Behaviour*, 56:801–809.
- Theiss, S.M., Davies, W.I.L., Collin, S.P., Hunt, D.M. and Hart, N.S. 2012. Cone monochromacy and visual pigment spectral tuning in wobbegong sharks. *Biology Letters*, 8:1019–1022.
- Van Dyck, H. 2012. Changing organisms in rapidly changing anthropogenic landscapes: the significance of the “Umwelt”-concept and functional habitat for animal conservation. *Evolutionary Applications*, 5:144–153.
- Virzi, T., Boulton, R.L., Davis, M.J., Gilroy, J.J. and Lockwood, J.L. 2012. Effectiveness of artificial song playback on influencing the settlement decisions of an endangered resident grassland Passerine. *Condor*, 113:846–855.
- Vorobyev, M. and Osorio, D. 1998. Receptor noise as a determinant of colour thresholds. *Proceedings of the Royal Society of London B*, 265:351–358.
- Whitmore, A.V. and Bowmaker, J.K. 1989. Seasonal variation in cone sensitivity and short wavelength absorbing visual pigments in the rudd *Scardinius erythrophthalmus*. *Journal of Comparative Physiology A*, 166:103–115.
- Wilson, C.J. and McKillop, I.G. 1986. An acoustic scaring device tested against European rabbits. *Wildlife Society Bulletin*, 14:409–411.