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BRADLEY F. BLACKWELL
ESTEBAN
FERNÁNDEZ-JURICIC

Behavior and Physiology in the Development and Application of Visual Deterrents at Airports

In the first major treatise on the science of wildlife damage management, Conover (2002) dedicated a short review of visual stimuli used to deter wildlife from specific areas or resources. The brevity of the review reflects the fact that these techniques have traditionally been developed over short periods and used to confront an immediate problem, generally through trial and error. Because humans perceive visual stimuli differently than other animals (Schwab 2012), deterrents based on human perception likely fall short in saliency of the stimuli (i.e., how well the stimuli stand out against a background). However, assessment of visual stimuli (both deterrents and cues) in the context of animal sensory physiology and behavior holds promise for the development of novel and more effective methods to mitigate negative human–wildlife interactions.

As Conover (2002) noted, visual deterrents are generally intended to provoke a fear response. Examples include scarecrows or other human forms, object movement (e.g., Mylar tape; Dolbeer et al. 1986), predator models (Conover 1982, 1985; Conover and Perito 1981), animal effigies (Avery et al. 2002; Seamans 2004), methods that provoke neophobia (e.g., coyote [*Canis latrans*] response to novel objects; Windberg 1997), and methods that combine movement and neophobia (e.g., use of lasers in bird dispersal [Blackwell et al. 2002, Gorenczel et al. 2002] and fladry against wolves [*C. lupus*; Musiani et al. 2003]). We can also include the use of border collies (*C. familiaris*) against birds at airports (Sodhi 2002) and other

dogs to protect livestock against mammalian predators (Rondinini and Boitani 2007) and contact with wild ungulates (Gehring et al. 2010). Visual stimuli that cue alert responses, as opposed to provoking fear, have been investigated relative to deer–vehicle collisions (D’Angelo et al. 2006, Blackwell and Seamans 2009) and in eliciting desired behavioral responses in birds (e.g., avoiding collision with static objects [Martin 2011]; enhancing detection and response to approaching aircraft [Blackwell and Bernhardt 2004; Blackwell et al. 2009, 2012a; Fernández-Juricic et al. 2011]). In this chapter we distinguish between visual methods that serve as the primary deterrent or cue and color cues used as conditioned stimuli in the context of chemical repellents (Chapter 3). We refer to visual stimuli intended to provoke fear and cues designed to enhance detection of objects as *visual deterrents*.

The immediate and long-term effectiveness of visual deterrents varies by species (e.g., Koehler et al. 1990, Mason 1998), season, group size (Dolbeer et al. 1986), habitat, and even legal constraints (Conover 2002). Moreover, the effectiveness of visual deterrents (or lack thereof) targeting birds or mammals is inherently linked to detectability, discriminability, and memorability, the three factors that govern design of animal signals (Guilford and Dawkins 1991; see also Endler 1992). In this initial section of the chapter, unless otherwise cited, we relate the discussion of these factors to Guilford and Dawkins (1991).

The environment through which the signal is trans-

mitted, the sensory capabilities of the receiving animal, and the cognitive processing of the receiver affect detectability of natural signals. Signal discriminability connotes that the receiver recognizes in the signal stimuli some category by which a particular behavior (e.g., flight, avoidance of a prey item) is warranted. Memorability of the signal is linked to learning, where the signal is eventually associated with a particular outcome. From the perspective of natural signals, Guilford and Dawkins (1991) assigned these three factors as components of strategic signal design and tactical design, or of signal efficacy.

Whereas strategic design in animal signaling is concerned with whether or why (in terms of fitness) the receiver responds appropriately, the second component—efficacy—affects the probability that the signal will reach its target destination and elicit a response. For instance, a signal might be salient because it is both easily detectable and occurs within the context of familiar habitat (e.g., coyote response to an intruder's sign or a novel object within the animal's territory; see Windberg 1997). Taken another way, if this same coyote encountered a novel object outside its territory, though the object is readily visible, it would likely show little interest simply because there is not an apparent intent (i.e., fitness consequence) to the signal.

Efficacy in animal signaling also entails aspects of what Guilford and Dawkins (1991) termed the receiver's "psychological landscape," or the cognitive processing of the signal that takes place behind the immediate sensory organs (in this case the eyes). Specifically, an animal's signal might be composed of cues important within one context but intended for another. For example, Guilford and Dawkins (1991) note that peacock (*Pavo cristatus*) tail coloration (i.e., the eye spots) will draw the immediate attention of the peahen from a vigilance perspective, but divert her attention to indicators of male fitness.

Unquestionably, signaling and signal reception by animals are multifaceted and complex (Endler 1990, 1992; Endler and Théry 1996). For a visual deterrent to effectively communicate some a priori risk to a target animal or cue that attracts the animal's attention, we must ask what traits or conditions are required for detectability, both to reinforce signal strength and to extend the period of effectiveness. Our purpose in the

remainder of this chapter is to discuss the importance of visual physiology, behavior, and ecological context as components in the design and effective use of visual deterrents against mammals and birds. We review briefly (1) vision in mammals and birds relative to other sensory paths and deterrent efficacy, (2) threat recognition in animals, and (3) how visual deterrents are currently used in the airport environment, as well as the efficacy of these methods.

Vision as a Sensory Pathway

Vertebrates have two types of photoreceptors: rods and cones (McIlwain 2006, Schwab 2012). Rods deal with dim conditions and are not activated by bright light. The ability to perceive color is dependent on the number of different visual pigments present in the cone photoreceptors (Cuthill 2006). Animals with a single visual pigment cannot perceive color but can determine differences in brightness of a signal (Land and Nilsson 2002). Animals with two or more visual pigments can perceive color. This capability is explained by the way the visual system works. Light entering the retina stimulates the visual pigments of the photoreceptors to different degrees (depending on the wavelength distribution of light and the peak sensitivity of the visual pigments). The visual system at the retinal level (amacrine cells, bipolar cells, horizontal cells, ganglion cells) uses stimulation ratios (instead of absolute stimulation values of a given visual pigment type) to estimate how much each photoreceptor is stimulated compared to the others, and then sends this information to the visual centers in the brain (Land and Nilsson 2002). Color perception is based on these stimulation ratios, which will vary depending on the number of visual pigments in the retina and the wavelength peak sensitivity of each visual pigment (Gouras 2007). Animals with two visual pigments are known as dichromats, three visual pigments as trichromats, four visual pigments tetrachromats, and so on.

Mammals

The relevance of the visual systems of mammals varies widely across taxa (e.g., Langley 1983, and references therein) because some species, such as ungulates, rely

more on olfaction and hearing than on vision. However, dogma often suggests limitations to ungulate vision that are inaccurate. For example, white-tailed deer (*Odocoileus virginianus*) and fallow deer (*Dama dama*) are not color-blind. Both species are dichromatic with peak sensitivity at 450–460 nm (i.e., “blue”) and at 537 nm (i.e., “green”). Their eyes also contain rod cells (up to 90% of the photoreceptors in the retina) that are activated only under dim conditions (Jacobs et al. 1994; see also VerCauteren and Pipas 2003, Warren et al. 2008). In addition, like other mammals active at night, ungulates possess a tapetum lucidum (Dukes 1969, D’Angelo et al. 2008) that reflects incidental light back through the retina and associated photo-pigments a second time, further enhancing vision in dim light.

The visual capability of deer at night is not necessarily limited to changes in brightness or intensity of the stimuli, however, but is dependent upon the intensity and spectra (i.e., wavelengths that compose the hue or color) of ambient lighting (e.g., presence of street lighting) and the time of exposure (Jacobs et al. 1994, VerCauteren and Pipas 2003, D’Angelo et al. 2008). As we alluded above, detection of a signal is but one component of signal effectiveness. Attempts to exploit signal detection in white-tailed deer via roadside, wavelength-specific light cues (i.e., those visually detectable by deer) synchronized with vehicle approach at night lead ironically to an increased chance of deer–vehicle collisions because of the confusion caused by the visual cues (D’Angelo et al. 2006). In contrast, Blackwell and Seamans (2009) showed that vehicle-based lighting that is more visually detectable to white-tailed deer enhanced detection and response to approaching vehicles. We suspect the difference in responses of deer in these studies is due to the application or saliency of light signals (roadside versus on the vehicle) relative to the potential threat (the vehicle). Importantly, however, findings from both studies highlight the interplay of brightness and spectra relative to deer response to reflected and direct vehicle lighting.

As with ungulates, the importance of the visual pathway to canids also varies with species and context (e.g., dominance of vision over other senses depends on ambient lighting; Langley 1983). Jacobs et al. (1993) examined the visual pigments of the domestic dog, is-

land gray fox (*Urocyon littoralis*), red fox (*Vulpes vulpes*), and Arctic fox (*Alopex lagopus*). According to the authors, besides rods, each of the four genera are (like ungulates) dichromatic, sharing one cone cell with peak absorption at ~555 nm (“green”) and a second cone cell with peak absorption from 430 to 435 nm (“blue”). We note, however, that there is little evidence that canids necessarily respond to color signals, whereas movement and novelty have played more of a role in deterrent efficacy (e.g., Windberg 1997, Mason 1998, Musiani et al. 2003) than considerations for spectral sensitivity of the target animal.

Birds

Unlike most mammals, vision represents a primary sensory pathway for birds (Walls 1942) and is highly developed, as evidenced by the relative size of the eyes to the skull (in some species the combined weight of the eyes exceeds that of the brain; Sillman 1973). Further, birds have visual systems that differ substantially from mammalian vision, including higher temporal visual resolution and sensitivity in a broader range of the spectrum (e.g., ~370–700 nm; Cuthill 2006, Martin 2011, Fernández-Juricic 2012). Birds are tetrachromats, with four types of visual pigments in their cone photoreceptors, and species differ at the level of the visual pigment sensitive to shorter wavelengths (Hart and Hunt 2007). Some species are ultraviolet sensitive (with a visual pigment peaking at 355–380 nm) or violet sensitive (with the visual pigment peaking at 402–426 nm). The peak sensitivity of the three other visual pigments in birds varies as follows: short-wavelength sensitive (427–463 nm), medium-wavelength sensitive (499–506 nm), and long-wavelength sensitive (543–571 nm). Additionally, birds have organelles within each cone photoreceptor known as oil droplets; these organelles filter light before it reaches the visual pigment, thereby enhancing color discrimination (Cuthill 2006). Birds also have rods, but in diurnal species they amount to about 20% of the photoreceptors (Querubin et al. 2009).

Sillman (1973) contended that no treatment of the biology of birds is sufficient without consideration of vision. The effective development and use of visual deterrents against birds must also consider the complexity of their visual systems, as well as the context of

the stimulus relative to the desired behavioral response (Blackwell 2002).

Common Properties of Mammalian and Avian Visual Systems

Despite the aforementioned differences, the visual systems of mammals and birds share a characteristic that can have implications for the development of visual deterrents. Both taxa process visual information in similar ways (see Dowling 2012).

Photoreceptors are responsible for converting optical information into a neural signal. Several photoreceptors are generally connected to a single retinal ganglion cell (which transfers information from the retina to the brain through the optic nerve) via different cells (amacrine, bipolar, horizontal). The group of photoreceptors that connect to a given ganglion cell forms a receptive field. Receptive fields of adjacent ganglion cells overlap in such a way that a given receptive field (on center) is surrounded by another receptive field (off center). When light hits the on-center receptive field, the associated ganglion cell is stimulated. When light hits the off-center receptive field, the associated ganglion cell is stimulated. However, when light simultaneously hits both the on- and off-center receptive fields, both ganglion cells inhibit each other, decreasing the cell's firing rate. The bottom line is that mammalian and avian visual systems at the retinal level work on the basis of differences in stimulation between center and surrounding receptive fields, rather than absolute changes in light intensity. This means the visual system is tuned to how much a given object reflects light relative to the light reflected from the background (Land and Nilsson 2002), rather than the absolute properties of the object (e.g., total amount of light reflected or wavelength reflected).

One implication of how the visual system processes visual information is that we cannot establish how color or light intensity is perceived by other species, because the number and properties of light-sensitive components of the retina (e.g., visual pigments, oil droplets; Cuthill 2006) influence the perceptual experience. These light-sensitive components will influence the stimulation ratios that an object (e.g., signal) and its visual background generate on the retina and, consequently, the visual contrast response. Visual deterrents

will be processed in a similar way. However, we can theoretically estimate the visual saliency of a deterrent for a given visual system.

Mathematical models (Vorobyev and Osorio 1998, Endler and Mielke 2005, Montgomerie 2006), used with freely available software (such as AVICOL; see Gomez 2006), can estimate visual contrast (i.e., chromatic, based on hues, and achromatic, based on brightness). These visual contrast models provide an estimate of how much an object stands out from the background. The required information to parameterize the models includes the reflectance of the object, reflectance of the visual background, and irradiance (spectral properties of the ambient light), which can be measured with an off-the-shelf spectrometer. Additionally, visual contrast models require empirical information on visual parameters of the target species (or a related species), metrics that are currently available in the literature, including sensitivity of the visual pigments and oil droplets (Hart and Hunt 2007) and relative density of cone photoreceptors (Hart 2001). These models can be used to establish the color and brightness that would enhance the visual contrast of a deterrent for a given species, assuming that the most salient deterrents for a given visual system could enhance an avoidance response. This assumption can be tested empirically through behavioral experiments. Overall, this sensory approach to develop visual deterrents can narrow the range of visual deterrents that have the highest chance, due to their visual saliency, of triggering a desired behavioral response.

Innate versus Learned Responses to Signals

Following our discussion of how we can enhance the saliency of a visual deterrent by better understanding the sensory system of the target species, it is logical to ask whether the characteristics of the deterrent are inherently meaningful. In other words, do the characteristics of the deterrent have the potential to stimulate innate avoidance or antipredator behaviors (Caro 2005), as with some natural signals? Or will the stimulus require a period of learning accompanied by reinforcement via other stimuli, for example, enhancing apparent predation risk to ring-billed gulls (*Larus delawarensis*; Conover 1987) or American crows (*Corvus brachyrhynchos*; Marzluff et al. 2010)? Inglis and

Isaacson (1984) demonstrated that exposure of wood-pigeon (*Columba palumbus*) wing marks is aversive to conspecifics, and that these marks might serve as a natural visual alarm (see also Murton 1974). In contrast, Shivik et al. (2003) noted that use of disruptive visual stimuli (e.g., fladry) against wolves can decrease predation, but does not produce or stimulate an aversion to the resource.

Also, natural signal colors from potential prey, such as warning-colored or aposematic prey (Poulton 1890, Guilford 1990, Gamberale-Stille and Guilford 2003) or other food resources (Herrera 1985, Altshuler 2001, Honkavaara et al. 2004), seem to be adapted for producing maximal differences in stimulation of avian photoreceptors (Finger and Burkhardt 1994, Vorobyev et al. 1998), serving as cues that stimulate innate or learned responses to the resource. Innate avoidance by birds of aposematic patterns characteristic of potential vertebrate prey is common (e.g., Rubinoff and Kropach 1970; Smith 1975, 1977; Caldwell and Rubinoff 1983). Innate and learned avoidance of aposematic invertebrate prey (e.g., yellow and black banding patterns) by birds has also been demonstrated (Schuler 1982, Schuler and Hesse 1985, Lindström et al. 1999). Any exploitation of behavioral responses to aposematic coloration for deterrent design must also consider that the primary context for application would likely entail deterrence of foraging, as opposed to provoking a sense of fear. Findings by Avery et al. (1999) with regard to bird avoidance of certain seed colors hold promise for the development of seed coatings to deter bird predation of newly seeded crops. Similarly, color treatments might also reduce avian mortality due to consumption of pesticide-treated baits or seeds (e.g., de Almeida et al. 2010).

In the context of antipredator behavior and our ability to exploit these behaviors, particularly salient visual signals from predators include aspects of size, shape, and movement pattern (e.g., Tinbergen 1948, Blumstein et al. 2000, Veen et al. 2000, Goth 2001; see also Inglis and Isaacson 1984). These same visual signals are also important in learned antipredator responses (e.g., Marzluff et al. 2010) and in response to novel threats. Chamois (*Rupicapra r. rupicapra*) in the Swiss Alps fled the approach of paragliders (possibly perceived as raptors because of flight dynamics) by as much as 900 m (2,953 feet; Schnidrig-Petrig and Ingold 2011). Similar escape behaviors in response to

the presence of aircraft have been observed in other mammals, such as mountain sheep (*Ovis canadensis*) disturbance by helicopters (Bleich et al. 1994) and hauled-out ringed seal (*Phoca hispida*) disturbance by fixed-wing aircraft and helicopters (Born et al. 1999). Necropsies and examination of associated injuries of birds struck by aircraft indicated that antipredator responses occurred before collision (Bernhardt et al. 2010). The efficacy of visual deterrents intended to elicit a fear response is also linked to similar predator traits (e.g., Boag and Lewin 1980, Avery et al. 2002, Seamans 2004), and there is potential to enhance the risk perceived by an animal relative to unnatural stimuli (e.g., Ydenberg and Dill 1986, Frid and Dill 2002, Stankowich and Blumstein 2005).

Visual Deterrents at Airports

Cleary and Dolbeer (2005:111–135) provide the most current review of control techniques, including visual deterrents, available for use at airports. These techniques include the use of natural predators such as trained falcons (Blokpoel 1976) or dogs, both of which have gained popularity in recent years because they are intended as nonlethal management approaches. In addition, Mylar flagging for short-term applications against birds, predator and prey effigies, and handheld lasers continue to be used at airports. Here we examine in greater detail the use of handheld lasers, effigies, and more recent advances in visual deterrents.

Lasers

A common application in the use of lasers against birds stems from findings by Blackwell et al. (2002) related to marked avoidance responses by captive Canada geese (*Branta canadensis*) to a moderate-power, 650-nm laser (Fig. 2.1).

However, Blackwell et al. (2002) also noted that wavelength sensitivity does not connote deterrence. They cited research reporting long-wavelength sensitivity in European starlings (*Sturnus vulgaris*), rock pigeons (*Columba livia*), and mallards (*Anas platyrhynchos*), yet captive groups of these species exhibited no avoidance or only a limited response to treatment from moderate-power, 630-nm (starlings) and 650-nm lasers (all three species). Ambient conditions or context



Fig. 2.1. Captive Canada geese moving perpendicular to (away from) a laser beam from a moderate-power (i.e., 5–500 mW), 650-nm laser in experiments conducted by Blackwell et al. (2002). Laser power specifications from U.S. Department of Labor, Occupational Health and Safety Administration; see http://www.osha.gov/dts/osta/otm/otm_iii/otm_iii_6.html. Photo credit: Bradley F. Blackwell

(e.g., captive versus free-ranging birds, light conditions surrounding a roost that can affect dark adaption by retinal photopigment and subsequent sensitivity to laser beams and beam spots, or predation risk outside a roost) likely affect potential responses to laser treatment. Sherman and Barras (2004) found that Canada goose response to a 650-nm laser was limited by ambient lighting and pond size. Similarly, Gorenzel et al. (2002) found that American crows occupying urban roosts responded to moderate-power, 630- and 650-nm lasers, but quickly reoccupied roosts. In an evaluation of moderate-power, 473- and 534-nm lasers against white-tailed deer, VerCauteren et al. (2006) noted that deer detected laser treatments, but the devices were ineffective as dispersal tools. In reference to findings by Blackwell et al. (2002) relative to birds, the authors noted that differential effectiveness of lasers may be due to species-specific differences in threat perception and avoidance behavior.

Effigies

The effectiveness of effigies in eliciting a desired behavioral response (e.g., area avoidance or flight) is inherently linked to spectral and form attributes, presentation, movement, and context. Seamans (2004)

found that a hanging (as opposed to supine) taxidermy mount of a turkey vulture (*Cathartes aura*), susceptible to movement by wind and in full view of roosting vultures, resulted in abandonment of a roost used during fall migration (Fig. 2.2).

In another study, Avery et al. (2002) used carcasses and taxidermy mounts of turkey and black vultures (*Coragyps atratus*) to disperse mixed roosts of vultures from communication towers. But in a test of a floating, mold-injected plastic Canada goose effigy as an area repellent against territorial pairs of Canada geese during late summer, Seamans and Bernhardt (2004) found no effect. Similarly, mold-injected plastic raptor models failed to deter European starlings from nest boxes (Belant et al. 1998). Unlike taxidermy mounts that were natural in appearance and form, as well as positioned such that erratic movement could occur, the plastic effigies lacked one or both of these attributes.

In contrast, Mason et al. (1993) deterred snow geese (*Chen caerulescens*) from agricultural fields via white plastic flagging, a cue typically used by hunters to decoy geese. In this case, however, systematic placement of the flagging, versus clumped placement used during hunting seasons, likely contributed to the deterrent effect. Effigies in the form of duck decoys (wood, cork, and mold-injected plastic composition) have been used successfully for generations to attract waterfowl, reinforcing the importance of context, movement, and placement relative to the effigy's intended effect. Moreover, an effigy's decoy effect and its aversive effect can be one in the same. For example, investigative flight behaviors by some species in response to an effigy (e.g., woodpigeons [*Columba palumbus*]) might be ideal responses to the hunter, but they might ultimately avoid the effigy altogether (Murton et al. 1974, Inglis and Isaacson 1984).

Recent Advances

Avian response to object approach is critical in the contexts of predator detection, foraging, flocking, and avoiding collisions with static or moving structures (Martin 2011). As suggested above, there is potential to exploit sensory systems to enhance natural behavioral responses to object approach. Blackwell et al. (2009) examined responses to approach by a ground-based vehicle and vehicle-lighting regimen by



Fig. 2.2. Taxidermy mount of a turkey vulture suspended as an effigy to deter roosting by conspecifics. Photo credit: Thomas W. Seamans

brown-headed cowbirds (*Molothrus ater*) and mourning doves (*Zenaida macroura*), as well as properties of the visual system for both species. The authors found that vehicle lighting (i.e., the visual cue) can influence the avoidance behavior by cowbirds and that reaction to vehicle approach and light treatments was also affected by ambient light. Avoidance behavior by doves was not affected by lighting treatments, but doves became alert more quickly (on average by 3.3 s) than cowbirds. In contrast, cowbirds took flight sooner than doves. The authors also found that doves have a wider field of vision and can detect objects at a greater distance due to their higher visual acuity; however, cowbirds might flush earlier to reduce predation-risk costs associated with lower ability to visually track a given object. In extending their findings to reducing bird collisions with aircraft, Blackwell et al. (2009) suggested that there is potential to design vehicle-mounted

lighting that will enhance avian alert behavior and, subsequently, response to aircraft approach. However, the authors also recognized the role of species-specific antipredator strategies in response to approaching threats and that vehicle lighting might not yield the same behavioral responses across all bird species.

Some airports have incorporated use of radio-controlled (RC) aircraft to disperse birds (see Transport Canada 2002). As noted above, there is evidence that birds respond to full-size aircraft via antipredator behaviors (Bernhardt et al. 2010), and researchers now use RC aircraft to better understand how to exploit avian antipredator behaviors relative to aircraft approach (Blackwell et al. 2012a; S. Lima et al., Indiana State University, unpublished data). For instance, Blackwell et al. (2012a) fitted an RC aircraft with pulsing lights and calculated chromatic contrast (see above)



Fig. 2.3. Radio-controlled aircraft approaching a group of captive Canada geese in experiments designed to quantify detection of and response to aircraft approach and lighting treatment (Blackwell et al. 2012a). Photo credit: Gail Keirn

with lights on (pulsing) versus off. They estimated that Canada geese would perceive the aircraft with lights as a more visually salient object than the same aircraft without lights. The authors tested this hypothesis in a behavioral experiment measuring responses of geese to RC aircraft approaches (Fig. 2.3). They found that geese were alerted to the approach of the RC aircraft with the lights on 4 s earlier than with the lights off. Four seconds could be enough time for birds to engage in evasive maneuvers (Bernhardt et al. 2010) and to avoid a collision. Future studies will explore lights at other wavelengths based on the spectral sensitivity of the visual systems of bird species with a high frequency of strikes to enhance the observed behavioral response.

More recent RC aircraft designed to mimic raptors are proving effective in stimulating antipredator responses and dispersing flocking species, including gulls (E. Fernández-Juricic, unpublished data; see also Blackwell et al. 2012a).

Summary

Visual recognition of the treatment (e.g., postconsumption detection of a secondary repellent and the

associated learned avoidance, stimulation of antipredator behaviors via predator effigies or laser dispersal, avoidance of disruptive stimuli such as fladry) is a common factor for nonlethal methods to deter wildlife from using areas or resources. In mammals, visual repellents generally rely on novelty or stimulation of antipredator behaviors. However, use of dogs to protect livestock might disrupt attacks by large predators (e.g., coyotes or wolves) but might not provoke a fear response (Gehring et al. 2010). Further, visual deterrents that rely on color detection by mammals must consider both visual capabilities of the target species and the context of application, for example, lighting cues (D'Angelo et al. 2006; Blackwell et al. 2002, 2012a; Blackwell and Seamans 2009). The context of application is critical with regard to birds, as well, but the complexities of avian visual configuration (Blackwell et al. 2009, Fernández-Juricic 2012) must also be understood. Specifically, is the visual deterrent or cue salient to the particular species in the given context? We contend that one can increase the period of effectiveness of a visual deterrent and decrease the degree of habituation by considering the sensory and behavioral ecology of the target species, the context of application, and how the method might be integrated

with other techniques to enhance perception of predation risk (Ydenberg and Dill 1986, Frid and Dill 2002).

Future evaluations of visual deterrents used against wildlife, particularly in airport applications, should include integrating methods to enhance antipredator behavior. We encourage further investigation of the use of visual barriers (Blackwell et al. 2012b) against deer and exploitation of natural alarm signals in the form of effigies (Inglis and Isaacson 1984, Avery et al. 2002, Seamans 2004). In addition, we suggest that quantifying the effects of wavelength and pulse frequency of aircraft lighting, as well as chromatic and achromatic contrast of aircraft, can aid in enhancing avian response to aircraft approach (Blackwell et al. 2009, 2012a; Fernández-Juricic et al. 2011).

LITERATURE CITED

- Altshuler, D. L. 2001. Ultraviolet reflectance in fruits, ambient light composition and fruit removal in a tropical forest. *Evolutionary Ecology Research* 3:767–778.
- Avery, M. L., J. S. Humphrey, D. G. Decker, and A. P. McGrane. 1999. Seed color avoidance by captive red-winged blackbirds and boat-tailed grackles. *Journal of Wildlife Management* 63:1003–1008.
- Avery, M. L., J. S. Humphrey, E. A. Tillman, K. O. Phares, and J. E. Hatcher. 2002. Dispersing vulture roosts on communication towers. *Journal of Raptor Research* 36:45–50.
- Belant, J. L., P. P. Woronecki, R. A. Dolbeer, and T. W. Seamans. 1998. Ineffectiveness of five commercial deterrents for nesting starlings. *Wildlife Society Bulletin* 25:264–268.
- Bernhardt, G. E., B. F. Blackwell, T. L. DeVault, and L. Kutschbach-Brohl. 2010. Fatal injuries to birds from collisions with aircraft reveal antipredator behaviors. *Ibis* 151:830–834.
- Blackwell, B. F. 2002. Understanding avian vision: the key to using light in bird management. *Proceedings of the Vertebrate Pest Conference* 20:146–152.
- Blackwell, B. F., and G. E. Bernhardt. 2004. Efficacy of aircraft landing lights in stimulating avoidance behavior in birds. *Journal of Wildlife Management* 68:725–732.
- Blackwell, B. F., G. E. Bernhardt, and R. A. Dolbeer. 2002. Lasers as non-lethal avian repellents. *Journal of Wildlife Management* 66:250–258.
- Blackwell, B. F., T. L. DeVault, T. W. Seamans, S. L. Lima, P. Baumhardt, and E. Fernández-Juricic. 2012a. Exploiting avian vision with aircraft lighting to reduce bird strikes. *Journal of Applied Ecology* 49:758–766.
- Blackwell, B. F., E. Fernández-Juricic, T. W. Seamans, and T. Dolans. 2009. Avian visual configuration and behavioural response to object approach. *Animal Behaviour* 77:673–684.
- Blackwell, B. F., and T. W. Seamans. 2009. Enhancing the perceived threat of vehicle approach to white-tailed deer. *Journal of Wildlife Management* 73:128–135.
- Blackwell, B. F., T. W. Seamans, J. L. Belant, K. C. VerCauteren, and L. A. Tyson. 2012b. Exploiting antipredator behavior in white-tailed deer for resource protection. *Wildlife Society Bulletin* 36:546–553.
- Bleich, V. C., R. T. Bowyer, A. M. Pauli, M. C. Nicholson, and R. W. Anthes. 1994. Mountain sheep, *Ovis canadensis*, and helicopter surveys: ramifications for the conservation of large mammals. *Biological Conservation* 70:1–7.
- Blokpoel, H. 1976. Bird hazards to aircraft: problems and prevention of bird/aircraft collisions. Clarke, Irwin, Ottawa, Ontario, Canada.
- Blumstein, D. T., J. C. Daniel, A. S. Griffin, and C. S. Evans. 2000. Insular tammar wallabies (*Macropus eugenii*) respond to visual but not acoustic cues from predators. *Behavioral Ecology* 11:528–535.
- Boag, D. A., and V. Lewin. 1980. Effectiveness of three waterfowl deterrents on natural and polluted ponds. *Journal of Wildlife Management* 44:145–154.
- Born, E. W., F. F. Riget, R. Dietz, and D. Andriashuk. 1999. Escape responses of hauled out ringed seals (*Phoca hispida*) to aircraft disturbance. *Polar Biology* 21:171–178.
- Caldwell, G. S., and R. W. Rubinoff. 1983. Avoidance of venomous sea snakes by naive herons and egrets. *Auk* 100:195–198.
- Caro, T. 2005. Antipredator defenses in birds and mammals. Chicago University Press, Chicago, Illinois, USA.
- Cleary, E. C., and R. A. Dolbeer. 2005. Wildlife hazard management at airports. Second edition. U.S. Department of Transportation, Federal Aviation Administration, Office of Airport Safety and Standards, Washington, D.C., USA.
- Conover, M. R. 1982. Comparison of two behavioral techniques to reduce bird damage to blueberries: methiocarb and a hawk-kite predator model. *Wildlife Society Bulletin* 10:211–216.
- Conover, M. R. 1985. Protecting vegetables from crows using an animated crow-killing owl model. *Journal of Wildlife Management* 49:643–645.
- Conover, M. R. 1987. Acquisition of predator information by active and passive mobbers in ring-billed gull colonies. *Behaviour* 102:41–57.
- Conover, M. R. 2002. Resolving human–wildlife conflicts. CRC Press, Boca Raton, Florida, USA.
- Conover, M. R., and J. J. Perito. 1981. Response of starlings to distress calls and predator models holding conspecific prey. *Zeitschrift für Tierpsychologie* 57:163–172.
- Cuthill, I. C. 2006. Color perception. Pages 3–40 in G. E. Hill and K. J. McGraw, editors. *Bird coloration: mechanisms*

- and measurements. Harvard University Press, Cambridge, Massachusetts, USA.
- D'Angelo, G. J., J. G. D'Angelo, G. R. Gallagher, D. A. Osborn, K. V. Miller, and R. J. Warren. 2006. Evaluation of wildlife warning reflectors for altering white-tailed deer behavior along roadways. *Wildlife Society Bulletin* 34:1175–1183.
- D'Angelo, G. J., A. Glasser, M. Wendt, G. A. Williams, D. A. Osborn, G. R. Gallagher, R. J. Warren, K. V. Miller, and M. T. Pardue. 2008. Visual specialization of an herbivore prey species, the white-tailed deer. *Canadian Journal of Zoology* 86:735–743.
- de Almeida, A., H. T. Zarate do Couto, and A. F. de Almeida. 2010. Camouflaging of seeds treated with pesticides mitigates the mortality of wild birds in wheat and rice crops. *Scientia Agricola* 67:76–182.
- Dolbeer, R. A., P. P. Woronecki, and L. Bruggers. 1986. Reflecting tapes repel blackbirds from millet, sunflowers, and sweet corn. *Wildlife Society Bulletin* 14:418–425.
- Dowling, J. E. 2012. The retina: an approachable part of the brain. Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA.
- Dukes, T. W. 1969. The ocular fundus of normal white-tailed deer (*Odocoileus virginianus*). *Bulletin of the Wildlife Disease Association* 5:16–17.
- Endler, J. A. 1990. On the measurement and classification of colour in studies of animal colour patterns. *Biological Journal of the Linnean Society* 41:315–352.
- Endler, J. A. 1992. Signals, signal conditions, and the direction of evolution. *American Naturalist* 139:S125–S153.
- Endler, J. A., and P. W. Mielke Jr. 2005. Comparing entire colour patterns as birds see them. *Biological Journal of the Linnean Society* 86:405–431.
- Endler, J. A., and M. Théry. 1996. Interacting effects of lek placement, display behavior, ambient light, and color patterns in three neotropical forest-dwelling birds. *American Naturalist* 148:421–452.
- Fernández-Juricic, E. 2012. Sensory basis of vigilance behavior in birds: synthesis and future prospects. *Behavioural Processes* 89:143–152.
- Fernández-Juricic, E., J. Gaffney, B. F. Blackwell, and P. Baumhardt. 2011. Bird strikes and aircraft fuselage color: a correlational study. *Human–Wildlife Interactions* 5:224–234.
- Finger, E., and D. Burkhardt. 1994. Biological aspects of bird coloration and avian color vision including ultraviolet range. *Vision Research* 34:1509–1514.
- Frid, A., and L. M. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6:11. <http://www.consecol.org/vol6/iss1/art11>.
- Gamberale-Stille, G., and T. Guilford. 2003. Contrast versus colour in aposematic signals. *Animal Behaviour* 65:1021–1026.
- Gehring, T., K. C. VerCauteren, and J-M Landry. 2010. Livestock protection dogs in the 21st century: is an ancient tool relevant to modern conservation challenges? *Bioscience* 60:299–308.
- Gomez, D. 2006. AVICOL: a program to analyze spectrometric data. <https://sites.google.com/site/avicolprogram/>.
- Gorenzel, P. W., B. F. Blackwell, G. D. Simmons, T. P. Salmon, and R. A. Dolbeer. 2002. Evaluation of lasers to disperse American crows from night roosts. *International Journal of Pest Management* 48:327–331.
- Goth, A. 2001. Innate predator-recognition in Australian brush-turkey (*Alectura lathami, Megapodiidae*) hatchlings. *Behaviour* 138:117–136.
- Gouras, P. 2007. Webvision: the organization of the retina and visual system. <http://webvision.med.utah.edu>.
- Guilford, T. 1990. The evolution of aposematism. Pages 23–61 in D. L. Evans and J. O. Schmidt, editors. *Insect defenses: adaptive mechanisms and strategies of prey and predators*. State University of New York, Albany, USA.
- Guilford, T., and M. S. Dawkins. 1991. Receiver psychology and the evolution of animal signals. *Animal Behaviour* 41:1–14.
- Hart, N. S. 2001. Variations in cone photoreceptor abundance and the visual ecology of birds. *Journal of Comparative Physiology* 187A:685–698.
- Hart, N. S., and D. M. Hunt. 2007. Avian visual pigments: characteristics, spectral tuning, and evolution. *American Naturalist* 169:S7–S26.
- Herrera, C. M. 1985. Aposematic insects as six-legged fruits: incidental short-circuiting of their defense by frugivorous birds. *American Naturalist* 126:286–293.
- Honkavaara, J., H. Siitari, and J. Viitala. 2004. Fruit colour preferences of redwings (*Turdus iliacus*): experiments with hand-raised juveniles and wild-caught adults. *Ethology* 110:445–457.
- Inglis, I. R., and A. J. Isaacson. 1984. The responses of woodpegeons (*Columba palumbus*) to pigeon decoys in various postures: a quest for a supernormal alarm stimulus. *Behaviour* 90:224–240.
- Jacobs, G. H., J. F. Deegan II, M. A. Cognale, and J. A. Fenwick. 1993. Photopigments of dogs and foxes and their implications for canid vision. *Visual Neuroscience* 10:173–180.
- Jacobs, G. H., J. F. Deegan II, J. Neitz, B. P. Murphy, K. V. Miller, and R. L. Marchinton. 1994. Electrophysiological measurements of spectral mechanisms in the retinas of two cervids: white-tailed deer (*Odocoileus virginianus*) and fallow deer (*Dama dama*). *Journal of Comparative Physiology* 174A:551–557.
- Koehler, A. E., R. E. Marsh, and T. P. Salmon. 1990. Frightening methods and devices/stimuli to prevent mammal damage—a review. *Proceedings of the Vertebrate Pest Conference* 14:168–173.
- Land, M. F., and D. E. Nilsson. 2002. *Animal eyes*. Oxford University Press, Oxford, United Kingdom.
- Langley, W. M. 1983. Relative importance of the distance senses in grasshopper mouse predatory behavior. *Animal Behaviour* 31:199–205.

- Lindström, L., R. V. Alatalo, and J. Mappes. 1999. Behavioral ecology: reactions of hand-reared and wild-caught predators toward warningly colored, gregarious, and conspicuous prey. *Behavioral Ecology* 10:317–322.
- Martin, G. 2011. Understanding bird collisions with man-made objects: a sensory ecology approach. *Ibis* 153:239–254.
- Marzluff, J. M., J. Walls, H. N. Cornell, J. C. Withey, and D. P. Craig. 2010. Lasting recognition of threatening people by wild American crows. *Animal Behaviour* 79:699–707.
- Mason, J. R. 1998. Mammal repellents: options and considerations for development. *Proceedings of the Vertebrate Pest Conference* 18:325–329.
- Mason, J. R., L. Clark, and N. J. Bean. 1993. White plastic flags repel snow geese (*Chen caerulescens*). *Crop Protection* 12:497–500.
- McIlwain, J. T. 2006. An introduction to the biology of vision. Cambridge University Press, Cambridge, United Kingdom.
- Montgomerie, R. 2006. Analyzing colors. Pages 90–147 in G. E. Hill and K. J. McGraw, editors. *Bird coloration: mechanisms and measurements*. Harvard University Press, Cambridge, Massachusetts, USA.
- Murton, R. K. 1974. The use of biological methods in the control of vertebrate pests. Page 211 in D. Price-Jones and M. E. Solomon, editors. *Biology in pest and disease control*. Blackwell Scientific, Oxford, United Kingdom.
- Murton, R. K., N. J. Westwood, and A. J. Isaacson. 1974. A study of woodpigeon shooting: the exploitation of a natural animal population. *Journal of Applied Ecology* 11:61–81.
- Musiani, M., C. Mamo, L. Boitani, C. Callaghan, C. C. Gates, L. Mattei, E. Visalberghi, S. Breck, and G. Volpi. 2003. Wolf depredation trends and the use of fladry barriers to protect livestock in western North America. *Conservation Biology* 17:1538–1547.
- Poulton, E. B. 1890. The colours of animals: their meaning and use, especially considered in the case of insects. Kegan Paul, Trench, Trübner.
- Querubin, A., H. R. Lee, J. M. Provis, and K. M. B. O'Brien. 2009. Photoreceptor and ganglion cell topographies correlate with information convergence and high acuity regions in the adult pigeon (*Columba livia*) retina. *Journal of Comparative Neurology* 517:711–722.
- Rondinini, C., and L. Boitani. 2007. Systematic conservation planning and the cost of tackling conservation conflicts with large carnivores in Italy. *Conservation Biology* 21:1455–1462.
- Rubinoff, I., and C. Kropach. 1970. Differential reactions of Atlantic and Pacific predators to sea snakes. *Nature* 228:1288–1290.
- Schnidrig-Petrig, R., and P. Ingold. 2001. Effects of paragliding on alpine chamois *Rupicapra rupicapra rupicapra*. *Wildlife Biology* 7:285–294.
- Schuler, W. 1982. Zur function von warnfarben: die reaction junger stare auf wespenähnlich swartz-gelbe attrappen. *Zeitschrift für Tierpsychologie* 58:66–78.
- Schuler, W., and E. Hesse. 1985. On the function of warning coloration: a black and yellow pattern inhibits prey-attack by naïve domestic chicks. *Behavioral Ecology and Sociobiology* 16:249–255.
- Schwab, I. R. 2012. Evolution's witness: how eyes evolved. Oxford University Press, Oxford, United Kingdom.
- Seamans, T. W. 2004. Response of roosting turkey vultures to a vulture effigy. *Ohio Journal of Science* 104:136–138.
- Seamans, T. W., and G. E. Bernhardt. 2004. Response of Canada geese to dead goose effigy. *Proceedings of the Vertebrate Pest Conference* 21:104–106.
- Sherman, D. E., and A. E. Barras. 2004. Efficacy of a laser device for hazing Canada geese from urban areas of northeast Ohio. *Ohio Journal of Science* 104:38–42.
- Shivik, J. A., A. Treves, and P. Callahan. 2003. Nonlethal techniques for managing predation: primary and secondary repellents. *Conservation Biology* 17:1531–1537.
- Silliman, A. 1973. Avian vision. Pages 349–387 in D. S. Farner, J. R. King, and K. C. Parkes, editors. *Avian biology. Volume 3*. Academic Press, New York, New York, USA.
- Smith, S. M. 1975. Innate recognition of coral snake pattern by a possible avian predator. *Science* 187:759–760.
- Smith, S. M. 1977. Coral-snake pattern recognition and stimulus generalization by naïve Great Kiskadees (Aves: Tyrannidae). *Nature* 265:535–536.
- Sodhi, N. 2002. Competition in the air: birds versus aircraft. *Auk* 119:587–595.
- Stankowich, T., and D. T. Blumstein. 2005. Fear in animals: a meta-analysis and review of risk assessment. *Proceedings of the Royal Society B* 272:2627–2634.
- Tinbergen, N. 1948. Social releasers and the experimental method required for their study. *Wilson Bulletin* 60:6–51.
- Transport Canada. 2002. Wildlife control procedures manual. TP 11500 E. Third edition. Transport Canada, Safety and Security, Aerodrome Safety Branch, Ottawa, Ontario, Canada.
- Veen, T., D. S. Richardson, K. Blaakmeer, and J. Komdeur. 2000. Experimental evidence for innate predator recognition in the Seychelles warbler. *Proceedings of the Royal Society B* 267:2253–2258.
- VerCauteren, K. C., J. M. Gilsdorf, S. E. Hygnstrom, P. Fioranelli, J. A. Wilson, and S. Barras. 2006. Green and blue lasers are ineffective for dispersing deer at night. *Wildlife Society Bulletin* 34:371–374.
- VerCauteren, K. C., and M. J. Pipas. 2003. A review of color vision in white-tailed deer. *Wildlife Society Bulletin* 31:684–691.
- Vorobyev, M., and D. Osorio. 1998. Receptor noise as a determinant of colour thresholds. *Proceedings of the Royal Society B* 265:351–358.

- Vorobyev, M., D. Osorio, A. T. D. Bennett, N. J. Marshall, and I. C. Cuthill. 1998. Tetrachromacy, oil droplets and bird plumage colours. *Journal of Comparative Physiology* 183A:621–633.
- Walls, G. L. 1942. The vertebrate eye and its adaptive radiation. Hafner, New York, New York, USA.
- Warren, R. J., K. V. Miller, and M. T. Pardue. 2008. Visual specialization of an herbivore prey species, the white-tailed deer. *Canadian Journal of Zoology* 86:735–743.
- Windberg, L. A. 1997. Coyote responses to visual and olfactory stimuli related to familiarity with an area. *Canadian Journal of Zoology* 74:2248–2253.
- Ydenberg, R. C., and L. M. Dill. 1986. The economics of fleeing from predators. *Advances in the Study of Behavior* 16:229–249.