



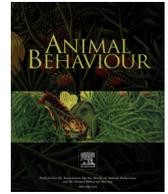
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No single solution: application of behavioural principles in mitigating human–wildlife conflict

Bradley F. Blackwell^{a,*}, Travis L. DeVault^a, Esteban Fernández-Juricic^b, Eric M. Gese^c,
Lynne Gilbert-Norton^d, Stewart W. Breck^c^a U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, Ohio Field Station, Sandusky, OH, U.S.A.^b Department of Biological Sciences, Purdue University, West Lafayette, IN, U.S.A.^c U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, Fort Collins, CO, U.S.A.^d Department of Wildland Resources, Utah State University, Logan, UT, U.S.A.

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There is no proverbial silver bullet for mitigating human–wildlife conflict, but the study of animal behaviour is foundational to solving issues of coexistence between people and wild animals. Our purpose is to examine the theoretical and applied role that behavioural principles play in understanding and mitigating human–wildlife conflict, and delineate gaps in behavioural theory relative to mitigating these conflicts. Specifically, we consider two different, yet contemporary, examples of human–wildlife conflict: animal–vehicle collisions and carnivore depredation of livestock. Although ostensibly unrelated, both conflict areas share common themes relative to animal behavioural responses to disturbance and perception of risk. We first place the effects on wildlife due to these conflicts in the scope of population sustainability, and then examine current research relative to the following three questions. How is behavioural ecology relevant to these particular areas of conflict? Are advances toward understanding the mechanisms by which animals process information and make decisions being translated into management methods? How might management efforts be affected over time by individual behaviours, method integration and habituation/sensitization? Regarding animal–vehicle collisions, only in the last decade have researchers applied an antipredator theoretical framework with sensory ecology to understand aspects of marine mammal, terrestrial mammal and bird responses to vehicle approach, speed and associated stimuli. However, the size and speeds of modern vehicles demand that we improve economic models and possibly develop novel theoretical frameworks to better predict animal responses to vehicle approach. Within the context of carnivore–livestock depredation, our understanding of individual predator behaviour relative to perceived risk and factors contributing to the development of problem individuals will influence the efficacy of the most promising, nonlethal management approaches (e.g. distractive techniques, reproductive inhibition and olfactory barriers). In both cases, successful management is contingent upon a mechanistic understanding of how animals respond to disturbance and the information utilized to assess risk.

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Human history is rife with poorly planned responses to problems occurring between people and wildlife. These responses have all too often resulted in a limited, short-term resolution, alienated some stakeholders, failed completely or exacerbated problems (see Conover, 2002; Murton, 1971; Wright, 1980). Human needs for

space, shelter and food will continue to ensure some degree of perceived 'trespass' when it comes to wildlife, a situation that paves the way for human–wildlife conflicts (i.e. situations occurring 'whenever an action by either humans or wildlife has an adverse effect on the other'; Conover, 2002, page 4).

Nonlethal management approaches are critical to mitigating human–wildlife conflicts (Shivik, 2006) and more sustainable from ecological and social perspectives (e.g. these methods avoid negatively affecting nontarget species, polarizing stakeholder groups; Treves & Naughton-Treves, 2005; Woodroffe, Thirgood, & Rabinowitz, 2005). Understanding the behaviour of the target species is

* Correspondence: B. F. Blackwell, U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, Ohio Field Station, Sandusky, OH, 44870, U.S.A.

E-mail address: bradley.f.blackwell@aphis.usda.gov (B. F. Blackwell).

central to the efficiency and efficacy of nonlethal methods (e.g. development of repellents and methods to provoke animal fear; Conover, 2002; animal response to human disturbances; Blumstein, 2006; Bejder, Samuels, Whitehead, Finn, & Allen, 2009), although the role of behaviour is sometimes not explicitly acknowledged in management policies or practices.

Our goals for this review are to (1) examine the theoretical and applied role that behaviour plays in understanding and mitigating human–wildlife conflicts, particularly as related to larger and long-term conservation efforts, and (2) delineate gaps in behavioural theory relative to mitigating current human–wildlife conflicts. Ultimately, we seek to find opportunities for animal behaviour-related research to develop new knowledge of critical value for conservation practitioners, information which could lead to a stronger application of conservation behaviour principles. We focus on two very different, yet contemporary, examples of human–wildlife conflict: animal–vehicle collisions and carnivore depredation of livestock. The development of nonlethal management for both conflict areas finds its conceptual grounding in understanding how animals initially respond to human disturbances or perceived risk (e.g. Frid & Dill, 2002), but also how animals adapt to levels and periodicity of human-related risk (e.g. Lima & Bednekoff, 1999).

We will first consider the effects on wildlife due to these conflicts in the scope of population sustainability. Specifically, what are the conservation implications, if any, in reducing mortality associated with these conflicts via integration of behaviourally based, nonlethal methods (e.g. see Caro, 2007)? We will then examine current research in these areas relative to the following questions. (1) How is behavioural ecology (including social and sensory aspects that affect resource use and antipredator strategies; Caro, 2005) relevant to the particular area of conflict? (2) How are advances toward understanding the mechanisms by which animals process information and make decisions (e.g. Blumstein & Fernández-Juricic, 2010) being translated into management methods? (c) How might management efforts be affected over time by individual behaviours, method integration and habituation/sensitization (e.g. Bejder et al., 2009)? Importantly, we will not delve into the complex aspects of human behaviour as related to mitigating these two areas of human–wildlife conflict, as others have addressed these dimensions (see Baruch-Mordo, Breck, Wilson, & Broderick, 2009; Huijser et al., 2008; Madden & McQuinn, 2014).

ANIMAL–VEHICLE COLLISIONS

Scope of the Problem

Animal–vehicle collisions (AVCs), whether on roads or railways, or in shipping lanes or the air, represent an evolutionarily novel threat to wildlife (DeVault, Blackwell, Seamans, Lima, & Fernández-Juricic, 2015; Lima, Blackwell, DeVault, & Fernández-Juricic, 2015). AVCs are generally viewed, at least initially, from the perspective of property damage and threats to human safety (e.g. DeVault, Blackwell, & Belant, 2013; Huijser et al., 2008). However, myriad species are affected by AVCs without subsequent damage to a vehicle or human injury (e.g. Fahrig & Rytwinski, 2009; Glista, DeVault, & DeWoody, 2008; Mckenna, Mckenna, Malcom, & Berenbaum, 2001; Soluk, Zercher, & Worthington, 2011). This lack of records for nondamaging AVCs can veil real threats to population sustainability (Lima et al., 2015), and hamper our ability to quantify suspected, severe population effects and to understand and manage this problem.

Estimates of the magnitude of collision-related mortality across taxa are variable, yet the ecological losses when viewed as additive to other anthropogenic sources of mortality (including indirect

effects of roads, railways and shipping lanes, as well as animal collisions with anthropogenic structures; Dorsey, Olsson, & Rew, 2015; Hovick, Elmore, Dahlgren, Fuhendorf, & Engle, 2014; Loss, Will, & Marra, 2014) are staggeringly high and affect a wide range of taxa worldwide. For large and medium-sized mammals in North America, collisions with automobiles account for about 9% of all known mortality (Collins & Kays, 2011). In Europe, automobiles are generally responsible for 5–10% of the mortality of ungulates (Seiler & Helldin, 2006). Vehicle collisions also pose severe threats to some terrestrial mammal species of conservation concern such as Florida panthers, *Puma concolor coryi* (Schwab & Zandbergen, 2011), eastern quolls, *Dasyurus viverrinus*, and Tasmanian devils, *Sarcophilus laniarius* (Jones, 2000).

Smaller vertebrates often compose the majority of casualties when comprehensive surveys are conducted (González-Gallina, Benítez-Badillo, Rojas-Soto, & Hidalgo-Mihart, 2013), despite being greatly underestimated in road-mortality surveys (Santos, Carvalho, & Mira, 2011; Teixeira, Coelho, Esperandio, & Kindel, 2013). For example, along some roads, reptiles and amphibians (especially frogs and toads) can account for >90% of all vertebrates killed by automobiles (Ashley & Robinson, 1996; Glista et al., 2008; Smith & Dodd, 2003), and road mortality can have severe adverse effects on some herpetofauna populations (Beebee, 2013; Mazerolle, Huot, & Gravel, 2005).

Birds also experience substantial losses from vehicle collisions, with annual estimates of 200 million individuals in the U.S.A. (Loss et al., 2014), 13.8 million in Canada (Bishop & Brogan, 2013), and 350 000 to 27 million individuals across several European countries (Erritzøe, Mazgajski, & Rejt, 2003), considering mortality by automobiles only. More birds are killed in the U.S.A. and Canada by vehicles than by collisions with communication towers, wind turbines and hunting (Calvert et al., 2013; Conover, Dinkins, & Haney, 2013; DeVault, 2015). Mortality from vehicles probably contributes to significant population declines for some bird species (Kociolek, Clevenger, St Clair, & Proppe, 2011; Mumme, Schoech, Woolfenden, & Fitzpatrick, 2000; Summers, Cunningham, & Fahrig, 2011; see also Bujoczek, Ciach, & Yosef, 2011), including species of conservation concern (e.g. southern cassowary, *Casuarus casuaris johnsonii*; Goosem, Moore, Byrnes, & Gibson, 2011). In addition to collisions with automobiles, birds are often struck by aircraft (DeVault et al., 2013). In the U.S.A., the Federal Aviation Administration maintains a database of wildlife–aircraft collisions or ‘strikes’, with >13 000 bird strikes reported annually under a voluntary reporting system (Dolbeer, Wright, Weller, & Begier, 2014).

Unfortunately, data for road mortality of insects are limited and vary widely by taxa (Mckenna et al., 2001; Soluk et al., 2011), although the number of insects killed by automobiles is undoubtedly extremely high (Lima et al., 2015, and citations therein). Data are similarly limited on the population-level effects of animal–train collisions (Dorsey et al., 2015) and vessel collisions involving marine mammals (Knowlton & Kraus, 2001; Neilson, Gabriele, Jensen, Jackson, & Straley, 2012; see also Lima et al., 2015).

Conceptual and Empirical Approaches to Understanding AVCs

One of the most important assumptions to test from a conceptual perspective as related to AVC is that an animal’s response to vehicle approach is similar to its response to predator approach. This assumption has been indirectly corroborated in some studies. An examination of injuries to birds struck by aircraft revealed that fatal injury locations were predominantly ventral, suggesting that birds had taken evasive action in response to the aircraft, albeit too late (Bernhardt, Blackwell, DeVault, & Kutchbach-Brohl, 2010). Additionally, escape response by free-ranging turkey vultures,

Cathartes aura, to terrestrial vehicle approach appears to be based on threshold distances between the vehicle and the birds (DeVault, Blackwell, Seamans, Lima, & Fernández-Jurícic, 2014).

Given that there is some empirical support for this assumption, animal responses to anthropogenic disturbances are expected to follow the same economic principles as those used by prey when avoiding predators (Frid & Dill, 2002; Møller, Nielsen, & Garamzegi, 2008). Furthermore, if animals respond to risk based on relative costs and benefits (e.g. Blumstein, Fernández-Jurícic, Zollner, & Garity, 2005; Frid & Dill, 2002; Stankowich & Blumstein, 2005; Ydenberg & Dill, 1986), there is potential to enhance the perceived risk in association with vehicle approach in order to accelerate escape responses (e.g. longer flight initiation distances, FID) and ultimately minimize collision risk (Blackwell & Bernhardt, 2004). For instance, poor acoustic detectability in modern recreational watercraft powered by jet engines is thought to be a primary factor contributing to collisions involving marine mammals (Miksis-Olds, Donaghay, Miller, Tyack, & Reynolds, 2007; Nowacek, Thorne, Johnston, & Tyack, 2007). One approach to enhance perceived risk and effect desired behavioural responses in this and other scenarios involves developing stimuli that are detectable and resolvable from a sensory perspective (Tyrrell & Fernández-Jurícic, 2015), and ecologically salient/contextually relevant for the study species (Beason, 2004; see also below). Another possibility is to enhance perceived benefits, but we are unaware of any such research with regard to animal response to vehicle approaches.

The first step in developing novel stimuli is to tune the stimulus to the sensory system of the target species (Blackwell & Fernández-Jurícic, 2013). This basic step would require that (1) individuals respond to stimulus manipulations and (2) certain components of the sensory space of the target species that are outside of the sensory space of humans can be used to minimize human effects. For instance, flicker or the pulse rate (Hz) of particular wavelengths can cause discomfort and ultimately lead to avoidance (reviewed in Wilkins, 2016). However, the capacity to perceive flicker varies between species (Healy, McNally, Ruxton, Cooper, & Jackson, 2013) and is higher in birds than in humans (Lisney et al., 2011). The implication is that a visual stimulus with a light pulsing at frequencies higher than 60 Hz would be perceived as a steady light by humans, but as a flickering light by most bird species.

We cannot overemphasize the relevance of tuning the sensory stimuli to the target species in order to avoid wasting precious time and limited financial resources. For instance, golden eagles, *Aquila chrysaetos*, have been shown to collide with wind turbines (Smallwood & Thelander, 2010), which is a cause of concern given their conservation status. One proposed solution was to fit wind turbines with ultraviolet lights (UV; hidden to the visual sensory system) so that golden eagles might detect them earlier. However, a behavioural experiment testing the effects of UV lights did not find significant changes in golden eagle behaviour (Hunt, McClure, & Allison, 2015). The main reason for the lack of behavioural response appears to be that the golden eagle does not have visual pigments sensitive to the UV portion of the spectrum (Doyle et al., 2014).

A greater degree of saliency of stimuli is expected to generate a stronger stimulation in the sensory centres of the brain, effects that can potentially influence animal responses to vehicle approach. One possibility is that more salient stimuli might enhance detection and shorten the time to initiate the escape response. For instance, Blackwell et al. (2012) increased the saliency of a radio-controlled aircraft approaching a group of Canada geese, *Branta canadensis*, by pulsing aircraft-mounted lights at 2 Hz, compared with the same aircraft with lights off, and found that individuals shortened their alert times by 4 s. Visual saliency differences between treatments were corroborated with perceptual models tuned to the Canada

goose eye (Blackwell et al., 2012). Additionally, Blackwell and Seamans (2009) developed vehicle lighting that better corresponded to the visual capabilities of white-tailed deer, *Odocoileus virginianus* (i.e. spectra within 400–537 nm and with consideration of rod dominance at night), and found that these more salient stimuli increased deer flight initiation distances relative to standard, incandescent vehicle lighting. However, other possibilities that have not been adequately tested in the context of AVC is that more salient stimuli from a vehicle could delay escape due to attraction responses, or produce a perceptual overload or supra-stimulus that overwhelms the neural-processing capacity and delays behavioural responses (see Blackwell & Seamans, 2009). Untangling these possibilities is an area of potentially fruitful research.

Conservation practitioners should also be aware that when using a novel stimulus to manipulate the behaviour of a target species, the stimulus might also cause the same response in nontarget species. For instance, noise tuned to the auditory system of a brood-parasite species might repel individuals from breeding in patches with a high abundance of migratory species. The question then is whether the migratory species themselves might be negatively (or positively) influenced by the same stimulus (see Gall & Lucas, 2010; Lucas, Velez, & Henry, 2015; Ortega, 2012). This issue has also been of particular concern regarding some marine mammal species such as the harbour porpoise, *Phocoena phocoena*, which is affected by acoustic deterrents used against *Halichoerus grypus* and *Phoca vitulina* seals (Brandt et al., 2013).

Addressing these unanticipated, sensory-related behavioural responses is sometimes overlooked, but it is of foremost importance. Specifically, the sensory systems of different taxa vary substantially (e.g. Collin, 1999; Lucas et al., 2015), even in species that are closely related phylogenetically (Moore, Pita, Tyrrell, & Fernández-Jurícic, 2015). Furthermore, between-species variation in sensory systems can influence escape responses. For instance, differences in alert distances for brown-headed cowbirds, *Molothrus ater*, and mourning doves, *Zenaida macroura*, in response to terrestrial vehicle approach were associated with variations in their visual acuity (Blackwell, Fernández-Jurícic, Seamans, & Dolan, 2009). Modelling efforts are sorely needed to establish how stimuli might negatively or positively influence nontarget species depending on the degree and direction of between-species differences in sensory configuration. Also, as alluded to in our earlier example of the brood parasite, these differences in response to novel stimuli might ultimately influence community composition. Furthermore, at the empirical level, there is a need for better understanding of the sensory traits that can influence vehicle detection and approach perception (e.g. auditory thresholds, visual acuity, motion perception, etc.) for species of conservation/management concern. Research efforts should be invested in characterizing the association between these sensory traits with other life-history traits (e.g. body mass) at the interspecific level, efforts that would provide indirect ways of predicting sensory configuration for species that have not been studied at the sensory level or species that cannot be studied due to ethical limitations (e.g. endangered species). For example, variations in visual acuity have been shown to be related to body mass: larger species tend to have higher visual acuity (Kilte, 2000).

The aforementioned economic framework (e.g. Frid & Dill, 2002) allows for the empirical manipulation of different factors that are expected to increase the costs of a late escape. More importantly, manipulating some of these factors, such as speed and approach distance, can provide insight into the rules that animals might use when deciding to escape from vehicle approaches, and ultimately their chances of survival. There are at least four rules that have been proposed in the literature that have application to

the AVC context: spatial margin of safety; temporal margin of safety; dynamic spatial margin of safety; and 'flush early and avoid the rush', or the FEAR, hypothesis (Blumstein, 2010; Cárdenas, Shen, Zung, & Blumstein, 2005; Samia & Blumstein, 2015). Animals show a temporal margin of safety when their FIDs increase with vehicle speed but their flight initiation times do not vary with speed. Animals show a spatial margin of safety when their flight initiation times decrease with an increase in vehicle speed, but their FIDs do not vary with speed. Animals show a dynamic spatial margin of safety when the threshold to escape is given by a fixed percentage of the alert distance before initiating escape. Finally, the FEAR hypothesis predicts that animals should minimize the costs of monitoring an approaching threat by escaping immediately after detection of the vehicle.

Few researchers have tested these hypotheses in the context of AVC. For instance, Blackwell, Seamans, and DeVault (2014) studied flight response by free-ranging white-tailed deer to an approaching vehicle (20–90 km/h) at night and found support for the spatial margin of safety. Based on this finding, the authors recommended management of roadside vegetation at collision 'hotspots' to maintain line-of-sight between animals and approaching vehicles. This management recommendation was intended to increase the probability that white-tailed deer would detect approaching vehicles and respond effectively at these sites. Additional research independently corroborated the necessary focus on vehicle speed and line of sight as management objectives for reducing deer–vehicle collisions (Meisingset, Loe, Brekkum, & Mysterud, 2014).

In addition, DeVault et al. (2015) developed video playback methodology to expose brown-headed cowbirds to virtual vehicle approach at different speeds in order to establish at which points birds would be struck by a vehicle, but without causing harm to the animals. Brown-headed cowbirds showed a spatial margin of safety, but most importantly they could not maintain this escape rule at vehicle speeds ≥ 120 km/h. Similar support for a spatial margin of safety has been found in turkey vultures (DeVault et al., 2014). The results of the three aforementioned vehicle-approach studies run counter to predictions of the FEAR hypothesis (Blumstein, 2010; Samia & Blumstein, 2015), although no formal empirical test of this hypothesis has been conducted in the context of vehicle approaches. Overall, findings by Blackwell et al. (2014) and DeVault et al. (2014, 2015) suggest that escape occurs at a fixed vehicle–animal separation distance, which might be species specific, and that higher vehicle speeds probably overwhelm the economic rules animals use to decide when to escape. The implication is that animals might not have the perceptual and cognitive mechanisms necessary to deal with the high speeds of certain vehicle encounters (e.g. commercial aircraft during some phases of flight, cars on high-speed roads). This possible weakness in anti-predator strategies relative to vehicle approach underscores an opportunity for the integration of modelling and empirical approaches to establish, at least from a conceptual perspective, what options managers can test to minimize the frequency of AVCs. An initial step would be to modify existing economic models with each of the aforementioned escape rules to predict which rule would lead to greater changes in survival at extremely high speeds. This approach would allow us to predict which species might be more or less vulnerable to AVC.

As suggested above, selection of appropriate cues to increase the detectability of an approaching vehicle could modify the effects of high speeds. In other words, if a vehicle is detected earlier, and assuming a positive relationship between alert distance and FID (Blumstein et al., 2005), then we would expect animals to have more time to estimate the optimal escape distance. One way of increasing detectability is by using sensory beacons. A recent study

tested this very possibility by developing lights tuned to the visual sensitivity of the brown-headed cowbird visual system (Doppler, Blackwell, DeVault, & Fernández-Juricic, 2015). In a seminatural experiment, groups of cowbirds were approached by a radio-controlled aircraft at different speeds with lights off, lights on pulsing, and lights on steady. Cowbird alert behaviour was greatly compromised at high speeds with lights off, but this effect (although statistically significant) was less pronounced with lights pulsing (Doppler et al., 2015). Interestingly, the speed effect was no longer significant with lights on steady (Doppler et al., 2015). More studies along these lines (e.g. modifying colour or size of vehicles) can bring new insight into strategies to enhance vehicle detectability. Also, novel conceptual approaches or modifications of current approaches would benefit by considering other factors that have proven relevant in predator–prey interactions: directness of approach (e.g. Lima, 1993; Stankowich & Coss, 2005), individual condition, experience with vehicles and context of the perceived risk (Carrete & Tella, 2010; DeVault et al., 2015; Mumme et al., 2000; Sol, Timmermans, & Lefebvre, 2002) and recognition of risk (Blackwell & Fernández-Juricic, 2013; DeVault et al., 2015; Lima et al., 2015).

Animal Vulnerability to AVC

Whereas economic principles appear to be at play in how animals detect and respond to vehicle approaches, conservation practitioners should also consider the potential differential vulnerability of species or individuals within populations to AVC (Cook & Blumstein, 2013). As in predation scenarios, AVC mortality rates vary by sex, age and temperament (Mumme et al., 2000; Møller, Erritzøe, & Erritzøe, 2011; St Clair & Forrester, 2009), and experience and context (Donaldson, Finn, Bejder, Lusseau, & Calver, 2012; Mumme et al., 2000; Wolf & Croft, 2010), as well as vehicle type (Lima et al., 2015). Cook and Blumstein (2013) also noted that social animals are less prone to AVC.

Diet is also thought to be a key factor in species vulnerability to AVC, with omnivorous and herbivorous mammals and birds experiencing higher rates of mortality (Cook & Blumstein, 2013). Specifically, because diet is associated with range size, mobility and animal speed, these life-history traits can contribute to more frequent exposure to roads and vehicles (Cook & Blumstein, 2013). Scavengers were not reported as particularly vulnerable to AVC, but this finding might relate more to the type of vehicle, such as terrestrial versus aircraft (Blackwell & Wright, 2006).

Certainly, animals foraging to support offspring might take greater risks near roads (sensu Lima & Bednekoff, 1999) than during nonreproductive periods (Legagneux & Ducatez, 2013). Similarly, changes to activity periods (e.g. greater nocturnality) in response to increasing human disturbance (i.e. perceived risk) can enhance access to anthropogenic resources (Ditchkoff, Saalfeld, & Gibson, 2006), but also contribute to AVCs (Cook & Blumstein, 2013; Laurian et al., 2008; Lee, Croft, & Ramp, 2010). In some instances, conditioning via direct provisioning of resources results in decreased perceived risk of humans, but enhanced probability of AVC (Donaldson et al., 2012). Avian scavenging of road-killed animals on and near airports (indirect provisioning) has also been identified as a hazard contributing to bird strikes, particularly involving raptors and vultures (Blackwell & Wright, 2006). Furthermore, terrestrial animals might adjust behavioural risk, taking in use of roads to exploit thermoregulation (e.g. reptile basking) and improved predator detection and foraging opportunities (Meek, 2014). In addition, ambient light conditions on road surfaces can concentrate animals on roads, thus increasing collision-related mortality (Horváth, Kriska, Malik, & Robertson, 2009).

In summary, antipredator theory (Frid & Dill, 2002) provides a starting point to understand and mitigate AVCs. Because components characteristic of predators, such as form, gaze, posture and directional changes during approach, are largely missing in vehicle approaches and because vehicle speeds are greater, economic models (e.g. Blumstein, 2010; Cooper & Blumstein, 2014; Ydenberg & Dill, 1986) should be improved or novel theoretical approaches developed for adequately predicting animal responses to vehicles. Such improvements must consider the interplay of sensory ecology with risk perception and the rules governing escape decision making, as well as factors that influence species or individual vulnerability to human-associated risks such as AVC.

COEXISTING WITH CARNIVORES

Across millennia the greatest source of conflict between humans and carnivores is from carnivores killing livestock (Conover, 2002; Karlsson & Johansson, 2010; Shivik, 2006; Treves & Karanth, 2003), a problem that is increasing in some areas (Mech, 1998; Treves et al., 2002). In the U.S.A., losses of sheep and lambs to predators (mostly coyote, *Canis latrans*) were estimated to be 247 200 head with a loss of \$20.5 million to farmers and ranchers in 2009 (National Agricultural Statistics Service, 2010). Similarly, cattle and calf losses from predators were estimated to total 220 000 head, representing a loss of \$98.5 million in 2010 (National Agricultural Statistics Service, 2011). In the U.K., lamb losses from red fox, *Vulpes vulpes*, predation is estimated to be 1–2% of lambs born (Macdonald et al., 2000), with losses in some flocks reaching 15% (Heydon & Reynolds, 2000) and perceived losses up to 0.26 lambs per ewe (Moberly, White, Webbon, Baker, & Harris, 2003). In Africa, depredation of cattle, goats and sheep by African lions, *Panthera leo*, leopards, *Panthera pardus*, and cheetahs, *Acinonyx jubatus*, can be substantial (Loveridge, Wang, Frank, & Seidensticker, 2010; Sillero-Zubiri & Laurenson, 2001). In the Gir Forest Sanctuary of India, Asiatic lion, *Panthera leo persica*, predation has been blamed for the annual loss of 1900–2000 domestic animals as late as 1995 (Singh & Kamboj, 1996). In the Annapurna region of Nepal, reported losses to snow leopards, *Panthera uncia*, were estimated to be only 2.6% of livestock but represented almost a quarter of the average annual Nepali per capita income (Oli, Taylor, & Rodgers, 1994). These losses can threaten the livelihood of individual producers and herders with the impetus leading to localized targeting of carnivores by individual producers, or wide-scale eradication of carnivores by federal, provincial or state agencies. In addition to livestock depredations, carnivores are responsible for direct predatory attacks on humans (e.g. Dhanwatey et al., 2013; Hadas et al., 2014), pets (Poessel, Breck, Teel, Shwiff, & Crooks, 2013), other nonagricultural animals associated with people (e.g. guard llamas and guard dogs) and the destruction of property (e.g. Baruch-Mordo, Breck, Wilson, & Theobald, 2008; Clark et al., 2005; Ziegler, 2004).

Lethal Control of Carnivores

Carnivore population declines can result from lethal control in association with economic losses, or historical beliefs and misconceptions (Loveridge et al., 2010; Sillero-Zubiri & Laurenson, 2001; Sillero-Zubiri, Reynolds, & Novaro, 2004). By the early 1900s, wolves, *Canis lupus*, mountain lions, *Puma concolor*, and grizzly bears, *Ursus arctos*, were systematically eradicated across North America, particularly in the U.S.A., to reduce the perceived and real threat posed to livestock (Wagner, 1988). In Africa, Frank, MacLennan, Hazzah, Bonham, and Hill (2006) reported the decimation of the African lion population covering large areas of Masai land in Kenya, with negative attitudes towards carnivores being a

primary driver of the decline. Other large carnivores (e.g. Amur tigers, *Panthera tigris altaica*, dholes, *Cuon alpinus*, jaguars, *Panthera onca*, wolves, grizzly bears) now inhabit only a fraction of their historical range in large part as a direct result of human persecution in response to livestock depredations. Moreover, in more rural environments, lethal control is commonly employed to manage these species, and often control is implemented at the population level in a nonselective fashion (Jaeger et al., 2001; see also below).

Behavioural Research and Application to Carnivore Conflicts

Integrating a theoretical approach to the management of human–carnivore conflict faces two important hurdles. First, over the course of most of human history, stopping carnivores generally meant killing them, with little need or desire to understand carnivore behaviour. Only in the last few decades has society changed its views of carnivores and pressed for the need for nonlethal methods in place of lethal management (Treves & Karanth, 2003). Thus, we have very little history to help guide our nonlethal efforts in stopping predatory species that are intelligent and keenly adapted to killing animals that resemble our livestock. Second, management to mitigate carnivore conflicts is usually driven by the need for an immediate resolution of a problem. This often places management action ahead of consideration of a theoretical framework toward carnivore behaviour, which has probably limited the contribution of basic behavioural sciences towards solving human–carnivore conflicts. For example, many of the initial developments and testing of nonlethal control techniques were precipitated by the need to provide livestock producers with a ‘toolkit’ of methods, but with little knowledge or consideration of behavioural theory. However, after several decades of trial and error to reduce conflict between humans and carnivores, we believe some theoretical frameworks have been useful to help inform management actions, whereas other areas have been less valuable. Taking a similar approach to that with AVC, we offer insight into relevant work in this area and suggest a number of theoretical underpinnings of animal behaviour that may help bridge the gap between theory and application for the development of more effective, nonlethal methods of control.

As noted earlier, theoretical developments in understanding behavioural responses of animals to human-associated risk (Lima & Bednekoff, 1999) and anthropogenic disturbance (Frid & Dill, 2002) offer a good deal of overlap between theory and application, and perhaps two of the most productive areas for developing more applicable theory. In many situations involving human disturbance or threat, carnivores behave similarly to prey species (Ordiz, Støen, Delibes, & Swenson, 2011). Recent work on black bears, *Ursus americanus*, in urban environments clearly demonstrates that bears perceive people as a potential risk, but that failures in natural food resources prompt greater risk-taking behaviour in proximity to people (Baruch-Mordo et al., 2008; Johnson et al., 2015; Lewis et al., 2015). Here, two major assumptions of the risk allocation hypothesis, that animals are energy limited and have perfect information about their risk regimen (Lima & Bednekoff, 1999), are problematic in bear use of anthropogenic resources. First, energy constraints are varying and second, bears have enough time to assess human-related risk (see also Ferrari, Sih, & Chivers, 2009). For example, Baruch-Mordo et al. (2008) modelled the energetic requirements of black bears and demonstrated that hazing (i.e. chasing an animal from an area or valued resource) had little merit as long as garbage and other human food sources were available. The energetic discrepancy between gains from anthropogenic versus natural foods only grew when natural food resources were limited in the environment. As such, tolerance of human-associated risk increased as well. Similarly, Till and Knowlton (1983) showed that

depredation rates on domestic sheep (i.e. risk-taking behaviours) increased when coyotes were energetically challenged during whelping and provisioning of pups, and that removing pups from a territorial, depredating breeding pair reduced predation rates on sheep. In subsequent research, sterilized coyotes reduced predation rates on domestic lambs six- to eight-fold without affecting social behaviour and territory maintenance (Bromley & Gese, 2001a, 2001b). Thus, anticipating how carnivores might shift their behaviour in response to available resources and in relation to the relative costs associated with anthropogenic 'predatory stimuli' is critical for carnivore–conflict mitigation.

Complementing management strategies intended to lessen the energetic reward associated with risk-taking behaviours are efforts designed to modify or interrupt a carnivore's predatory sequence (i.e. killing livestock; Knowlton, Gese, & Jaeger, 1999; Shivik, 2006). Here, we emphasize that the predatory sequence involves detection, attack, capture and consumption of prey. Attempts to disrupt one part of this sequence by nonlethal tools are not always successful due to the effects of learning on the part of the carnivore. For many years, aversive conditioning was advocated as a nonlethal method to deter predation on livestock (Knowlton et al., 1999). While aversive conditioning successfully deterred prey consumption, it did not reduce the likelihood of an attack and capture, and subsequent death of young animals (Burns, 1983; Burns & Connolly, 1980). The use of plastic collars around the neck of sheep to disrupt the attack behaviour of coyotes (they usually attack by biting the neck) led to the coyotes adapting their attack behaviour to the hindquarters of the sheep. In essence, carnivores learn and adapt their strategies based upon previous experience with nonlethal tools.

Disruptive stimuli (e.g. object movement, bursts of light or sound) are important tools in nonlethal methods of control (Bomford & O'Brien, 1990; Koehler, Marsh, & Salmon, 1990; Linhart, 1984; Linhart, Dasch, Johnson, Roberts, & Packham, 1992). However, over time their effectiveness at deterring predators erodes. Changing locations of devices or patterns of stimuli, as well as integrating across several techniques maintains the effects of novelty and surprise and reduces habituation effects over the short term (Conover, 2002; Dolbeer, Holler, & Hawthorne, 1994). For instance, territorial alpha coyotes are more likely to approach a novel object (i.e. a capture device) outside of a home range or territory where the effects of familiarity and novelty are simultaneously reduced (Harris & Knowlton, 2001; Windberg & Knowlton, 1990; Woodruff & Keller, 1982). Novelty can have a greater impact inside individual carnivore territories through the effects of neophobia and avoidance. Wolves have been temporarily deterred from entering or approaching areas with the use of flagging or fladry (an ancient method from Europe using strips of flagging hanging from a rope as disruptive stimuli) applied to fencing (Musiani et al., 2003; Shivik, Treves, & Callahan, 2003; Lance, Breck, Sime, Callahan, & Shivik, 2010). However, electrified fladry (Lance et al., 2010) has been shown to be a more effective tool; exploiting a wolf's inherent neophobia and reinforcing fear of novel objects through delivery of an electronic shock that prolongs effectiveness (Lance et al., 2010).

Notably, the recently developed radio-activated guard (RAG) box and the movement-activated guard (MAG) devices (Breck, Williamson, Niemeyer, & Shivik, 2002; Shivik & Martin, 2001; Shivik et al., 2003), which are two behaviourally contingent methods, have been applied to deter livestock depredation by wolves and are successful in minimizing potential habituation effects. Specifically, the RAG box is a scare device activated by the signal of a radiocollared animal, but only when in the vicinity of the pasture. The MAG device is similar, but activated by a passive infrared detector, which sets off lights and sounds to scare

carnivores from the pasture. Once again, the efficacy of these methods suffers from effects of previous experience and learning. Several field evaluations have shown that carnivores might attempt to enter a pasture to access livestock from a different direction after encountering a RAG or MAG device. Another downside is that while one producer has a RAG or MAG device that deters the carnivores, the 'problem' simply gets transferred to the neighbouring producer without such devices.

Other recent efforts have exploited the territorial defence behaviour of scent marking by carnivores. This 'biofence' concept originated in Botswana as a means to keep African wild dogs, *Lycaon pictus*, from leaving protected reserves and entering farmlands to depredate livestock. Biofences, however, have had limited success in altering wolf pack movements (Ausband, Mitchell, Bassing, & White, 2013) or movements of individual coyotes (Shivik, Wilson, & Gilbert-Norton, 2011). Habituation effects might be more pronounced when only using artificial scent marks, as occasional physical confrontation at territorial borders used in conjunction with scent marking is necessary for maintaining territories in natural settings (Gese, 2001; Mech & Boitani, 2003). Conflicts between neighbouring territorial conspecifics often lead to death or loss of territorial space; thus these conflicts are generally avoided (Mech & Boitani, 2003). Knowledge of fundamental behaviours and sensory abilities may lead to more effective use of 'natural' barriers or deterrents that exploit a carnivore's innate aversion to avoid conflicts with conspecifics. Clearly, each device or method has limitations, and long-term efficacy is a continual arms race between behavioural adaptability and nonlethal tool development.

Another important area of research relates to the growing interest and development of theory on individual variability in behaviour. Individual variability plays a large role in carnivore adaptation to human-dominated environments (Gehrt, Riley, & Cypher, 2010; Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004) and, probably, differential responses to management methods. Some of this variability is likely to relate to personality traits of animals and presents a fundamental challenge in designing and implementing comprehensive nonlethal tools. Some animals are shy, bold or wary, and these personality traits can be context dependent. Thus, individuals differentially habituate to previously novel approaches.

Individual carnivore response to management tools is undoubtedly also shaped by experience, learning and behavioural adaptation (Baker & Timm, 1998). Alpha and older animals are often more resistant to nonselective removal techniques than younger animals (Knowlton et al., 1999; Mitchell, Jaeger, & Barrett, 2004). Coyotes subjected to intensive removal in rural systems often shift diurnal movement patterns to avoid or reduce human contact (Kitchen, Gese, & Schauster, 2000). Yet large-scale efforts to identify and remove problem individuals using generalized, simplistic measures such as social status (e.g. alpha pair; see Gese, Ruff, & Crabtree, 1996) or territory overlap with livestock operations (Timm & Connolly, 1980) often do little to address the behaviour of specific individuals (Linnell, Odden, Smith, Aanes, & Swenson, 1999).

Understanding and targeting behaviour at the individual level (sensu Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004) could improve selective removal of problem individuals from otherwise viable and ecologically meaningful carnivore populations, thereby promoting public and stakeholder tolerance towards carnivores. Variation in individual behaviour has generally been viewed as noise in management methods research. Recent studies, however, have begun to investigate the effects of personality traits on management outcomes. For example, Darrow and Shivik (2009) found that differential response by coyotes to a

scare device was a function of behavioural type; bold individuals approached the device to consume food significantly more often than shy animals. Interestingly, the results also showed that bold coyotes were subordinate in dyadic competitive food trials, which suggests that, in coyotes at least, boldness might be a separate construct from social status. This might in part be because social status is not a fixed state in coyotes and can fluctuate according to context. Alternatively, subordinate coyotes might take more risks to increase individual advantage within coyote populations. Determining how to measure individual personality traits in a natural setting could improve management efforts. However, many carnivore species are studied via radiotelemetry or GPS locations, and determining boldness or aggressiveness in individuals that are rarely observed is challenging. One possibility could be to use distance of a predator to novel management tools or humans as an indirect measurement for boldness, as in other personality research (Sih, Cote, Evans, Fogarty, & Pruitt, 2012).

Boldness might also be context specific, with individual predators increasing bold and aggressive behaviour towards humans in environments with reduced levels of persecution (Baker & Timm, 1998; Timm, Baker, Bennet, & Coolahan, 2004). Moreover, a lack of persecution or harassment can encourage some individuals to alter temporal patterns of activity and habituate to human presence (Timm et al., 2004), thus increasing the potential for carnivore conflict. Observations of wild coyote packs suggests that sociality also has an effect on boldness, in that large groups will confront larger predators, such as wolves, and exploit kills through increased numerical advantage and aggression potential (Atwood & Gese, 2008). Some individuals might also learn to rely on numerical advantage and aggression in urban environments. Timm et al. (2004) showed that the number of human–coyote conflicts involving more than one coyote is increasing, particularly in urban settings. Given the expansion to and increased density of carnivores in human-dominated landscapes, understanding the role of socially mediated boldness or aggression in carnivore conflicts is warranted. Increasing the efficacy of identifying and selectively targeting problem individuals proactively has the potential to improve carnivore management; at present intervention is generally reactive. Moreover, understanding individual response to management techniques as a function of behavioural type and context could improve the ability to match the most effective tool to a given problem individual. Current ecological enquiry focuses on the effects of personality differences on risk-taking behaviour, activity patterns and survival (Sih et al., 2012; Wolf & Weissing, 2012). In line with current ecological interest in state–behaviour feedback systems (Sih et al., 2015), future predator management would likely benefit from research that integrates proximate and ultimate causes for individual variation.

Contribution to Conservation

Although lessons have been learned in pursuit of nonlethal techniques to manage human–carnivore conflicts (Knowlton et al., 1999), many more questions remain. Behavioural theory has proved useful in some cases, while new theory must be investigated to open new avenues of research and development. Increasing our understanding of carnivore behaviour relative to availability, energetic reward and risk associated with anthropogenic resources will limit unnecessary use of lethal control. For example, the RAG box, described above, has application only in areas with radiocollared animals, but it plays a critically important role in deterring endangered carnivores (often radiocollared for other research purposes) from depredating livestock. In South Africa, implementing the use of livestock guard dogs helped increase tolerance of farmers to cheetahs. In addition, sightings of cheetahs

also increased in the area (Rust, Whitehouse-Tedd, & MacMillan, 2013), suggesting an efficient mitigation technique that modifies predator behaviour, as well as proving to be a cost-effective method with immediate conservation implications. In the northern Rocky Mountains of the U.S.A., testing of new, larger breeds of livestock guardian dogs imported from eastern Europe is currently underway in an attempt to find a dog breed less vulnerable to wolf predation and still a reliable guardian of livestock. Even translocating problem animals may be appealing from a population standpoint and has proven successful in some situations (e.g. Weise et al., 2015), but translocation can also lead to transferring the problem to another area, or reduced survival of the translocated individuals (e.g. Bradley et al., 2005; Fontúrbel & Simonetti, 2011).

We emphasize that combining several tools, rotating among methods, ‘mixing it up’, and thinking outside the box will be needed to continue to advance research of nonlethal techniques to deter or reduce conflicts between livestock producers and carnivores (Shivik, 2006). Demonstrating that nonlethal methods will reduce conflicts between humans and carnivores, but can also be cost-effective (e.g. McManus, Dickman, Gaynor, Smuts, & Macdonald, 2015), will be necessary to convince producers and farmers to adopt such measures.

CONCLUSIONS AND FUTURE DIRECTIONS

The reality of wildlife management and conservation today is that practitioners are confronted with human–wildlife conflict (Conover, 2002), and management options can prove ineffective and negatively affect sensitive populations (Treves & Naughton-Treves, 2005; Woodroffe et al., 2005). For the animal that traverses habitats divided by roads, railways, shipping lanes or busy airspace, the risk of vehicle collision is evolutionarily novel with regard to vehicle size, speed and generally unvarying direction in approach (Lima et al., 2015). Antipredator behaviour theory provides a foundation for understanding this problem, but the size and speeds of modern vehicles demand that we improve economic models and possibly develop novel theoretical frameworks to better predict animal responses to vehicle approach. The challenge is to improve our understanding of the sensory world of the target species along with their antipredator behaviours, particularly as related to those stimuli associated with vehicle approach, so as to best enhance detection and response.

Similarly, although carnivores are generally apex predators, these species express behaviours associated with perception of human-related risk (Baruch-Mordo et al., 2008; Johnson et al., 2015; Lewis et al., 2015; Ordiz et al., 2011), and their behavioural responses can be exploited to mitigate conflicts. As with AVC, we must ask which stimuli are salient, which constitute a level of risk that outweighs a readily available resource reward, and how these stimuli can be presented so as to minimize potential habituation. Physical barriers and husbandry serve in large part to thwart carnivore depredation of livestock. However, individual predator behaviour within the context of both the livestock operation and coexistence in human-dominated landscapes will dictate how nonlethal approaches, including distractive techniques, reproductive inhibition and olfactory barriers, are integrated with the possibility of limited lethal control. Furthermore, altering management methods from widescale indiscriminate control to understanding individual carnivore behaviour and identifying problem individuals will increase tolerance for coexistence with apex predators in the environment.

In summary, animal behaviour as a discipline has an immense potential to make contributions to conservation ecology and wildlife management that can help guide research and innovative applications. In this review, we have identified gaps in current

behavioural theory that can provide opportunities for novel, conceptual advances in research related to mitigating multiple areas of human–wildlife conflict, as well as providing methods that can also be put to direct use by conservation practitioners.

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