

Animal reactions to oncoming vehicles: a conceptual review

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ABSTRACT

Animal–vehicle collisions (AVCs) are a substantial problem in a human-dominated world, but little is known about what goes wrong, from the animal’s perspective, when a collision occurs with an automobile, boat, or aircraft. Our goal is to provide insight into reactions of animals to oncoming vehicles when collisions might be imminent. Avoiding a collision requires successful vehicle detection, threat assessment, and evasive behaviour; failures can occur at any of these stages. Vehicle detection seems fairly straightforward in many cases, but depends critically on the sensory capabilities of a given species. Sensory mechanisms for detection of collisions (looming detectors) may be overwhelmed by vehicle speed. Distractions are a likely problem in vehicle detection, but have not been clearly demonstrated in any system beyond human pedestrians. Many animals likely perceive moving vehicles as non-threatening, and may generally be habituated to their presence. Slow or minimal threat assessment is thus a likely failure point in many AVCs, but this is not uniformly evident. Animals generally initiate evasive behaviour when a collision appears imminent, usually employing some aspect of native antipredator behaviour. Across taxa, animals exhibit a variety of behaviours when confronted with oncoming vehicles. Among marine mammals, right whales *Eubalaena* spp., manatees *Trichechus* spp., and dugongs *Dugong dugon* are fairly unresponsive to approaching vehicles, suggesting a problem in threat assessment. Others, such as dolphins Delphinidae, assess vehicle approach at distance. Little work has been conducted on the behavioural aspects of AVCs involving large mammals and automobiles, despite their prevalence. Available observations suggest that birds do not usually treat flying aircraft as a major threat, often allowing close approach before taking evasive action, as they might in response to natural predators. Inappropriate antipredator behaviour (often involving immobility) is a major source of AVCs in amphibians and terrestrial reptiles. Much behavioural work on AVCs remains to be done across a wide variety of taxa. Such work should provide broad phylogenetic generalizations regarding AVCs and insights into managing AVCs.

Key words: animal–object collisions, animal–vehicle collisions, antipredator behaviour, avoidance, sensory, wildlife strikes.

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I. INTRODUCTION

Animal–vehicle collisions (AVCs) are a substantial problem in an increasingly human-dominated world (Conover, 2002). In many cases, concerns about AVCs centre on human safety and property, but effects on animal populations are likely severe. Seiler & Helldin (2006) suggest that billions of vertebrates are killed every year in collisions with cars, trains, boats, and aircraft, and that numbers are steadily increasing as infrastructure networks expand, vehicle speed increases, and the fleet of vehicles swells annually. Together, the negative effects on animal populations and associated direct and indirect consequences to humans (i.e. property damage, injury/death, ecosystem services) pose substantial research and management challenges.

For example, recent estimates suggest there are 1.5 million collisions annually between deer and automobiles in the United States alone, with thousands of personal injuries and many dozens of fatalities, as well as damage to vehicles (Conover *et al.*, 1995; Conover, 2002). Wildlife–aircraft collisions (strikes) in U.S. civil aviation annually lead to over \$600 million in damages (Dolbeer *et al.*, 2012) and over 200 people have died as a result of bird strikes over the last two decades (Richardson & West, 2000; Dolbeer *et al.*, 2012). Concerns about AVCs also centre on mortality experienced by endangered species such as manatees (Nowacek, Johnson & Tyack, 2004a) and North Atlantic right whales (*Eubalaena glacialis*) (Rolland *et al.*, 2012). Finally, terrestrial motorized vehicles have been found to have pervasive influences on animals and their populations (Fahrig & Rytwinski, 2009; Taylor & Goldingay, 2010).

Our goal is to provide some conceptual insight into, and a review of what is known about, the reactions of animals to oncoming vehicles when collisions might be imminent. We consider traditional motorized vehicles (e.g. automobiles, aircraft, boats) and review what is broadly understood about the effects of roads and vehicle traffic on animal populations, what is currently known about the way in which animals perceive and avoid imminent collisions with vehicles, and what happens when a collision occurs. Much

of our discussion concerns the degree to which behavioural principles regarding habituation, object avoidance, and predator avoidance yield insights into AVCs. Because we will be focused on the immediate reactions to oncoming vehicles, we will not generally address the role of vehicles in habitat selection or population demography, but initially consider these factors only in a broader context. We will also not address the influence of vehicular noise or other general disturbances on animals and their populations.

This review is organized into three major sections. The first deals with the effects of roads, terrestrial vehicles, and aquatic vehicle traffic as relatively novel threats to animal populations. We then move into the various conceptual issues surrounding AVCs. The third section covers empirical information on the behavioural aspects of AVCs. The latter section is organized taxonomically and highlights the taxonomic differences in what is known about animal–vehicle interactions, and the limitations in gaining that information. Our focus is necessarily on vertebrates, which are the animals that have received most attention. We also consider human pedestrians in our review, as human failures in crossing roadways might provide some insights into AVCs in general.

II. ROADS AND VEHICLES AS NOVEL THREATS

Our knowledge of animal mortality rates due to roads and vehicles is relatively poor. However, several reviews (Clevenger, Chruszcz & Gunson, 2003; Forman *et al.*, 2003; Seiler & Helldin, 2006; Roedenbeck *et al.*, 2007; Fahrig & Rytwinski, 2009) have summarized the detrimental effects of roads on animal populations as: (i) direct mortality due to collisions; (ii) hindrance to natural movement patterns and reduced access to resources and mates; (iii) disturbance caused by noise, dust, light, and heavy metal pollution, leading to the degradation of habitat quality; and (iv) habitat loss caused by human disturbance effects, including road construction. These effects can be direct (i.e. species that make use of roads) or indirect (i.e. species that avoid roads

but whose predators are influenced by road mortality; Fahrig & Rytwinski, 2009). Additionally, mortality effects can be exacerbated in animals that exhibit no road or traffic avoidance (Jaeger *et al.*, 2005).

Vehicle speed seems to be a critical factor in successful avoidance behaviours (e.g. Erritzoe, Mazgajski & Rejt, 2003; Van Langevelde & Jaarsma, 2004; Ramp, Wilson & Croft, 2006; Seiler & Helldin, 2006; see also Wang & Frost, 1992). For instance, Legagneux & Ducatez (2013) found that birds increased the distance at which they would flee from an approaching vehicle in roads with higher speed limits, presumably to reduce the chances of collision. However, despite these behavioural adjustments, animals may have difficulty estimating approaching distance/time at high speeds. Farmer & Brooks (2012) found that a 30 km/h increase in road speed limit increased mortality of different vertebrate species from 10 to 75%.

Some species are attracted to roads for resources (e.g. carrion or corridors), but have the cognitive and physical abilities that allow them to avoid collisions with oncoming vehicles, minimizing mortality effects (Fahrig & Rytwinski, 2009). Also, some species might avoid roads but have small movement ranges, territory sizes, and high reproductive rates, which would reduce the population-level consequences of road mortality (Fahrig & Rytwinski, 2009).

Given the broad population-level effects of roads, it is important to delineate vulnerability to AVC or negative road effects which are expected to vary substantially across species. For example, species that occur at low densities and have low reproductive rates, long generation times, large home ranges/high intrinsic mobility (e.g. large mammals and carnivores), as well as species that are habitat generalists, are most susceptible to additive mortality from roads, particularly AVCs (Forman *et al.*, 2003). Interestingly, some insect species fit these criteria as well. For example, Soluk, Zercher & Worthington (2011) suggest that the relatively low population size and long adult lifespan of dragonflies (Odonata, Anisoptera) makes them one of the few non-vertebrate groups likely to be impacted by direct AVC mortality. Further, species flight behaviour near roads is a critical metric of potential mortality. At high traffic-volume sites, near wetlands in Illinois USA dragonfly mortality was high although fewer animals attempted to cross (Soluk *et al.*, 2011). Most importantly, the significance of AVC mortality to dragonflies is more pronounced when considering that 63% of species found in the United States are species of conservation concern and, worldwide, 15% of Odonata species are threatened with extinction (Soluk *et al.*, 2011).

Similarly, Beebe (2013) reports that amphibians, among the most seriously declining animal groups, are exceptionally vulnerable to road-associated mortality, and markedly susceptible to AVCs. For example, amphibians (and reptiles) are susceptible to collision mortality due to basking behaviour on roads, association of visual cues from road surfaces with cues from preferred habitats, seasonal episodic movements, lack of avoidance of roads, and failure to respond appropriately to oncoming vehicles (see below).

Overall, amphibians have been involved in 6 to >90% (mean 57%) of mortalities associated with road collisions based on studies on four continents (Beebe, 2013; see also Glista, DeVault & DeWoody, 2008).

Data on population-level consequences of aquatic mammal mortality associated with vehicle collisions are limited. Neilson *et al.* (2012) note that relative to global incidences of whale–vessel collisions, there are no standardized criteria to evaluate eyewitness collision reports or assess injuries to stranded whales. Vessel speed and size appear to be important factors in predicting whale–vessel collisions and outcomes. For example, the tendency of humpback whales (*Megaptera novaeangliae*) to remain on the surface or North Atlantic right whales to remain submerged at 0.5–2.5 m enhances the frequency of collisions and propeller injuries (Neilson *et al.*, 2012).

In both terrestrial and aquatic systems, the effects of direct vehicle mortality on population persistence will vary depending upon the ‘area’ avoidance behaviour, as adapted from Jaeger *et al.*’s (2005) ‘road’ avoidance behaviour. Area or road avoidance behaviour comprises the avoidance of disturbance (e.g. noise, emissions, other pollutants, etc.) associated with roads or shipping lanes but not including avoidance to vehicles themselves. Vehicle avoidance is dependent upon traffic volume, but not necessarily the size of road or shipping lane (i.e. animals might avoid crossing when traffic is frequent, but learn to cross successfully during intervals of low traffic volume; Jaeger *et al.*, 2005). We suggest that differences across taxa in detection of vehicle approach, processing stimuli, and responding appropriately (critical factors to vehicle avoidance behaviour and AVCs) represent one of the least studied areas of road ecology and an important gap in understanding the response of animals to vehicle approach.

III. SOME CONCEPTUAL POINTS

In the context of vehicle avoidance, how will an animal react to an approaching vehicle at close quarters? This is not an easy question to address, because moving vehicles are, evolutionarily speaking, very novel in the world of animals. It seems likely that an animal’s reaction will involve some aspect of its antipredator repertoire (see also Frid & Dill, 2002), although in many instances a vehicle may initially be perceived more as a benign large object than a threat. However, lacking a general theory of object avoidance, it is conceptually useful to organize our discussion around well-studied antipredator behavioural phenomena (Lima & Dill, 1990; Caro, 2005).

Figure 1 shows schematically the behavioural stages of an encounter with an oncoming vehicle, and provides an additional framework for our discussion. These stages cover object detection, threat assessment, and evasion. Success is required at all stages of an encounter if a collision is to be avoided (Fig. 1). Failures to avoid a collision can occur at any stage of the encounter, and such failures vary across taxa

(see below). We deal with these general stages in turn, and then consider additional conceptual aspects of AVCs.

(1) Vehicle detection and distractions

In many cases, vehicle detection would not seem to be an issue in AVCs – how can a large and often noisy vehicle go completely undetected? This seems especially germane to animals with acute hearing (mammals) or excellent vision (especially birds; Blackwell *et al.*, 2009b). Furthermore, visual ‘looming detectors’ (Rind & Simmons, 1999), neurological systems devoted to assessing the direct approach of an object, appear to be present in arthropods, fish, amphibians, birds, and mammals (Sun & Frost, 1998; Carlile, Peters & Evans, 2006; Card & Dickinson, 2008), hence an approaching vehicle should be readily detectable. The same may apply to looming sounds (Zahorik, Brungart & Bronkhorst, 2005), especially when coupled with motion of the sound source (Bach *et al.*, 2009; Ghazanfar & Maier, 2009 see also Cappe *et al.*, 2009).

Vehicle detection theoretically should not be a problem in many species, but the detection of a vehicle does require the presence of visual and auditory cues that match the sensory capacity of the animal in question (Martin, 2011). We know that sensory systems differ substantially across animals, which means that some will favour certain sensory modalities over others (e.g. snakes may favour chemosensory over acoustic cues). There are undoubtedly some animals with limited perceptual abilities that may not be able to detect a vehicle until it is very close. Such animals might include those with limited vision or hearing, or those whose perceptual abilities are tuned to a specific predator signal. Furthermore, the physical configuration of visual systems can impose certain sensory constraints, which could affect the timely detection of moving vehicles (Martin, 2011). For instance, some bird species with bigger eyes tend to have narrower visual coverage (or larger blind areas, Fernández-Juricic, Erichsen & Kacelnik, 2004; Martin & Coetzee, 2004). These blind areas can negatively affect predator detection (Kaby & Lind, 2003; Devereux *et al.*, 2006), and could similarly affect the detection of vehicles; even aircraft might not be quickly detected if a bird is approached from its blind direction. On the other hand, increased eye size in birds is associated with greater visual acuity (Kiltie, 2000). Based on the positive relationship between body size and eye size (Brooke, Hanley & Laughlin, 1999; Garamszegi, Moller & Erritzoe, 2002; Burton, 2008), larger species may generally be able to detect a vehicle from further away than smaller species (see Blackwell *et al.*, 2009b).

Another relevant visual property is an animal’s ability to detect a vehicle against a given background. This ability can be estimated through visual contrast (chromatic/achromatic; Endler, 1990; Montgomerie, 2006) between the vehicle and the visual background: the higher the contrast, the greater the likelihood of perceiving a given object. There is considerable evidence indicating that ecological conditions (e.g. spectral properties of the light, visual background) that favour visual contrast lead to a higher chance of detection

of prey or predators (e.g. Théry, Pincebourde & Feer, 2008; Cazetta, Schaefer & Galetti, 2009; Macedonia *et al.*, 2009), and the same may apply to the detection of vehicles. For instance, one way of enhancing vehicle detection is to equip it with lights (Blackwell & Bernhardt, 2004), which could potentially increase its visual saliency. However, responses to vehicular lighting may vary depending on ambient light conditions as well as properties of the lights themselves. For instance, Blackwell *et al.* (2009b) found that brown-headed cowbirds (*Molothrus ater*) respond to a light-equipped vehicle more quickly under cloudy conditions when the lights pulsed, but not under sunny conditions, in which constant lighting proved more effective. However, high-intensity lights approaching at high speeds may cause disability glare (i.e. surplus light bounces within the eye chamber reducing visual contrast; Koch, 1989), which could overwhelm the visual system and reduce the chances of a successful avoidance manoeuvre.

One of the problems in studying animal responses to moving vehicles is that of distinguishing detection from the lack thereof. In other words, an animal may be aware of a vehicle well before it responds overtly. Such overt responses may, in many cases, reflect threat recognition rather than detection *per se* (see below). Overall, however, given the variability in sensory modalities and sensory properties within a modality, we expect that variation across species in their ability to detect vehicles will be associated with specific sensory constraints. More research along these lines would be particularly valuable.

Distractions may also be an important issue in vehicle detection, as a distracted animal may fail to detect an object that it might normally detect at a much greater distance. For instance, in predator–prey interactions, a bird distracted by feeding is much more likely to be killed by a hawk than one in an alert state (Roth, Lima & Vetter, 2006; see also Lima & Bednekoff, 1999). Distraction resulting from limited attentional abilities is likely to be a general phenomenon in animals (Dukas, 2002). However, the role for distractions in AVCs has not been examined in any systematic manner. Distractions have been addressed in pedestrian–automobile collisions (see below) and may underlie avian mortality at wind farms (Smallwood, Ruge & Morrison, 2009) and the tendency for hunting raptors to be struck by aircraft near airport runways (Blackwell & Wright, 2006). The increase in deer–automobile collisions during the rutting season is often cited as evidence for distraction-driven AVCs (Sullivan, 2011), although this too has not received rigorous study. It also seems likely that distractions are more of an issue when dealing with an object not perceived to be very dangerous, and vehicles may often fit that description. In any case, this matter of distractions and AVCs should be amenable to experimental study (see also Dukas, 2002).

(2) Threat assessment and habituation

Success in avoiding a collision requires that a detected vehicle is eventually considered to be a threat (Fig. 1). We suspect, however, that many animals do not routinely perceive

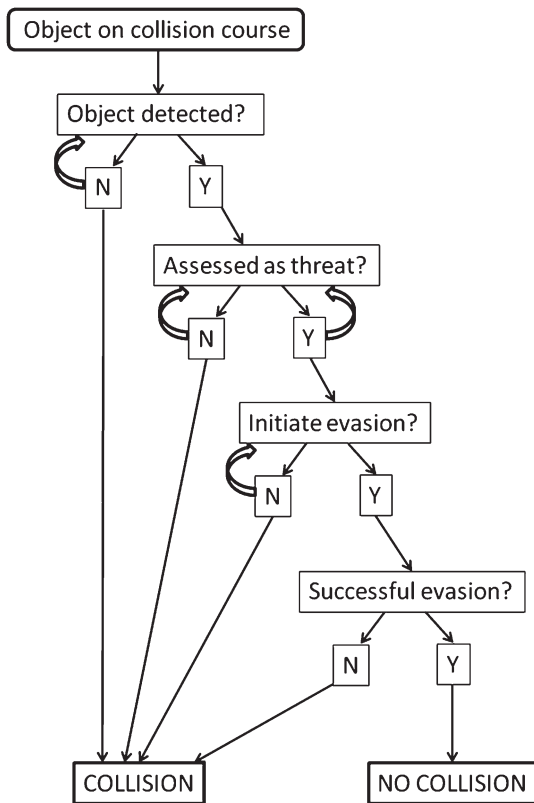


Fig. 1. Key behavioural steps in avoiding a collision with an object on a collision course. Failure ('N') at any step, from detection through to evasion, will result in a collision. No collision occurs only when all steps are completed successfully ('Y'). Curved arrows indicate a step in which initially unsuccessful behavioural action could be reversed with enough time to proceed to the next step. For instance, an object not initially detected might be detected as it looms larger in an animal's visual field; a detected object might initially not be perceived as a threat, but as it approaches, that initial assessment could change, and evasive action may be delayed even during the assessment of a potentially serious threat. In the case of threat assessment, the curved arrow from 'Y' indicates a process in which the threat perceived increases over time.

vehicles as predatory threats in a strict sense, especially those animals with well-developed perceptual abilities. For instance, in birds many aspects of predator recognition are innate and influenced by details of appearance or behaviour (Curio, 1993; Edelaar & Wright, 2006), and are also strongly influenced by learning (Levey *et al.*, 2009). Similar sorts of well-developed predator recognition are probably the norm across the animal world (see also Walther, 1969), hence it seems unlikely that vehicles will be routinely mistaken as predators (but see Schnidrig-Petrig & Ingold, 2001). Furthermore, even the behavioural responses triggered by neurological looming detectors are controlled by cognitive processes, and thus are not simply reflexive reactions (Tresilian, 1999; Carlile *et al.*, 2006). Hence, in many cases threat assessment likely involves the realization that a collision is imminent, rather than an assessment of a predatory threat

per se. Nevertheless, such an alarming realization will likely evoke some sort of antipredator response.

Some degree of habituation to moving vehicles is probably typical in a variety of animals, and thus an important aspect of threat assessment. Simply put, animals in all but the most remote areas are exposed to vehicles of all kinds on a daily basis. Because vehicles are not threatening in most situations, habituation is a likely outcome. For instance, birds that spend much time flying well above the tree line will very often see many different types of aircraft both near and far. These aircraft usually stay on a stable heading and never engage in any threatening behaviour. The same can be said for automobiles limited to well-defined roads (but see Fahrig & Rytwinski, 2009). Such habituation is likely to be context dependent (Hemmi & Merkle, 2009), and vehicles out-of-place or behaving oddly may well evoke a heightened response.

An alternative interpretation to habituation is that some individuals in populations are more risk-prone and thus suffer higher mortality due to road collisions than less risk-prone individuals. For instance, Carrete & Tella (2010) found that burrowing owls (*Athene cunicularia*) have a strong repeatability in their flight initiation distances, suggesting that individuals may distribute in the landscape depending on behavioural syndromes. Along these lines, Evans, Boudreau & Hyman (2010) found that song sparrows (*Melospiza melodia*) living in urbanized areas are bolder towards humans and have higher levels of territorial aggression compared to those in rural areas. The implication is that mortality due to vehicle collisions may influence the phenotypic distribution of populations, particularly those close to areas with high road or traffic volumes.

An important implication of threat assessment under strong habituation is that animals may be lulled into situations that make lethal AVCs more likely, such as feeding by roads or active airport runways. For instance, a habituated bird may detect an airplane on its take-off roll, but wait until the last instant before flushing, which could increase chances of a bird strike. There would probably be far fewer AVCs in the absence of this sort of habituation, but such an early response to any kind of threat would probably magnify the negative effects of many modern activities on animal populations due to limitations in the availability of disturbance-free areas.

On the other hand, there are several examples of novel motorized vehicles being used as threats in the study of antipredator behaviour (often small radio-controlled vehicles; Rodriguez-Prieto *et al.*, 2009; Thaker *et al.*, 2010). It seems likely that habituation to these vehicles will be fairly rapid (e.g. Thaker *et al.*, 2010; but see Rodriguez-Prieto *et al.*, 2009), but this has not usually been addressed. Furthermore, there appear to be no direct comparisons of animal responses to vehicles *versus* real predatory threats (but see Blackwell *et al.*, 2012). However, several studies show that animals react to humans approaching on foot earlier than to motorized vehicles (Walther, 1969; Stankowich, 2008) as long as the vehicles maintain a normal speed, which suggests considerable habituation to the latter. Nevertheless,

some species clearly avoid activity near roads during times of high traffic (Fahrig & Rytwinski, 2009; Benitez-Lopez, Alkemade & Verweij, 2010), and others may never fully habituate to motorized vehicles (Fahrig & Rytwinski, 2009).

A major conceptual limitation in understanding threat assessment is the lack of a predictive theory of the avoidance of novel objects. Indeed, how one might approach such a theory is not clear, given the evolutionary novelty of moving vehicles. The Risk-Disturbance Hypothesis (RDH) proposed by Frid & Dill (2002) addresses this situation, and is focused on cautious responses to novel vehicles and other disturbances. The crux of the RDH is that an animal's response to such situations is likely to reflect its trade-off-driven responses to predatory threats, as this is the context in which an animal is likely to respond. The RDH is intuitive and appealing, but ultimately descriptive in nature. In other words, the RDH cannot be used to predict the optimal response to a novel vehicle (as there often is little or no risk), nor can it predict the degree to which learning will lessen threat perception (perhaps to complete habituation). Ultimately, the perceived threat associated with moving vehicles may just be a matter of empirical investigation and prove to be idiosyncratic across species and contexts.

One potentially general approach here is the use of flight initiation distance (distance between the vehicle and the animal at the time of some sort of evasive response) as an empirical index of threat assessment. Flight initiation distance (FID) has been used extensively in the study of prey responses to predators in multiple taxa and ecological contexts (Frid & Dill, 2002; Stankowich & Blumstein, 2005; Stankowich, 2008; Burger *et al.*, 2010). The use of FID may allow one to assess the factors that influence the threat associated with an approaching object, such as speed, size, direction of approach, etc. FIDs could also be used to assess novel technologies that enhance animal avoidance behaviour, such as lighting systems in aircraft (Blackwell & Bernhardt, 2004) and ground-based vehicles (Blackwell & Seamans, 2009). A similar measure is alert distance (distance between a vehicle and an animal when the latter becomes clearly alerted to the former), which could also yield useful information in many contexts (Fernández-Juricic, Jimenez & Lucas, 2001).

(3) Evasive behaviour

As outlined earlier, an animal that finds itself in a close encounter with an oncoming vehicle is likely to rely on its antipredator behavioural repertoire in its reactions. Simply moving away from the line of the vehicle's travel will be an effective evasive response in most cases. However, such behaviour is not necessarily the best response to an oncoming predator, and thus not an action likely to be observed in all taxa in response to a vehicle.

Perhaps the worst possible antipredator-driven evasive reactions would be those that do not involve movement away from the vehicle. Several species might respond by freezing to avoid detection, much as they would with terrestrial predators (e.g. Cooper, Caldwell & Vitt, 2008; Cresswell *et al.*, 2009; see also Blackwell *et al.*, 2009b). Deer often

freeze in response to approaching vehicles, probably in an effort to assess the situation as well as avoid detection. Also, turtles are known to retreat into their shells while on a busy road. Still, other species such as mormon crickets (*Anabrus simplex*) or small frogs may simply be too slow to evade a vehicle. Species with inappropriate or ineffective defensive responses are those most likely to be greatly affected by road-associated mortality (Glista *et al.*, 2008; Fahrig & Rytwinski, 2009).

Social animals with active avoidance behaviours might also be compromised by an antipredator imperative of maintaining group cohesion in the face of a threat (Lima, 1993; Krause & Ruxton, 2002; Caro, 2005). Such behaviour might explain the tendency of deer to follow others across the road once a panicked response to a vehicle has begun; these followers are often the ones struck by a vehicle (see also Lee, Croft & Ramp, 2010). Similar socially based escape tactics (Lima, 1993) might bring entire flocks of birds in contact with flying aircraft (e.g. Marra *et al.*, 2009).

(4) Are 'defective' animals involved in AVCs?

Animals that are struck by vehicles might conceivably be less able to detect or avoid vehicles than others in their population. For instance, limited evidence suggests that dolphins struck by motorboats might be physically compromised in some way (Wells & Scott, 1997). There have also been many suggestions that immature birds are relatively prone to being struck by aircraft because of their relative inexperience (Blokpoel, 1976), although this has not been demonstrated empirically. Such observations are analogous to those from natural predator-prey systems in which substandard prey are disproportionately taken by predators (Temple, 1987; Lima, 2002). However, a recent study has challenged some of these views. Bujoczek, Ciach & Yosef (2011) found that individuals from three bird species involved in collisions with cars were in better body condition compared to those that died as a result of predation, which is reasonable given that predators tend to target those animals in a population with lower chances of escape. The implication is that the mortality associated with road collisions does not necessarily involve individuals with low fitness potential, which can negatively affect populations.

(5) Predator-naive animals

The above discussion raises the interesting issue of AVCs in places without many native predators. Assuming that the basis of vehicle avoidance is antipredator behaviour, animals lacking natural predators (and thus well-developed antipredator behaviour) would likely be particularly vulnerable to AVCs. A similar argument could be made of those species that face lower predation risk because of large body size or weaponry. Such animals might not avoid open areas like roadways, or have little fear of an approaching novel object.

Oceanic islands are well known for predator-naive animals (Blumstein, Daniel & Springett, 2004), especially regarding terrestrial predators (Cox & Lima, 2006). One might thus

expect a greater problem with AVCs on such islands than in mainland settings, but we know of no definitive studies on this matter. However, increasing highway traffic in the Galapagos Islands has become a major source of mortality in birds (Gottdenker *et al.*, 2008) and lizards (Tanner & Perry, 2007). Australian mammals are frequently struck by motorized vehicles (Lee *et al.*, 2010), but this problem is not obviously worse than that with mammals in North America or Europe (see Taylor & Goldingay, 2010). Some comparative AVC work on this matter would be worth pursuing.

(6) Cognitive abilities and AVCs

Animals with greater cognitive abilities might be better able to recognize the novel threat imposed by modern vehicles and respond appropriately. The difficult part in assessing this idea is measuring cognitive abilities. Recent studies (see Sol *et al.*, 2007) have correlated several aspects of innovation and intelligence with forebrain size in birds. Similar findings exist in mammals as well (Sol *et al.*, 2008). This sort of analysis could be conducted with respect to AVCs, perhaps most easily with birds, but no such work exists to date. Nevertheless, one cognitively advanced group of birds—the corvids (crows and jays)—is relatively under-represented in AVC data sets (Kelly, O’Callaghan & Bolger, 2001; Dolbeer *et al.*, 2012). Carr-Lewty (1943) noted that rooks (*Corvus frugilegus*) often inhabit airfields but are struck by aircraft far less often than other birds. Corvids are also under-represented in mortality estimates at wind farms (Smallwood *et al.*, 2009). Along these lines, dolphins (another cognitively advanced group) appear to be involved in fewer AVCs than other large marine mammals (Wells & Scott, 1997).

IV. EMPIRICAL STUDIES AND OBSERVATIONS

The mortality resulting from AVCs has been the focus of several studies (see Section I), but behavioural reactions to oncoming vehicles have been studied in surprisingly few species. The work available is a somewhat haphazard mix of topics and species, although some common themes are apparent. For instance, the species studied are often those involved in some sort of overarching environmental matter, such as disturbances due to military aircraft operations or energy extraction in ecologically sensitive areas. Popular and charismatic species, such as large marine mammals, tend to receive the most attention, especially those that are rare and subject to excessive AVC mortality. AVCs that involve matters of public safety or loss of property also receive some attention, including automobile collisions with large mammals (Conover, 2002) and bird strikes in aviation (Dolbeer *et al.*, 2012; DeVault, Blackwell & Belant, 2013). Work on collisions with the moving blades of wind turbines is also receiving increased attention (Arnett *et al.*, 2008). There are few studies outside of the above themes.

Existing empirical work usually covers observational studies or simply collections of anecdotal accounts of animal–vehicle encounters. There are obvious limitations to experimental approaches to studying animal reactions to oncoming vehicles, not the least of which is the danger to the experimenter in driving at large mammals or flying aircraft into flocks of birds. Such constraints are least problematic in the marine environment, and thus experimental work is most prominent in studies of marine animals.

We start with a consideration of marine mammals and then terrestrial mammals. We then cover birds, reptiles and amphibians, fish, invertebrates, and human pedestrians.

(1) Marine mammals

Property damage and danger to humans are often minimal in AVCs involving marine mammals. Accordingly, the main focus here is on the animals themselves. Some of the more pressing matters in marine AVCs involve whales, manatees, and dugongs, all of which are endangered in some way and subject to frequent AVCs. Nowacek *et al.* (2004a) examined the response of North Atlantic right whales (*Eubalaena glacialis*) to sound recordings of approaching large vessels and actual approaching vessels. The whales did not respond overtly to these acoustical stimuli, although such sounds may be generally stressful (Rolland *et al.*, 2012). The whales did, however, respond fairly vigorously to the broadcasts of right whale alert calls, suggesting that they do not associate the sound of ocean-going vessels with an imminent threat. There is apparently no information on potential evasive action taken by right whales when collision is imminent. However, other whale species seem less vulnerable to collisions, perhaps because they engage in effective evasive behaviours when approached, much like large ungulates faced with loud, novel threats like trucks or low-flying aircraft (see below). Perhaps the right whales studied by Nowacek *et al.* (2004a) were stressed in some way such that they were less responsive than they would have been otherwise (this population is known to be in decline). The surface-feeding tendencies of these whales also leave them vulnerable to collisions (Parks *et al.*, 2011).

Recent work suggests that manatees and dugongs are also fairly unresponsive to approaching motorized boats, until they get very close. Miksis-Olds *et al.* (2007) used hydrophonic playbacks in the field to simulate the close approach (to about 10 m from a manatee) of both powered boats and jet skis. Florida manatees (*Trichechus manatus*) were more responsive to the sounds of faster boats and jet skis, which elicited quicker movement and retreat to deeper water. Such evasive manoeuvres are used by dugongs (*Dugong dugon*) to avoid sharks (Heithaus *et al.*, 2009), and may be similarly appropriate in manatees. It thus appears that these animals recognize approaching vehicles as a threat of some sort. Nevertheless, manatees often allowed very close approach (or were slow to respond), and a small number of non-responders were apparent in the animals studied. A much larger proportion of non-responding manatees was seen by Nowacek *et al.* (2004b), who used actual direct boat

approaches to within three body lengths of manatees. Fifty-one percent did not show much of a response, but those that did used manoeuvres similar to those described above; no major effect of boat speed on manatee responsiveness was observed.

This general lack of reaction to approaching boats is clearly the source of many problems for manatees. The biological basis of this low reactivity, however, is not entirely clear. Minimal threat assessment reflecting habituation is a likely problem, as the test subjects in both of the above studies probably had considerable experience with close approach by watercraft. Perhaps boat-naïve manatees would be similarly unreactive to boats, but there is no work on this matter. An inability to detect an approaching boat also seems unlikely, and manatees appear able to discern the direction of boat-like sounds (Colbert *et al.*, 2009). Another issue here is the apparent lack of serious natural predators faced by manatees, which might leave these large herbivores in a state of relative naivety regarding threats posed by large objects. Many manatees survive collisions with boats (Beck & Reid, 1995), but whether such survivors have learned to avoid further collisions is unknown.

Dugongs, on the other hand, have serious predators in the form of sharks (Heithaus *et al.*, 2009) and they are apparently stronger swimmers than manatees. Nevertheless, dugongs appear to be similarly unresponsive to approaching watercraft. Hodgson & Marsh (2007) found that an approach to within 50 m did not elicit any obvious response in dugongs; somewhat closer approaches would sometimes elicit a reduction in feeding behaviour. Approaches simulating a near collision would probably have elicited some evasive behaviour, but dugongs may well incur as much risk of collisions as manatees.

One would not expect marine mammals with high cognitive abilities like agile dolphins and killer whales (*Orcinus orca*) to be subject to AVCs, and that appears to be the case. However, bottlenose dolphins (*Tursiops truncatus*) are occasionally struck by watercraft in shallow water, although the victims appear to be physically compromised in some way (Wells & Scott, 1997). Dolphins will also change their heading and speed when approached by fast-moving watercraft, especially erratically moving jet skis (Nowacek & Wells, 2001). Dolphins are behaviourally aware of watercraft that shadow their movements at 100 m (Lemon *et al.*, 2006). Killer whales are not only aware of boats at 100 m, but also employ antipredator-like evasive manoeuvres in changing path and speed (Williams, Trites & Bain, 2002*b*); such effects can extend up to 500 m if the boat in question will intercept the whales' path of movement (Williams *et al.*, 2002*a*). This work is unique in that avoidance can be demonstrated to occur well before the vehicle and animal are in close proximity.

(2) Terrestrial mammals and ground vehicles

This category is one of the most common forms of AVCs experienced by most people and applies to terrestrial mammals of all sizes and habitats. AVCs involving large mammals can be particularly problematic for drivers,

vehicles, and animals (Conover *et al.*, 1995; Sullivan, 2011). Given the prevalence of AVCs involving mammals, there is remarkably little work on the behavioural aspects of mammal-vehicle collisions.

An exception of a sort involves work on flight-initiation distances in reaction to the approaches of various motorized vehicles, much of which involves large ungulates (see review by Stankowich, 2008). Unfortunately from our present perspective, these vehicles were travelling fairly slowly with little direct risk of a collision. However, an interesting pattern here is that humans on foot usually invoke a greater response than an approaching ground vehicle (passenger car, truck, snowmobile, etc.), suggesting that vehicles in general will be allowed a closer approach than a potential predator. A few papers also suggest that vehicles following predictable paths (established roads, etc.) are perceived as less threatening than those in unusual situations (Stankowich, 2008). This suggests a spatially specific habituation to vehicles that could ultimately bring animals into closer contact with vehicles and raise the probability of AVCs.

Given the prevalence of deer-automobile collisions in North America, and the resulting damage and injury (Conover *et al.*, 1995; Sullivan, 2011), it is surprising that the behavioural interaction between deer and moving vehicles remains virtually unstudied (but see D'Angelo *et al.*, 2006; Blackwell & Seamans, 2009). Nevertheless, anyone who frequently travels on rural roads and highways probably has experienced several near misses with panicked deer as they suddenly dart across traffic at an inopportune time, along with the apparent social interactions that cause deer to follow each other across the road and into the paths of automobiles (see also Faria, Krause & Krause, 2010 for similar effects in humans). These are phenomena worthy of study from a behavioural perspective, and might yield some insight into the reduction of such dangerous interactions. Work along these lines with kangaroos suggests that the more reactive species are the ones more likely to be struck (Lee *et al.*, 2010).

Pinnipeds can be vulnerable to vehicle approaches when on land or ice, particularly during the breeding season. For instance, the tendency of Weddell seals (*Leptonychotes weddellii*) to visually track snow-capable vehicles increased when the vehicle was closer, when the pups were exposed, and the distance to the ocean was large (van Polanen Petel *et al.*, 2007). However, these seals did not flee from the vehicles, perhaps due to the costs of locomotion or general naivety about land predators (in Antarctica).

Bats are also struck by automobiles on a fairly regular basis in some habitats (Lesinski, 2007; Gaisler, Rehak & Bartonicka, 2009), but the behavioural aspects of such interactions are largely unknown (but see Abbott, Butler & Harrison, 2012). Zurcher, Sparks & Bennett (2010) provide a rare exception in showing that the avoidance of roads by some bats (e.g. Kerth & Melber, 2009; Berthinussen & Altringham, 2012) is driven to some extent by close encounters with the vehicles themselves, with bats taking evasive action (reversing course) at close distances from moving vehicles.

(3) Mammals and aircraft

A section on mammals and aircraft would most intuitively be focused on bats. However, bat strikes in aviation have only recently received much attention (Biondi *et al.*, 2013), perhaps reflecting the relatively low risk posed by bat strikes (at least relative to large birds; Peurach, Dove & Stepko, 2009; but see Parsons *et al.*, 2009). Behavioural information on encounters between bats and aircraft appears to be non-existent.

Most studies on mammalian responses to flying aircraft involve large mammals. This is an odd combination of animals and vehicles, for it would seem that most large mammals do not have any serious aerial predators and thus aircraft would not be recognized as a threat. Furthermore, because there is no risk of a collision with aircraft well off the ground, no reaction could enhance or lessen the possibility of an AVC. These studies are still worth mentioning here, as low flying aircraft can be loud and perhaps close enough to the ground to be frightening once sighted. We note here that collisions with deer and other large mammals are actually a major threat to aircraft on the runway itself (DeVault *et al.*, 2008, 2011; Biondi *et al.*, 2011), but here we refer to aircraft well away from the runway environment (behavioural information on runway encounters is also entirely lacking).

Frid (2003) provides an unusually detailed behavioural study of the reaction of Dall sheep to fixed-wing aircraft and helicopters flying at low altitude (within 60 m of a sheep's altitude on a slope), one that is comparable to many studies of antipredator behaviour *per se*. These sheep could be surprisingly reactive to aircraft, with flight initiation distances up to 3 or 4 km in a few cases, although most reactions occurred within 200 m. Escape/avoidance behaviours involved a retreat to rocky slopes, which reflects the escape behaviour of sheep faced with a terrestrial predator. Sheep were much more reactive to helicopters than fixed-wing aircraft. This result suggests a simple noise effect, but sheep in the direct line of flight reacted much more than those off to the sides, which is consistent with a directly approaching threat and the general looming literature (Wang & Frost, 1992; Rind & Simmons, 1999). Caribou (*Rangifer tarandus*) appear to react similarly to low-flying aircraft (Calef, Debock & Lortie, 1976), exhibiting panic reactions to the direct approach of a (fixed-wing) aircraft under 60 m above ground level (AGL).

Ringed seals (*Pusa hispida*) hauled-out on ice also reacted (dropped into the water) to the direct approach of fixed-wing aircraft and helicopters flying at 150 m AGL. As with Dall sheep, the effect of helicopters was much stronger than that of the fixed-wing aircraft (Born *et al.*, 1999). The seals were less reactive when thermal conditions favoured being out of the water, suggesting a trade-off between some sort of perceived risk and the benefits of hauling-out, much as envisioned by the Risk-Disturbance Hypothesis of Frid & Dill (2002). It is interesting to note that these seals have no conceivable aerial predators, yet they did react to a direct aerial approach. In the seals and the above ungulates, it is not clear how much prior experience these animals had with low flying aircraft, hence habituation or sensitization effects cannot be assessed.

A study on alpine chamois (*Rupicapra rupicapra*) and aerial vehicles (Schnidrig-Petrig & Ingold, 2001) takes this issue of threat perception to another level. These relatively small ungulates apparently treat paragliders as avian predators. Paraglider enthusiasts soar along mountain ridge lines for rising air, much as golden eagles (*Aquila chrysaetos*) do. Upon sighting a paraglider, the chamois escaped to forested habitat, just as they do in response to eagles. Furthermore, time spent in non-preferred forest habitat was directly related to local paraglider activity. This degree of responsiveness does not reflect a response to noise, as none is made by paragliders, and habituation effects (if present) were not strong. In fact, these chamois did not respond much to loud jet aircraft at low altitude (Schnidrig-Petrig & Ingold, 2001). Apparently, a paraglider's shape and soaring behaviour are similar enough to that of an eagle to induce a strong threat perception (perhaps as a supernormal stimulus). Such a perception is remarkable, given that real eagles were present for comparison to the seemingly very different paragliders.

(4) Birds and aircraft

Unlike most mammals, many birds are clearly at risk to AVCs involving aerial vehicles, and bird strikes in aviation provide some of the more dramatic examples of AVCs and their aftermath (Dolbeer *et al.*, 2012; DeVault *et al.*, 2013). Birds would appear to have the agility and cognitive abilities to avoid aircraft, and this is likely the case in general (Blokpoel, 1976; Kelly, Bolger & O'Callaghan, 1999; Sodhi, 2002). Nevertheless, many thousands of bird strikes are reported each year in the United States, and such incidents are greatly under-reported (Dolbeer *et al.*, 2012). This situation likely reflects the sheer number of aircraft and birds in the air at any given time, rather than an acute vulnerability to such collisions.

The threat that bird strikes pose to aviation is clear, yet existing information on the behavioural reaction of birds to aircraft is mainly anecdotal and haphazard. The available observations suggest that birds may not usually treat flying aircraft as much of a threat (more of an obstacle), often allowing fairly close approach before taking evasive action. An early account along these lines was provided by a bird-knowledgeable Royal Air Force pilot (Carr-Lewty, 1943), who noted that, on close approach of an aircraft, birds in flight would generally avoid it. Blokpoel (1976) summarized similar anecdotal observations made by pilots, noting a case in which a flock of bean geese (*Anser* sp.) that was purposefully pursued by a plane (at fairly slow speed) did not attempt evasion until the plane was nearly in formation with the geese, whereupon they simply banked away from the plane. Similarly, snow geese (*Chen caerulescens*) in a large flock simply created an opening through which a plane could pass without changing their heading (Blokpoel, 1976); Jacobi (1996) describes similar behaviour in jackdaw (*Corvus monedula*) flocks. Observations made from within planes while studying nocturnal passerine migrants (using activated landing lights) indicate similar tendencies for birds to engage in evasive manoeuvres mainly when in close proximity to the plane (Bellrose, 1971;

Larkin *et al.*, 1975). However, birds flying at night are at an obvious disadvantage in detecting aircraft, and these studies actually recorded several collisions with the birds under observation.

In contrast to the above observations, birds may be relatively reactive to flyovers by loud aircraft. Conomy *et al.* (1998) found that resting/feeding ducks were responsive to overflights by loud, low-flying military aircraft (especially helicopters), often flushing into flight at distances of 1 km or more. Similarly, adult Antarctic penguins in breeding colonies clearly responded with alarm to noisy aircraft, even those 1 km away (see Harris, 2005, for a review); interestingly, these adult birds have no serious aerial predators, and it seems that noise is the main source of disturbance. By contrast, Conomy *et al.* (1998) found that dabbling duck species were fairly unresponsive to low-flying military aircraft.

These studies with military aircraft suggest a role for sound in the avoidance of aircraft by birds, and several have argued that the quieter civilian jet aircraft currently in use are more at risk to AVCs than the previous generation of aircraft (Burger, 1983; Sodhi, 2002; see also Tomlinson *et al.*, 1991). Noise also seems to be a factor in reactions of mammals to aircraft (see above). Noise can certainly be an important issue during the take-off roll of large aircraft, during which engine noise travels forward much faster than the aircraft. In fact, Tomlinson *et al.* (1991) found that caged pigeons (*Columba livia*) and gulls (*Larus* sp.) responded physiologically (increased heart rate) to just the sound of the take-off roll of a large jet aircraft, but not usually until the plane was within 300 m. However, at cruising speeds of typical passenger aircraft, the warning provided by noise to birds ahead of an aircraft is relatively minimal (Solman, 1976; Kelly *et al.*, 2001; Kelly & Allan, 2006).

There have been very few systematic studies of the behavioural reactions of flying birds to aircraft. Experimental studies involving the direct approach of aircraft towards birds have not been conducted on free-ranging birds. Kelly *et al.* (1999) provide the closest approximation to such work in a study of low-flying bird flocks crossing active runways at an airport in Ireland. These authors identified four basic types of responses. The first is a simple acceleration without change of direction. The remaining three are more complex avoidance behaviours, which are followed by the reestablishment of the original heading: 'S' type avoidance in which birds change direction at a right angle to the original heading to move around the rear of the plane, 'noose' type avoidance in which a flock performs a 360° loop away from the plane as it passes by, and a zig-zagging 'protean' response suggesting antipredator behaviour (Driver & Humphries, 1988). Most observations were on rooks, black-headed gulls (*Chroicocephalus ridibundus*), and woodpigeons (*Columba palumbus*). The majority of avoidance manoeuvres were 'S' type. Evasive responses did not occur until birds were in close proximity to the aircraft. No apparent response was observed in 12% of the close encounters, but no actual strikes were observed.

Generally lacking from studies of bird-aircraft interactions is the distance at which flying birds initiate avoidance

of nearby aircraft. The above observations clearly indicate that birds avoid close encounters with dodges and other behaviours, but perhaps these short-range observations are the only ones that observers are likely to make. Furthermore, given their perceptual abilities (Jones, Pierce & Ward, 2007), birds certainly have the opportunity to respond at a great distance, well before pilots or other observers are aware of their presence. Perhaps this is where the majority of avoidance takes place. Radar could be useful in making such assessments, but has seen only limited use in AVC work (Larkin *et al.*, 1975; Desholm *et al.*, 2006; Klope *et al.*, 2009). Overall, we suspect that most evasive behaviour by birds takes place at fairly close range, perhaps within 100–200 m of an aircraft, but long-distance reactions are certainly a possibility.

So, what goes wrong in AVCs involving birds and aircraft? Based on the locations of injuries received by birds struck by aircraft, Bernhardt *et al.* (2010) suggested that most such birds actually had initiated some sort of antipredator response, although apparently too late. Pilot reports of bird strikes (unstructured comments as summarized by Dolbeer, Washburn & Wright, 2004; R. A. Dolbeer, personal communication) also suggested that the struck birds attempted some sort of evasive manoeuvre in the majority of collisions (about 75%). Most reported evasive responses involved a dive or descent, although a variety of other responses were noted (climb, scatter). These responses are similar to those involved in successful avoidance manoeuvres. In about 25% of cases, however, pilots noticed no apparent attempt at avoidance. Dolbeer *et al.* (2004) also noted that collisions above 150 m AGL were usually associated with dive/descend responses, whereas a variety of responses was more apparent at lower altitudes. This effect of altitude could reflect species differences in typical flying altitudes rather than altitude-dependent avoidance behaviour in birds, but this matter is unclear. A few pilots reported that the struck birds were aggressively approaching the aircraft. This may seem unlikely, but Pennycuik (1972) described attacks on a light aircraft by large eagles. Aggressive responses towards light aircraft (BFB, personal observation) and helicopters by osprey (*Pandion haliaetus*) have also been observed (Carrier & Melquist, 1976).

We suspect that the biggest problem in bird strikes is that birds are often habituated to flying aircraft, and thus at risk of allowing dangerously close approaches. In many parts of the world, birds probably see flying aircraft dozens of times on many days. These aircraft do not act in any threatening way, and thus it seems inevitable that they will be treated as relatively benign flying objects. There are also several anecdotal reports of ground-feeding birds strongly habituated to aircraft take-offs near runways (Carr-Lewty, 1943; Blokpoel, 1976), although such birds may have learned to avoid disturbances associated with the runway itself. We suspect, however, that habituated birds would react with alarm towards an atypically-behaving aeroplane that made sudden and threatening moves towards them. There are obvious dangers in obtaining such observations,

but Carr-Lewty (1943) notes that otherwise passive flocks of birds were greatly disturbed when directly harassed by RAF pilots in 'high spirits'.

Some antipredator adaptations might put certain types of birds at greater risk of collision with aircraft. For instance, a common escape tactic for many high-flying birds under raptor attack is to allow the raptor to approach closely, whereupon a quick last-second dodge is used to evade capture (Lima, 1993). Such a tactic would clearly be fraught with danger when applied to aircraft (see also Bernhardt *et al.*, 2010). Relatively fast birds are able to outfly predators (even falcons) in level flight (Lima, 1993), and might attempt to do so when approached closely by (much faster) aircraft. Blokpoel (1976) noted that ducks and shorebirds may indeed attempt to outfly an aircraft until it gets very close, whereupon they dive or bank out of the way. Major, Dill & Eaves (1986) reported a similar tendency in dunlins (*Calidris alpina*) to attempt to outfly aircraft on take-off runs. Flock-level decision-making might also delay or confuse responses to approaching aircraft, which could leave entire flocks at risk from collisions.

(5) Birds and automobiles

Low-flying birds are frequently hit by automobiles (e.g. Mumme *et al.*, 2000; Erritzoe *et al.*, 2003; Kociolek *et al.*, 2011), but little has been published on the behavioural issues surrounding such AVCs. However, virtually any observant driver in all but the most urban areas could recount several such strikes and near misses of low-flying birds. In our experience, birds feeding on or very close to the road itself [vultures (Cathartidae), crows, etc.] are rarely struck by cars, they seem aware of approaching vehicles and vacate the road well before collision, although this effect may vary with the speed of the approaching vehicle (DeVault *et al.*, 2014). This sense of awareness is also obvious in places where cliff swallows (*Petrochelidon pyrrhonota*) nest under busy highway overpasses, under which several automobiles may pass per minute; these birds spend much of the day milling over the road but largely manage to avoid being struck (C. Brown, personal communication). In general, automobile–bird collisions tend to involve individuals crossing perpendicular to the road, and usually involve little or no overt reaction to the vehicle (SLL, personal observation). The most obvious explanation for these sorts of collisions is that the birds were in some way distracted, but this remains to be demonstrated.

(6) Birds and boats

We know of no situations in which collisions between boats and birds are a regular occurrence. However, several studies have addressed the reactions of birds to oncoming boats and larger vessels, mainly in the context of managing disturbances to birds (Burger, 1998; Burger *et al.*, 2010; Schwemmer *et al.*, 2011). Some seabirds are surprisingly reactive to oncoming recreational boats and larger vessels. For instance, black guillemots (*Cepphus grylle*) tend to flush into the air from approaching boats at about 250 m (Ronconi & St. Clair,

2002), and European shags (*Phalacrocorax aristotelis*) react similarly at several hundred meters (Velando & Munilla, 2011). All of the sea duck species studied by Schwemmer *et al.* (2011) flushed into flight on average at over 200 m from relatively large vessels, with common scoters (*Somateria mollissima*) reacting at 800 m. The distances at which these species flushed are entirely appropriate for 'escaping' from a surface vessel, but the nature of the threat perceived is not obvious: what threat faced by ocean-going birds would in any way be suggested by an ocean-going vessel? The early use of flight in the encounter perhaps suggests that approaching boats are somehow perceived as terrestrial (or non-flying) predators. Diving into the water is a more typical escape behaviour used against serious aerial predators like falcons (Lima, 1993). The perception of boats as threats is clear in defensive reactions of parental velvet scoters (*Melanitta fusca*), which aggressively approach boats that are approaching their (flightless) offspring (Mikola *et al.*, 1994).

Not all ocean-going birds are so reactive to such vessels. Marbled murrelets (*Brachyramphus marmoratus*) generally react to boats within about 50 m, and reactions tend to involve diving rather than flight (Bellefleur, Lee & Ronconi, 2009); most birds did not react with overt escape behaviour, apparently casually swimming away from the vessel's line of travel. This lower degree of reactivity is typical of many pelagic birds such as shearwaters (SLL, personal observation), and, of course, opportunistic species such as gulls might seek out vessels as sources of food.

(7) Amphibians and reptiles

Amphibians and reptiles can suffer much mortality on roads (Glista *et al.*, 2008), which in some cases puts an entire population at risk (Fahrig & Rytwinski, 2009). The behavioural issues here seem straightforward: amphibians and reptiles are often too slow to avoid a speeding vehicle (assuming that they perceive the oncoming threat). However, the situation can be even more problematic. Experimental work indicates that the antipredator responses of frogs, salamanders, and toads can enhance their vulnerability to automobile traffic (Mazerolle, Huot & Gravel, 2005). These amphibians became immobile when faced with automobile-related stimuli (lights, noise, and actual vehicles). Such immobility is effective against motion-sensitive predators, but not motorized vehicles. In fact, such a response both increases the risk of mortality during a given encounter and greatly lengthens the time necessary to cross a road (see also Litvaitis & Tash, 2008). Cooper *et al.* (2008) provide further insight into this problem, showing that frogs, which are potentially motion-sensitive predators, tend to freeze when approached by ground-level objects. Similarly, Andrews & Gibbons (2005) showed experimentally that three snake species become immobile at close quarters with a moving vehicle. Once again, this can only serve to lengthen the time necessary to cross a busy road, although snakes generally tend to cross roads fairly quickly in the absence of such encounters.

Aquatic reptiles are also at risk from collisions with boats, such as crocodilians (Grant & Lewis, 2010) and sea turtles

(Oros *et al.*, 2005; Hazel & Gyuris, 2006). Hazel *et al.* (2007) showed experimentally that green turtles (*Chelonia mydas*) in shallow water do react effectively to the direct approach of a 6-m boat, but only if that boat is moving slowly (4 km/h or 1.1 m/s); their tendency to react decreased markedly as boat speed increased to 11 and 19 km/h (both still fairly slow speeds). Their reactions mainly involved fleeing away from the track of the boat, although many crossed the track of the boat in an effort to flee to deeper water. Hazel *et al.* (2007) suggested that the turtles approached at higher speeds simply did not have adequate time to detect and respond to the boat. They suggest further that turtles were probably habituated to the sounds of boat motors (see also Samuel *et al.*, 2005), and mainly used vision to detect potential threats, which was limited to 12 m or less during the experiments. Indeed, turtles more than about 10 m from the track of the boat showed no response to its approach. Perhaps surprisingly, Wirsing, Abernethy & Heithaus (2008) used a boat to simulate predator attacks in a study on the escape behaviour of loggerhead turtles (*Caretta caretta*). These simulated attacks were, however, maintained at slow speed and in close proximity to a turtle.

(8) Fish

Relatively few AVC-related issues involving fish have received much attention, although collisions with boats may be a problem for large fish such as sturgeons (Brown & Murphy, 2010) and whale sharks (Speed *et al.*, 2008). An odd AVC issue is that involving the invasive silver carp (*Hypophthalmichthys molitrix*) in the Mississippi River drainage (Chick & Pegg, 2001), which can leap over 2 m into the air when disturbed (SLL, personal observation), and thus present a major hazard to fast-moving recreational boats. However, the reactions of fish to moving objects, such as towed fishing gear, has long been of interest to fisheries biologists. Much of this work has been reviewed recently, but some parallels and contrasts are worth highlighting relative to our present AVC focus.

Many fisheries-related studies focus (in essence) on how to enhance collisions between fish and objects such as nets towed by fishing vessels (Wardle, 1993; Ryer, 2008). This body of work makes explicit reference to the antipredator behaviour of various fishes, and how it can be used to enhance the capture of a given set of species or lower the bycatch of others (Ryer, 2008). Issues of vehicular avoidance come into play in work focused on the reactions of fish to survey vehicles and the resulting biases in estimating stock abundances (Stoner *et al.*, 2008). Considerations of antipredator behaviour are important here as well, especially when considering taxonomic variability in avoidance reactions (Stoner *et al.*, 2008). Visual stimuli (in the form of lights and the vehicle itself) and sound stimuli are relevant in avoidance (e.g. Ryer, Stoner & Iseri, 2009), although the latter have received less attention (Popper & Hastings, 2009). However, unlike the AVC work that we have considered so far, attraction can often be an issue of greater importance than avoidance with

respect to slowly moving underwater survey vehicles (Stoner *et al.*, 2008).

(9) Invertebrates

Collisions involving automobile windscreens and flying insects are undoubtedly the most numerous AVC in the modern world. There are probably many tens of millions of such collisions on any given summer evening. Virtually any invertebrate that crosses a road at an altitude under 2 m is at risk of death (e.g. Soluk *et al.*, 2011). However, such collisions are of little danger to humans or economic importance, and the species involved are rarely charismatic or popular. Hence, it is perhaps not surprising that this topic has received little attention (but see Seibert & Conover, 1991; Soluk *et al.*, 2011).

The antipredator looming responses of flying insects have nevertheless been studied in considerable detail (Rind & Simmons, 1999). Such looming responses are well developed, but did not evolve in an environment with large objects moving at 30 m/s: modern vehicles probably overwhelm the looming response of any insect. Smaller insects might ride the shock wave up and over a fast-moving vehicle, but larger insects will not be so fortunate. It seems possible that the looming responses of birds (Wang & Frost, 1992; Sun & Frost, 1998) could be similarly overwhelmed by fast-moving automobiles and aircraft, but this possibility is only recently under investigation (DeVault *et al.*, 2014). Of course, regardless of the perception of an approaching threat, many flightless invertebrates probably have no effective reaction to moving vehicles while crossing roads, much as the amphibians and reptiles discussed above.

(10) Pedestrians and automobiles

The phenomenon of humans crossing roadways may be analogous to road crossing by many other vertebrates. Humans know vehicles are potentially dangerous, but are largely habituated to their presence, which may put them at a considerable risk of collision. And as with other reasonably agile vertebrates, most roadway crossings by humans occur without incident. However, the sheer volume of roadway crossings by pedestrians will dictate a large number of collisions. Automobile–pedestrian collisions in the United States alone account for about 5000 fatalities and 70000 serious injuries each year (NHTSA, 2009). The number of collisions (including minor incidents) probably exceeds 100000 per year. Understanding what goes wrong when humans are struck by vehicles might shed some light on the more general phenomenon of AVCs.

As mentioned earlier, distractions may play a role in AVCs involving various mammals and birds. Distractions would seem to be important in pedestrian–vehicle collisions, but this has received relatively little study until recently. Such studies focus on the now prevalent use of mobile phones and other personal electronic devices. A study on pre-adolescent children in a simulated (video) road-crossing

environment indicated that mobile phone use increased the risk of collision, especially early in the experiment (Stavrinos, Byington & Schwebel, 2009). Other studies in simulated environments reached similar conclusions (Neider *et al.*, 2010; Stavrinos, Byington & Schwebel, 2011). Observations on mobile-phone-using college students crossing an active street were judged to be more unsafe than those made by non-users (Nasar, Hecht & Wener, 2008). Hatfield & Murphy (2007) present a similar study showing that mobile phone users are less vigilant and tend to cross roads more slowly. The tendency to miss even very unusual activity when using mobile phones has been termed ‘inattention blindness’ (Hyman *et al.*, 2010).

Distractions aside, a perfectly performing pedestrian would assess both the speed and distance of an approaching vehicle to determine whether ample time exists for a road crossing (as assumed by Das, Manski & Manuszak, 2005). However, recent studies using large-scale video simulations suggest that vehicular speed plays only a minor role in road-crossing decisions; rather, distance seems to be the most influential metric (Simpson, Johnston & Richardson, 2003; Oxley *et al.*, 2005; but see de Velde *et al.*, 2005). Basing decisions on distance to vehicle can work well if vehicles move at a predictable speed, but may be problematic otherwise. One mitigating factor here is that pedestrians tend to cross roads at a higher speed with a short gap between vehicles (i.e. when taking a greater risk; Ishaque & Noland, 2008). However, studies in simulated environments also indicate that certain classes of pedestrians – the old and the very young – often miscalculate margins of safety to the point of having frequent ‘negative’ margins of safety (essentially struck by the virtual vehicle; Oxley *et al.*, 2005; Wann, Poulter & Purcell, 2011). Miscalculations may also be induced by social information in groups of pedestrians (Faria *et al.*, 2010). Reactions by automobile drivers undoubtedly prevent many such miscalculation-driven collisions.

Do non-human animals miscalculate margins of safety in crossing roadways? Do they understand that margins of safety exist? Perhaps analogous forms of miscalculation accompany some types of AVCs, but we suspect that there is not much forethought or planning in decisions made by road-crossing (or runway-crossing) animals. It seems more likely that some form of ‘inattention blindness’ causes AVCs in certain taxa, but that remains to be demonstrated.

V. CONCLUSIONS

(1) Animal–vehicle collisions (AVCs) are a substantial problem, threatening not only human lives and property (Conover, 2002; Dolbeer *et al.*, 2012), but also entire populations of particularly vulnerable animals (Forman *et al.*, 2003; Fahrig & Rytwinski, 2009). This review focused on the behavioural reactions of various animals to oncoming vehicles in an effort to provide some insight into the underlying causes of AVCs.

(2) Just what exactly goes wrong during AVCs is not yet clear in many systems, but some generalizations are apparent at this point. For instance, the species for whom AVCs are a major conservation concern often fail profoundly in avoiding an oncoming vehicle. Those failures may occur in detection, threat assessment, or evasive behaviour (Fig. 1), although the precise point of failure in that sequence is often not clear. Such apparent failures apply most prominently to endangered marine mammals (e.g. Nowacek *et al.*, 2004a), some of which appear particularly slow to assess the threat posed by an oncoming vessel. For sea turtles (Hazel *et al.*, 2007), the failure here seems to be a function of a slow evasive response. This problem of profound failures applies perhaps more widely and acutely to amphibians, whose antipredator escape tactics (often immobility) are often inappropriate when used against motorized vehicles (Mazerolle *et al.*, 2005).

(3) Generalizations regarding the many behavioural issues that we raised are harder to make at this point. However, one such tentative generalization is that many animals are likely to be habituated to modern vehicles to the point where they are not perceived to be deadly threats. This topic has not received the systematic attention it deserves, but we suspect that it is particularly relevant in many birds and mammals. We do not suggest that habituation has proceeded to the point at which no reactions occur, but it may lead animals into problematic situations where collisions are more likely to occur (e.g. Bernhardt *et al.*, 2010). Such habituation could be particularly problematic when combined with high vehicle speed and inappropriate evasive responses. Given current information, we cannot reach even tentative generalizations about the other behavioural issues that we considered, such as the role of sensory constraints, distractions, cognitive abilities, and miscalculation in AVCs. All of these entities, however, are potentially important determinants of AVCs in any given system, and worthy of much more empirical attention, from both basic and applied perspectives.

(4) Given the scope of problems involving AVCs, surprisingly little systematic behavioural work has been done to date. This situation holds for just about every taxon. The reactions of marine mammals to oncoming vessels have been explored experimentally to the greatest extent. Similar behavioural work on terrestrial mammals is remarkably limited, especially related to encounters with automobiles. Much of the focus in dealing with mammalian AVCs is on channeling animals across or under roads in ways that preclude collisions (Glista, DeVault & DeWoody, 2009; Taylor & Goldingay, 2010) or providing warning to motorists about particularly problematic areas (Bruinderink & Hazebroek, 1996). Experimental behavioural work, however, should be feasible in many mammalian systems. There have also been many products (e.g. ‘deer whistles’) purporting to alter the behaviour of roadside animals that have little if any value in reducing AVCs (Hedlund *et al.*, 2004), but the entire sensory range of such animals has

hardly been explored from this perspective (see Blackwell & Seamans, 2009).

(5) A behaviourally based approach to lessening AVCs may be the least effective in reptiles and amphibians. Many such species exhibit inappropriate or slow reactions to vehicles. Thus the only viable approach is keeping such animals off roads (see Glista *et al.*, 2009; Taylor & Goldingay, 2010). However, behavioural work focused on interactions with oncoming vehicles can help outline the scope of the problem (e.g. Hazel *et al.*, 2007) and provide valuable information to enhance wildlife collision models (Litvaitis & Tash, 2008).

(6) By contrast, behavioural work may be an essential aspect of any program to manage AVCs involving birds, especially with respect to aviation. Because birds are difficult to herd or channel once in the air, an understanding of the sensory/behavioural interactions between birds and aircraft may be particularly important in decreasing bird strikes. Nevertheless, existing information on the behavioural reaction of birds to aircraft is mainly anecdotal and haphazard. These animals are not the easiest to manipulate in the field (aerial) environment, but experimental work should be possible in many respects. Comparative behavioural work covering avian species with the highest frequencies of damaging strikes (DeVault *et al.*, 2011; Dolbeer *et al.*, 2012) would be most useful. There are a number of questions that such work might consider, such as (i) the role of perceptual constraints in aircraft detection (e.g. Blackwell *et al.*, 2009b, 2012), (ii) the range at which birds tend to interact with aircraft, and (iii) how to get the attention of habituated birds to elicit earlier threat assessment and evasive behaviour.

(7) The development of a general and predictive theory of vehicle avoidance behaviour is desirable but not very likely at this stage. As we outlined earlier, the evolutionary novelty of motorized vehicles would seem to preclude such an approach. Future advances will thus rely mainly on systematic empirical studies covering a range of behavioural phenomena and as much taxonomic diversity as possible (see also Martin, 2011). Such a research program will likely yield useful taxonomic generalizations regarding AVCs. Constructs like the Risk-Disturbance Hypothesis (Frid & Dill, 2002) will also continue to provide a useful organizational theme for interpreting the results of this work.

(8) We strongly encourage as much experimental work as possible in future studies. We also encourage the use of actual or miniature vehicles to the extent that it is safe and feasible to do so. The resulting work will provide a unique view of AVCs and animal behaviour in general, and potentially many insights into ways of minimizing the risk of AVCs. Such work will complement many other approaches to the problem of AVCs, such as considerations of entire landscapes, the design of roads (Nielsen, Anderson & Grund, 2003; Seiler & Helldin, 2006; Ng, Nielsen & St. Clair, 2008), and habitat management around airports (Blackwell *et al.*, 2009a; DeVault *et al.*, 2013). We doubt that

AVCs can be entirely eliminated, but such a multifaceted approach should ultimately do much to minimize the problems caused by large moving objects in the modern world.

VI. ACKNOWLEDGEMENTS

We thank Michael Gerringer for providing helpful comments on the manuscript and help in its preparation. Support for B.F.B., T.L.D., and E.F.-J. was provided by the U.S. Department of Agriculture, Wildlife Services, National Wildlife Research Center.

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(Received 9 May 2013; revised 1 February 2014; accepted 4 February 2014; published online 25 March 2014)