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ARTICLE

Individual variation in avian avoidance behaviours in response to repeated, simulated vehicle approach

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Abstract: Birds exhibit variation in alert and flight behaviours in response to vehicles within and between species, but it is unclear how properties inherent to individuals influence variation in avoidance responses over time. We examined individual variation in avoidance behaviours of Brown-headed Cowbirds (*Molothrus ater* (Boddaert, 1783)) in response to repeated presentation of a simulated vehicle approach in a video playback scenario. We modeled temporal alert and flight behaviours to determine whether overall behavioural variation resulted primarily from variation within individuals (i.e., intraindividual variation) or between individuals (i.e., interindividual variation). We examined reaction norms (individual × treatment day) and whether birds showed plasticity in responses via habituation or sensitization. Repeatability in the response metrics for individuals was low (~0.22 for alert and flight), indicating that model variation was due primarily to within-individual variation rather than between-individual variation. We observed sensitization in alert responses over time, but no sensitization or habituation in flight responses. Our results indicate that individuals learned to anticipate the vehicle approach but did not vary their escape behaviour, suggesting that alert and flight behaviours might be affected differently by cues associated with oncoming objects or experience with them. We consider our findings in light of the ongoing development of strategies to reduce animal–vehicle collisions.

Key words: behaviour, bird strike, Brown-headed Cowbird, collision, *Molothrus ater*, repeatability, sensitization.

Résumé : Si les oiseaux présentent des variations intraspécifiques et interspécifiques des comportements d'alerte et de fuite en réaction aux véhicules, l'influence des propriétés individuelles sur les variations des réactions d'évitement avec le temps n'est pas bien établie. Nous avons examiné les variations individuelles des comportements d'évitement de vachers à tête brune (*Molothrus ater* (Boddaert, 1783)) en réponse à la présentation répétée d'une approche de véhicule simulée dans un scénario de reprise vidéo. Nous avons modélisé les comportements d'alerte et de fuite dans le temps afin de déterminer si les variations comportementales globales résultaient principalement de variations intraindividuelles ou interindividuelles. Nous avons examiné les normes de réaction (individu × jour du traitement) et si les réactions des oiseaux présentaient une plasticité sous forme d'accoutumance ou de sensibilisation. La répétabilité des mesures de réaction pour les individus était faible (~0,22 pour l'alerte et la fuite), ce qui indique que les variations modélisées étaient principalement dues à des variations intraindividuelles plutôt qu'interindividuelles. Nous avons noté une sensibilisation dans les réactions d'alerte avec le temps, mais aucune sensibilisation ou accoutumance dans les réactions de fuite. Nos résultats indiquent que les individus ont appris à anticiper l'approche d'un véhicule, mais n'ont pas modifié leur comportement d'échappement, ce qui porte à croire que les comportements d'alerte et de fuite des oiseaux pourraient être influencés différemment par des signaux associés à des objets se dirigeant vers eux ou par leur expérience individuelle de tels signaux. Nous discutons de nos constatations dans le contexte de l'élaboration de stratégies pour réduire les collisions entre animaux et véhicules. [Traduit par la Rédaction]

Mots-clés : comportement, impact d'oiseau, vacher à tête brune, collision, *Molothrus ater*, répétabilité, sensibilisation.

Introduction

Responses by animals to approaching predators or risky objects (e.g., vehicles) vary across species due to, among other things, differences in experience, antipredator strategies, and sensory capabilities (Blumstein et al. 2003; Stankowich and Blumstein 2005; Blackwell et al. 2009; Lima et al. 2015). Within species, responses to approaching threats can vary due to individual age, sex, condition, risk tolerance, and habituation/sensitization, as shown in birds (Mumme et al. 2000; Edelaar and Wright 2006; Møller 2010; DeVault et al. 2014, 2015; Borneman et al. 2016), mammals (Bejder et al. 2006; Andersen and Aars 2008; Li et al. 2011),

reptiles (Samia et al. 2016), and fish (Ferrari et al. 2007). Individual escape behaviours also might reflect differences in body condition or head orientation relative to the approaching threat, or distractions resulting from social interactions (Lima et al. 2015).

Individual personality also can contribute to how animals respond to risk (Sih et al. 2015), and variation across individuals might result from high individual repeatability in behaviours over time (Carrete and Tella 2010, 2011, 2013; Briffa 2013; Highcock and Carter 2014). Within-individual variability reflects the predictability or repeatability of an animal's behaviour (Briffa 2013). For example, Carrete and Tella (2010) found that breeding Burrowing

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Owls (*Athene cunicularia* (Molina, 1782)) exhibited relatively high repeatability (0.84–0.92; low within-individual variation) in flight initiation distance (FID) in response to human approaches toward burrows, and speculated that selection and distribution of breeding sites reflected different levels of individual tolerance to human disturbance. Subsequently, Carrete and Tella (2011) tested whether individuals invading urban environments were more tolerant of human disturbances, or alternatively were tame individuals from species with high levels of variation in tolerance to disturbance. The authors quantified FID in response to vehicle traffic for species inhabiting both rural and urban environments and concluded that urban invaders were tame individuals from species with generally higher variability in FID across individuals, thus indicating behavioural flexibility (Carrete and Tella 2011). However, their data reflected responses by focal birds to primarily tangential, unrepeated vehicle approaches, and thus their study did not explicitly investigate the role of within-individual variability in FIDs. Finally, Carrete and Tella (2013) reported that Burrowing Owls maintain unusually high individual consistency (repeatability ≥0.90) in their fear of humans throughout their lifetimes.

These aforementioned studies suggest that a better understanding of individual responses to anthropogenic threats can inform how human–wildlife conflicts might be managed (Blackwell et al. 2016). For instance, because animals respond to vehicles much as they do to predators (Frid and Dill 2002; Blackwell and Seamans 2009; Bernhardt et al. 2010), some assessment of risk (e.g., Frid and Dill 2002; Cooper and Frederick 2007) should be expected. If so, then how is perceived risk relative to vehicle approach expressed within and across individuals? Recent research focusing on enhancing detection of an approaching vehicle to exploit antipredator behaviours (e.g., Lima 1993; Blumstein et al. 2005; Caro 2005) indicated that speed and visual saliency of the approaching vehicle are important to alert and escape behaviours (Blackwell et al. 2009, 2012, 2014; Fernández-Juricic et al. 2011; DeVault et al. 2014, 2015; Doppler et al. 2015). However, our understanding of individual experience with repeated, noninjurious exposure to vehicle traffic is minimal (DeVault et al. 2017).

Our goal was to discern the role of individual variation in animal avoidance behaviours in response to vehicle approach through repeated exposures to this threat. One of the challenges inherent to this type of study is to control for the multiple confounding factors to which animals are subject in the field (e.g., variation in temperature, light intensity, individual identity). We addressed this shortcoming by exposing birds to a simulated vehicle approach in a video playback scenario (DeVault et al. 2015, 2017). We quantified variation in temporal alert and flight behaviours within and across individuals in response to a virtual, oncoming vehicle and assessed those metrics in terms of variation within and across individuals and with regards to habituation and sensitization. First, we proposed two alternative hypotheses to explain overall variation in alert and flight behaviours: (1) variation between individuals would drive overall variation (i.e., individuals would show relatively low within-individual variability; Carrete and Tella 2010, 2011, 2013), and (2) within-individual variability would drive variation in responses, suggesting that unpredictable behaviour in response to threat might be advantageous (Briffa 2013), or reflect a possible inconsistency in risk perception with regards to approaching vehicles as opposed to real predators (Lima et al. 2015). Second, we proposed two alternative hypotheses to explain the variation in alert and flight initiation behaviours over time: birds would show plasticity (Réale et al. 2007; Dingemanse and Dochtermann 2013) to repeated vehicle approaches via either (1) habituation (i.e., reduced alert and flight initiation responses with repeated exposures; DeVault et al. 2017) or (2) sensitization (i.e., enhanced alert and flight initiation responses with repeated exposures).

Materials and methods

Study animals

We used male Brown-headed Cowbirds (*Molothrus ater* (Boddaert, 1783); hereafter Cowbirds) as our model species because they are easy to capture in large numbers in our study area, stay healthy in captivity for several weeks following capture, and respond well to experiments involving simulated vehicle approach in a video playback scenario (DeVault et al. 2015). We captured Cowbirds using modified Australian crow traps at the National Aeronautics and Space Administration Plum Brook Station (Erie County, Ohio, USA) in April–May 2014 and held them in 2.4 m × 2.4 m × 1.8 m cages in an indoor aviary illuminated with natural lighting. Cowbirds were given water, white millet and sunflower seeds ad libitum, and meal worms (*Tenebrio molitor* Linnaeus, 1758) once weekly. The day before exposure to treatment, groups of three birds each were placed into separate holding cages (0.5 m × 1.0 m × 1.9 m). All Cowbirds used in our experiment were colour-banded for individual identification; following the experiment the bands were removed, and all birds were released unharmed. The Institutional Animal Care and Use Committee of the USDA National Wildlife Research Center approved all procedures used in this study (QA-2228).

Video playback

Procedures used to simulate vehicle encounter closely followed DeVault et al. (2015). Briefly, Cowbird groups (see below) were placed in an indoor viewing chamber with three walls (61 cm × 152 cm) and a ceiling (122 cm × 152 cm) of solid, gray composite material, a wire mesh floor (122 cm × 152 cm), and a fourth wall consisting of a high definition, 240 Hz, LED Samsung TV monitor with a visual surface of 58 cm × 102 cm. A black, thin plastic mesh screen (62 cm × 102 cm) was positioned 50 cm from the monitor to prevent close approach to the monitor and reduce the use of nonpictorial depth cues. The top, rear, and side walls of the chamber included a small opening for the placement of video cameras to record behaviours. Lighting within the chamber was supplied by the TV monitor and a compact fluorescent bulb (>1000 Hz). After each video presentation of the oncoming vehicle, experimental birds were removed from the viewing chamber, returned to their pre-assigned holding cages, and a new set of birds was placed in the chamber.

Video playback trials were conducted over 12 days from 6 to 23 May 2014 (Tuesday through Friday during each of the 3 weeks). Thirty-five groups of three Cowbirds each (105 individuals in total) were tested once per day during 4 consecutive days within 1 week (11 groups during the first week and 12 groups during the second and third weeks). Thus, each bird/group was exposed to treatment four times during the experiment, and each group remained intact during the experiment. We tested birds in groups of three instead of individually to reduce stress, given that Cowbirds are a flocking species (Lowther 1993). The number of times animals were exposed to our treatments followed Carrete and Tella (2010), who exposed individual Burrowing Owls to 2–5 approaches by humans.

Each video presentation showed a directly oncoming 2003 Ford F-250 gray pickup truck appearing to approach at 150 km/h (75 km/h actual approach played back at double speed (60 frames/ s); for detailed description of video recording and playback methods see DeVault et al. 2015). To begin a trial, a paused video file of an empty road was first placed on the monitor in "full-screen" mode. We then released a group of three Cowbirds inside the video chamber and closed the door to the chamber. The video remained paused for 15 min to allow Cowbirds to acclimate to their surroundings. We then played the video and recorded the birds' responses to the oncoming vehicle. Each video playback ended when the virtual vehicle "collided" with the video chamber. The entire approach, from the time the vehicle became visi-

ble on the screen (to human eyes) until colliding with the video chamber, lasted approximately 20 s.

Behavioural metrics

All experimental groups were filmed during video playback using four video cameras. We examined each video recording at approximately 0.1 s intervals. We recorded the time that each individual within a group showed an alert response and a flight response, relative to the marked end point (time of virtual collision) for the vehicle approach. We measured alert and flight responses at the individual level (e.g., the first individual in the group that reacted and each individual thereafter). Alert behaviour was defined as the sudden transition from an individual's baseline behaviour (e.g., loafing or preening) to a vigilance-related behaviour (e.g., head up with neck extended) in response to the approaching virtual vehicle. Flight response was defined as an obvious intent to avoid the simulated oncoming vehicle and involved running or flying towards the back or sides of the video chamber (DeVault et al. 2015). We scored flight behaviour at the initiation of the crouch to fly or the first step in a running response. Time-to-collision alert (TTC_{alert}) and time-to-collision flight (TTC_{flight}) represented the time (s) required for the vehicle to reach the birds' location at the onset of the respective behaviour. If a bird failed to show an alert response but showed a flight response, we scored TTC_{alert} as equal to TTC_{flight}. If a bird failed to show flight response, we scored TTC_{flight} as equal to zero. Greater values of TTC_{alert} and TTC_{flight} indicate an earlier response to the vehicle (DeVault et al. 2015).

Analyses

We quantified decomposition of variance of response variables relative to within- and between-individual components by using a generalized linear mixed models approach (Dingemanse and Dochtermann 2013). We used PROC GLIMMIX (SAS version 9.2; SAS Institute, Inc., Cary, North Carolina, USA), a lognormal distribution, identity link function, Gauss–Hermite Quadrature (QUAD) for parameter estimation, and the containment method for degrees of freedom (SAS version 9.2). The QUAD estimation technique maximizes log likelihood numerically, as opposed to approximating maximum likelihood (ML); ML generally underestimates random-effect standard deviations (Bolker et al. 2009). Also, our data were non-normal, thus we used QUAD estimation as opposed to restricted ML to estimate random effects (Bolker et al. 2009; Nakagawa and Schielzeth 2010). Because we selected a lognormal distribution, the GLIMMIX procedure models the logarithm of the response variable as a normal random variable (i.e., the mean and variance are estimated on the logarithmic scale, assuming a normal distribution, $\log(Y) \sim N(\mu, \sigma^2)$; SAS/STAT 9.2 User's Guide, Second Edition). As such, the GLIMMIX procedure will omit zero (e.g., see "Behavioural metrics" above) or negative responses from the analyses. We therefore added 0.001 to all cases where TTC_{alert} or TTC_{flight} = 0.000 (alert: n = 4 instances, for which the addition represented 0.04% of the mean alert response over 4 days; flight: n = 21 instances, for which the addition represented 0.15% of the mean flight response).

For TTC_{alert} and TTC_{flight}, we modeled the response relative to individual as *G*-side or conditional random effects (i.e., the response | random effect; Dingemanse and Dochtermann 2013) centred on the individual bird, and as nested designs involving the individual within group or week. We compared repeatability (r), defined as the ratio of between-individual variation (i.e., the variance across random intercepts of individuals) to that of between- and within-individual variation (i.e., residual error; Réale et al. 2007; Nakagawa and Schielzeth 2010; Dingemanse and Dochtermann 2013), for nested models via –2 log likelihood ratios and non-nested models via Akaike's information criterion corrected for small sample size (AIC$_c$; Burnham and Anderson 2002), which is an ML-based metric (Bolker et al. 2009). Values of r that approach 1 indi-

cate consistency of behaviour for an individual or large between-individual differences in a behaviour (Hitchcock et al. 2015). Based on published values for r in animal responses to human disturbance (e.g., Carrete and Tella 2010, 2013), we considered r to be low to moderate if ≤0.50. We calculated the standard error of r following Becker (1984). However, our results for nested models were identical to those for individual only, thus we report results for the non-nested model.

To examine whether birds showed habituation or sensitization to repeated exposure to treatment, we also examined reaction norms (i.e., individual × treatment day interaction). In other words, we examined the behavioural responses of individuals relative to the novelty of the treatment (Réale et al. 2007; Dingemanse and Dochtermann 2013). If birds habituated to the treatment, we would expect a negative and significant interaction effect of individual × day on the response variable. Alternatively, if sensitization occurred, the effect would be positive. We modeled the interaction of subject (i.e., individual as the conditional, random effect) and day of treatment (fixed effect; Réale et al. 2007). Again, we used QUAD as our estimation technique.

Results

Of 420 individual virtual vehicle encounters, we noted 21 instances where an individual within a group failed to show a flight response, and only a single group failed to show an alert or flight response to treatment during one vehicle approach. Based on our raw data (including instances where animals showed no response; raw score = 0.000), we obtained TTC_{alert} = 2.33 ± 1.35 s (range: 0.00–6.9 s) and TTC_{flight} = 0.67 ± 0.64 s (range: 0.00–4.2 s; Fig. 1). We found that repeatability for TTC_{alert} and TTC_{flight} was low (explaining ≤50% of model variation), indicating that within-individual variability was high relative to between-individual variability (Table 1). Model overdispersion was negligible for TTC_{alert}, but somewhat higher for TTC_{flight} (Pearson χ^2/df = 0.67 vs. 1.66, respectively). We attribute this difference in model overdispersion to greater within-individual variation (i.e., lower repeatability) observed for flight behaviour (Table 1).

We found that the interaction of individual × treatment day was positive and significant for TTC_{alert}, indicating that birds sensitized in alert response over the course of the experiment ($F_{[3,312]}$ = 33.09, P < 0.0001; Fig. 1). However, we found no significant interaction effect on TTC_{flight} (i.e., no sensitization or habituation) with repeated treatment ($F_{[3,312]}$ = 1.56, P = 0.198; Fig. 1).

Discussion

We found that repeatability in alert and flight behaviours by Brown-headed Cowbirds in response to simulated vehicle approach was low (<0.50), indicating that variation in avoidance behaviours rested primarily with the individual. Furthermore, we found that individuals appeared to sensitize in their alert responses with repeated vehicle exposures, although flight behaviour did not vary over the same time period.

With regard to low repeatability of alert and flight behaviours in response to simulated vehicle approach, we reason that two broad factors, not necessarily mutually exclusive, might have affected the behaviours that we observed. First, visually salient cues common to approaching predators (e.g., gaze, varying directionality in approach, varying approach speed), which might contribute to higher levels of repeatability in alert and flight responses, are missing in the evolutionarily novel threat of vehicle approach (Blackwell et al. 2014; DeVault et al. 2014, 2015; Lima et al. 2015). Thus, the manner in which individuals assess the threat from vehicle approach and process information relative to threat recognition and perceived risk could differ in some ways from that associated with predation (Stankowich and Blumstein 2005). This difference could be reflected in our result of low repeatability in response to simulated vehicles (<0.50) compared with earlier

Fig. 1. Time-to-collision alert (left-hand panels) and time-to-collision flight (right-hand panels) for Brown-headed Cowbirds (*Molothrus ater*) across four exposures (one each day on consecutive days) to the approach of a virtual vehicle in a video playback scenario. In the top three rows of panels, each line represents an individual bird (*n* = 33 in first week; *n* = 36 in second and third weeks); the bottom row of panels represents means ± 1 SE.
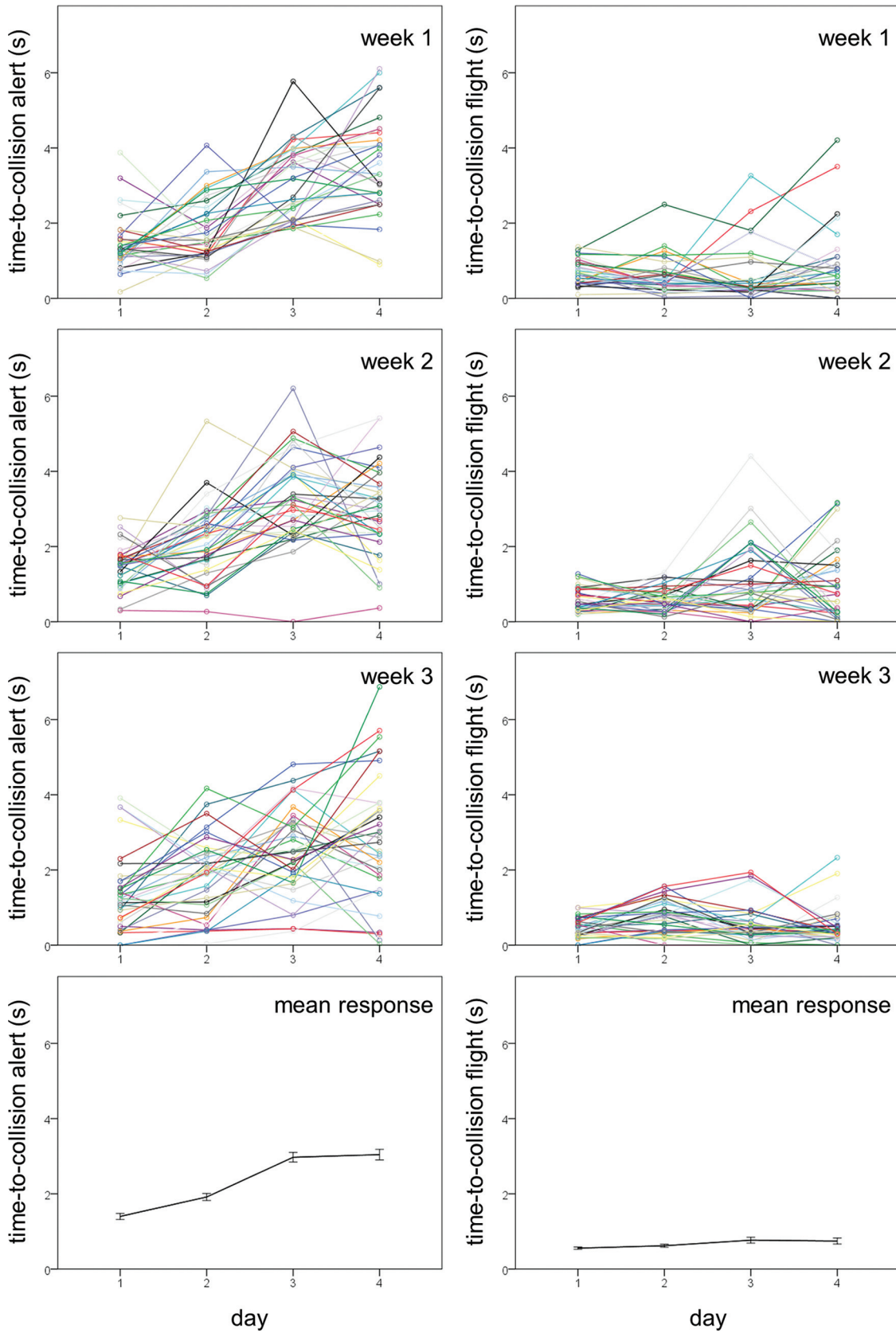
Table 1. Decomposition of variance in response variables for Brown-headed Cowbirds (*Molothrus ater*) exposed to virtual vehicle approach in video playback trials conducted over 12 days from 6 to 23 May 2014 (35 groups, 3 birds/group, 4 exposures over 4 consecutive days).

TTC model	Covariance parameter	Estimate	SE	r	SE
Alert	Intercept (Bird)	0.2960	0.0700	0.2719	0.0529
	Residual	0.7928	0.0632		
Flight	Intercept (Bird)	0.5342	0.1448	0.2184	0.0518
	Residual	1.9120	0.1523		

Note: Response metrics included time-to-collision (TTC) alert and flight. Repeatability (*r*), which is the variance attributable to across-individual effects, represents the ratio of covariance parameter for bird to overall model variance.

studies reporting high repeatability (0.84–0.92) in response to approaching humans (i.e., simulated predators; Carrete and Tella 2010). Alternatively, low repeatability of flight behaviour might reflect a strategy of individual unpredictability in behavioural response when under threat. For example, Briffa (2013) showed that increased within-individual variance in hermit crab (*Pagurus bernhardus* (Linnaeus, 1758)) startle responses was directly linked to cues from an external predator and suggested that such unpredictability could represent a strategy for reducing predation risk. Similarly, low repeatability in Cowbird response to simulated vehicle approach could conceivably be an adaptive response to uncertain risk associated with approaching threats.

We also suggest that unpredictability in response to vehicle approach need not be consistent between alert and flight behaviours. Specifically, our finding of sensitization in alert responses indicates that Cowbirds recognized the simulated vehicle approach as a threat and that some degree of learning occurred via anticipation of the vehicle approach. Animal sensitization to disturbance is not unusual, but possibly overlooked (Bejder et al. 2009; Blumstein 2016). For example, frequent disturbance might result in animals flushing at greater distances (White and Thurow 1985), expressing higher levels of stress hormones but without overt behavioural responses (Ellenberg et al. 2007), or even varying their stress-related responses according to the personality of the animal and consistency/duration of the disturbance (Ellenberg et al. 2009). Of particular interest in our findings, however, is the apparent disconnect between threat recognition (as measured by alert behaviour) and escape response.

In other words, sensitization in the alert response did not translate into earlier (enhanced) flight behaviour. Previous studies investigating the effects of onboard vehicle lighting on bird avoidance behaviours also have shown differential alert responses across lighting treatments, with little effect on flight responses (Blackwell et al. 2009, 2012; Doppler et al. 2015; but see Sheridan et al. 2015). Furthermore, our current results are inconsistent with findings from a recent study involving simulated vehicle approaches towards Rock Pigeons (*Columba livia* Gmelin, 1789). In that study, we found that individuals exposed repeatedly to passing vehicles had shorter FID (analogous to TTC_flight in the current study) than vehicle-naïve birds when confronted with a virtual, directly approaching vehicle, suggesting that pigeons habituated to vehicles (DeVault et al. 2017). It is possible that habituation and sensitization are species-specific traits (Blumstein et al. 2003; Blumstein 2016), even though prior research has reported strong correlations between alert and flight behaviours in predator–prey scenarios (e.g., Blumstein et al. 2005; Cárdenas et al. 2005). Thus, animals might learn to anticipate repeated, consistent disturbance in the form of vehicle approach (e.g., Mumme et al. 2000; Möller 2010), but also respond unpredictably, showing flight behaviour that could be adaptive in a predation scenario, but maladaptive in response to vehicles.

Our findings have implications for both management to reduce bird–vehicle collisions and directions for new research. First, ve-

hicle approach speed is a critical factor contributing to ineffective avoidance responses by birds (DeVault et al. 2014, 2015) and mammals (Blackwell et al. 2014), but more so if escape responses are highly variable because some reactions will likely be too late for successful avoidance even when the mean flight response is effective. Also, our results suggest avoidance behaviours are unlikely to be improved by repeated exposure to vehicles (see also DeVault et al. 2017). Thus, our results confirm earlier work suggesting that reduced vehicle speeds (e.g., via lowering posted speed limits on roads) would lead to fewer animal–vehicle collisions, especially in areas where collisions are frequent and such regulations are practical (Blackwell et al. 2014, DeVault et al. 2014, 2015). We also suggest that future work involving simulated vehicle approach, particularly experiments designed to maintain realistic vehicle approach speeds (e.g., DeVault et al. 2015), should pair repeatability in alert and flight responses to the same metrics during a simulated approach of a known predator, as well as investigation into plasticity of alert and flight responses with regard to efforts to enhance detection of approaching vehicles (Blackwell et al. 2012; Doppler et al. 2015).

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