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Exploiting avian vision with aircraft lighting to reduce bird strikes

Bradley F. Blackwell[1]*, Travis L. DeVault[1], Thomas W. Seamans[1], Steven L. Lima[2], Patrice Baumhardt[3] and Esteban Fernández-Juricic[3]

[1]*USDA/APHIS/WS National Wildlife Research Center, Ohio Field Station, 6100 Columbus Avenue, Sandusky, OH 44870 USA;* [2]*Department of Biology, Indiana State University, 600 Chestnut Street, Terre Haute, IN 47809 USA; and* [3]*Department of Biological Sciences, Purdue University, Lilly Hall G-302, 915 W. State Street, West Lafayette, IN 47907 USA*

Summary

1. Bird–aircraft collisions (bird strikes) represent a substantial safety concern and financial burden to civil aviation world-wide. Despite an increase in the rate of damaging bird strikes, necessary steps to develop a mitigation method outside of the airport environment have not been empirically tested.

2. We assessed whether use of aircraft lighting might enhance detection of and reaction to the approach of an aircraft in flight by Canada geese *Branta canadensis* Linnaeus, a species responsible for a high rate of damaging bird strikes. We used a novel approach by estimating the visibility to the goose visual system of a standard radio-controlled (RC) aircraft (standard aircraft) exhibiting either a 2-Hz alternating pulse of two lights, or lights off; and another RC aircraft designed to mimic a raptor (predator model). We then exposed wing-clipped Canada geese to the approach of each aircraft and quantified behavioural responses to respective treatments.

3. Estimates of chromatic and achromatic contrasts indicated that the standard aircraft with lights on was more salient to the visual system of the Canada goose than with lights off or the predator model.

4. At individual and group levels, quicker alert responses were observed to the standard aircraft with lights compared with the lights off and predator model. Goose groups showed similar responses to approaches by the standard aircraft and the predator model, suggesting use of antipredator behaviour to avoid the aircraft.

5. *Synthesis and applications.* Understanding animal sensory ecology and associated behaviours can aid the development of methods exploiting certain behaviours to reduce negative human–wildlife interactions. For example, reducing the frequency of bird strikes requires the integration of wildlife management efforts within and outside of the airport environment that target species resource use and response to disturbance, with mitigation techniques focused on the aircraft. Moreover, the design of aircraft lighting systems to enhance detection and avoidance by birds is contingent upon understanding avian visual ecology and behaviour. Based on spectral sensitivity in Canada geese, aircraft-mounted lights that peak in the ultraviolet/violet range (380–400 nm) are likely to produce the maximal behavioural effect.

Key-words: aircraft lighting, airport, antipredator behaviour, avian vision, bird strike, *Branta canadensis*, human–wildlife interactions, sensory ecology

Introduction

The frequency of wildlife–aircraft collisions (strikes), particularly involving birds, is increasing (Dolbeer 2011); such collisions lead to aircraft damage and downtime, as well as multiple safety issues. On a world-wide basis, direct and indirect costs to the civil aviation industry owing to bird strikes exceed $1·2 billion annually (Allan 2002). Furthermore, the bird-strike issue goes beyond the usual management of wildlife on airport property.

For example, in a recent analysis of strike data reported to the US Federal Aviation Administration (FAA; 1990–2009), Dolbeer (2011) found the percentage of all damaging strikes

*Correspondence author. E-mail: bradley.f.blackwell@aphis.usda.gov

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that occurred >152 m above-ground level (AGL) increased at a greater rate than those incidents occurring at ≤152 m AGL. Dolbeer (2011) attributed these altitudinal differences in strike rates to the effects of wildlife-hazard management efforts on US airports, which affect mainly bird activity in the vicinity of the airport. However, these efforts have little effect beyond airport property, as evidenced by the 2009 forced landing of US Airways Flight 1549 in New York's Hudson River owing to engine ingestion of multiple Canada geese, *Branta canadensis* Linnaeus, (Marra *et al.* 2009) at approximately 859 m AGL and 7 km from LaGuardia Airport, New York, NY (US National Transportation Safety Board, NTSB 2010). Thus, a major gap in effectively reducing bird-strike frequency is the manipulation of the interaction between birds and aircraft beyond airport property.

A central theme behind any nonlethal management of animals is to modify their behaviour (Sutherland 1998). Some of the proposed strategies to minimize bird strikes outside of the immediate airport environment include development of on-board systems that could make aircraft more visible to birds (thus, enhancing the probability of avoidance behaviours), such as modifications to lighting (Blackwell *et al.* 2009a) or paint schemes (Fernández-Juricic *et al.* 2011a). If birds are alerted to the approach of an aircraft at a greater distance, avoidance manoeuvres similar to those in response to aerial predators (e.g. Hilton, Cresswell & Ruxton 1999; Lind, Kaby & Jakobsson 2002; see also Bernhardt *et al.* 2010) might be initiated sooner, thus reducing the risk of a bird strike. For example, in situations involving avian response to approaching humans, alert response is positively correlated with flight-initiation distance (Blumstein *et al.* 2005). Similarly, Martin (2011) suggests exploiting sensory ecology to distract or divert birds from colliding with wind turbines or buildings (see also Poot *et al.* 2008). However, to date, there is no single on-board technology in use that is specifically designed to reduce bird strikes.

Developing a strategy to make aircraft more visible to birds and enhance avoidance responses requires a multi-disciplinary approach. First, the degree of visibility of an aircraft will depend on the sensory system of the target species. For instance, birds have visual systems that are quite different from human vision (e.g. wide lateral visual fields, higher temporal visual resolution, and sensitivity in a broader range of the spectrum; Cuthill 2006; Martin 2011). Thus, an effective on-board technology should produce stimuli salient to the target species' visual system. Second, a conceptual framework is necessary to allow generalization of responses to novel on-board technology across bird species that cause the most damaging strikes (Dolbeer *et al.* 2010; DeVault *et al.* 2011). Antipredator behaviour theory (e.g. Lima 1998; Caro 2005) has been applied successfully in human–wildlife interaction contexts (e.g. Frid & Dill 2002) and can provide such a framework (Blackwell & Seamans 2009; Bernhardt *et al.* 2010). Specifically, by exploiting sensory capabilities of target species and antipredator responses to novel stimuli, one might enhance avian detection and avoidance of aircraft (see Blackwell & Bernhardt 2004; Blackwell *et al.* 2009a). These are critical first steps in developing an on-board system intended to reduce bird strikes, because broad implementation of such systems depends on species responding to an aircraft with enough time to engage in avoidance manoeuvres.

In this study, we assessed whether aircraft lighting might enhance detection of and reaction to the approach of an aircraft by Canada geese, a species that causes a disproportionate degree of damage to US civil aircraft (DeVault *et al.* 2011). Our objectives were to (i) establish whether aircraft with lights on would be more visible to a Canada goose, considering specific properties of its visual system; (ii) quantify behavioural response of Canada geese to approach by an aircraft under preselected lighting treatments; and (iii) provide suggestions for aircraft lighting designs that will aid in reducing bird–aircraft collisions.

Materials and methods

ANIMALS

We obtained 58 adult, urban, resident Canada geese of undetermined sex, captured in June 2009. See Appendix S1 for details on animal care and maintenance.

EXPERIMENTAL DESIGN

Modelling visual perception in birds

We used visual contrast models (details in Appendix S2) to estimate how Canada geese would perceive the stimuli (i.e. two aircraft) in relation to the visual background. Using this modelling approach, we tested a critical assumption of our behavioural experiments that Canada geese would perceive the aircraft with lights on as more contrasting than the aircraft with lights off. Using visual contrast models is important owing to the aforementioned differences between the avian and human visual systems. We calculated chromatic and achromatic contrasts (Endler 1990), which estimate the ability of the visual system to distinguish an object from the background using cues related to colour and brightness of visual stimuli, respectively (Vorobyev & Osorio 1998; Osorio, Miklósi & Gonda 1999). This approach requires information on (a) the sensitivity of the retina to different wavelengths, (b) the light reflectance patterns of the stimuli and the background environment, and (c) the spectral characteristics of the ambient light. Details on the parameterization and calculation of the visual contrast models are presented in Appendix S2.

Experimental site and equipment

We conducted our experiment under semi-natural conditions in a 9·3-ha grass field in Erie County, OH, USA (41°22′N, 82°41′W) on 21 and 23 July 2009 between 0900 and 1715 hrs. (Appendix S1). We held each group of geese in a circular enclosure (~229 m^2) of 1·8-m high synthetic, 5-cm mesh fencing located in the centre of a 372-m^2 area of mixed grass (~4 cm in height; Fig. 1). The enclosure was intended to mimic grasslands within airport property, and allowed the geese ample freedom for responding to aircraft approach. We used a standard fixed-wing design, RC aircraft (Rascal 110; standard aircraft) and the Falco Robot GBRS©, designed to mimic a raptor (predator model), as our approach vehicles (Appendix S3). Engine noise was audible for each aircraft. However, we assumed that variations in wind conditions, noise from an on-site power generator (used

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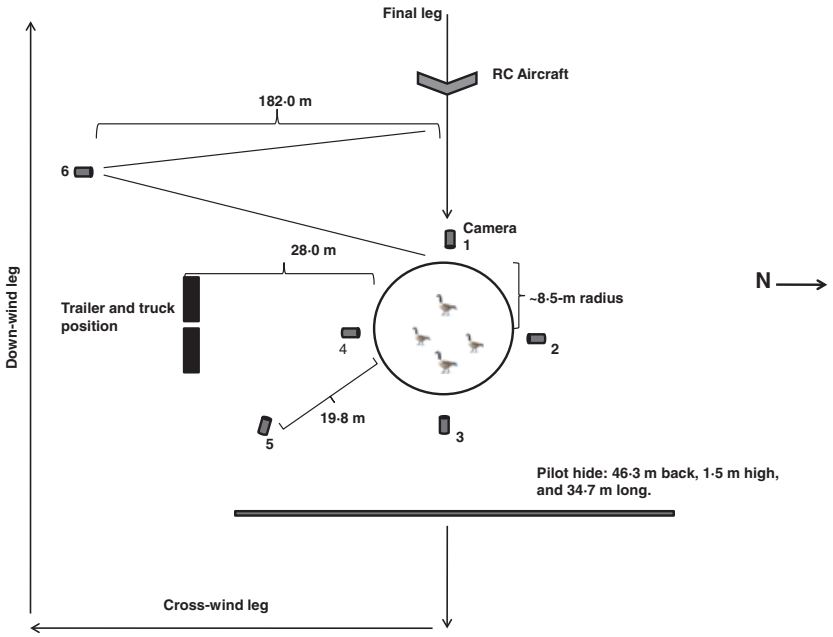

Fig. 1. Diagram of the experimental site and approach scenario used for the exposure of captive groups of Canada geese to the approach of radio-controlled (RC) aircraft. Camera positions are indicated by the numbers 1–6. The final leg of each standard-aircraft approach began approximately 550 m from the enclosure, whereas the predator model approached from 420 m.

to power our server/video recorder system; Appendix S1), and the fact that aircraft approached the enclosure from an upwind direction reduced possible confounding effects of differential engine sounds. All approaches were video-recorded (see Appendix S1).

Experimental protocol

We were limited to 58 birds and therefore used a repeated-measures approach to the experiment. We exposed 14 groups of geese, four birds per group, to three treatments (standard aircraft with lights off, standard aircraft with lights on, and predator model; two birds were held as potential replacements). The first two treatments involved the standard aircraft either with lights off or on, with the order randomly determined. Standard-aircraft approaches with lights on involved the alternating pulse (2 Hz) of two lights mounted on the landing gear (Appendix S3). A 2-Hz pulse is considered safe for civil aviation pilots (Rash 2004).

To assess response to the standard aircraft relative to antipredator behaviour, we exposed all groups to a third treatment consisting of the approach of the predator model. Tests prior to our experiment showed that the predator model generated antipredator behaviour in Canada geese (e.g. escape to water, aggregation of individuals; E. Fernández-Juricic, unpublished data). Because our focus was the response of geese to the standard aircraft with lights on or off, we used the predator model consistently as our third and last treatment.

Each goose group was allowed at least 15 min to acclimate to the enclosure. During acclimation the geese were, however, exposed to movement of the pilot and observer preparing aircraft for take-off (approximately 60 m from the enclosure), as well as noise from the generator (Appendix S1). These geese were urban birds habituated to people, traffic, and associated noise. Accordingly, we observed no behaviour suggesting that the geese were overly disturbed, as each goose group quickly began exploring the enclosure and foraging.

With the exception of take-off and landing, the general flight scenario for each treatment was similar, entailing a downwind, base, and final flight legs (Fig. 1). Each goose group could hear and view aircraft departure. We launched the standard aircraft from a gravel road 60 m southeast of the enclosure and climbed it to altitude on the downwind leg, approximately 550 m west of the enclosure. While the aircraft was in flight, the pilot and observer were positioned behind a hide to the east of the enclosure (Fig. 1). After completing an approach, the standard aircraft was landed (on the same gravel road), retrieved by the pilot, then positioned for the second treatment, or removed and the predator model prepared for the third treatment.

In contrast, we launched the predator model windward by hand from behind the hide (Fig. 1). Also, because of the smaller size and reduced visibility (from the pilot's perspective), the pilot climbed the aircraft to altitude on the downwind leg approximately 420 m west of the enclosure to begin the final approach. The final leg for both aircraft was a fully powered and direct approach upwind, descending linearly from approximately 150–6 m and flaring upward upon reaching the western edge of the enclosure, then banking and climbing to position for the landing.

The interval (mean ± SD) from take-off until landing for treatments involving the standard aircraft (1·9 ± 0·5 min) exceeded that of the predator model (1·0 ± 0·2 min) because of the longer final flying leg of the former. Intervals (mean ± SD) between flights within group (i.e. across three treatments per group) were consistent (5·2 ± 0·5 min). However, owing to problems with our outside camera (no. 6, Fig. 1), we obtained ground speed estimates (see Appendix S1) for only 12 standard-aircraft approaches with lights on, 11 standard-aircraft approaches with lights off, and 11 predator model approaches. Aircraft approach speeds (mean ± SD) were similar (standard aircraft with lights on: 114·1 ± 13·2 km hr^{-1}; lights off: 110·7 ± 8·0 km hr^{-1}; predator model: 102·2 km ± 13·0 km hr^{-1}).

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Behavioural metrics

We examined video footage of each group and measured behavioural responses relative to the time at which the aircraft was over the centre of the enclosure. Here, the same observer viewed video footage from each aircraft approach taken via camera five (Fig. 1) and measured the position of the aircraft relative to enclosure features. We recorded the time each individual within a group became alert and moved away (flight initiation) in response to aircraft approach (as per Blackwell *et al.* 2009a). We defined alert behaviour as the increase in vigilance-related behaviours (e.g. rate and proportion of time head-up scanning) in response to on-coming aircraft. An alert response involved a transition in an individual's behaviour from an undisturbed behaviour (e.g. pecking, preening, loafing, or general scanning) to a behaviour clearly directed towards the approaching aircraft; showing head up and neck extended, increased scanning, or crouching (Fernández-Juricic, Jimenez & Lucas 2001; Blackwell *et al.* 2009a). Furthermore, alert behaviour in response to aircraft approach had to be maintained by an individual until (i) the aircraft was over the centre of the enclosure, or (ii) transition to flight behaviour. Those birds that showed an alert response to aircraft take-off reverted to other behaviours before the aircraft began the final leg. We defined a flight response as a clearly differentiated transition in behaviour from, for example, loafing, pecking, foraging, or alert behaviour, to running, flight attempts, or sudden movement towards other members of the group in response to aircraft approach.

For each individual bird within a group we recorded alert time as the time (seconds) required for the aircraft to reach the centre of the enclosure from the point at which an individual showed alert behaviour in response to aircraft approach (as defined previously). Similarly, flight-initiation time was the time required for the aircraft to reach the centre of the enclosure from the point at which the individual initiated flight behaviour. Greater values of alert and flight-initiation times indicate an earlier response to approaching aircraft. For individuals that maintained alert behaviour through the aircraft's passage over the enclosure, without showing a flight response, we scored flight-initiation time as zero. In instances where an individual showed no alert behaviour but initiated a flight response, we scored alert time as equivalent to flight-initiation time. If a bird showed no alert or flight response, both time metrics were scored as zero.

As an additional metric of antipredator behaviour in response to aircraft approach, we measured neighbour distances within each goose group at the point of aircraft take-off and when the aircraft was over the centre of the enclosure. We used ImageJ (http://rsb.info.nih.gov/ij) to measure all pairwise neighbour distances from and to the centre of the body and distance between the head and the ground for each individual (individual height). We used pixels as our measurement unit and all distances were recorded from the same camera across trials. Because of distortion associated with distance of the individuals from the camera, we standardized pairwise distances as follows: distance between individual 1 and 2/[(individual 1 height + individual 2 height)/2]. We then used the standardized distances among all individuals to estimate an average neighbour distance per trial.

We included ambient light intensity (μmol m^{-2} s^{-1}), temperature, and wind as covariates in our models. We recorded ambient light intensity with a Li-Cor (Lincoln, Nebraska, USA) LI-250 Light Meter and LI-190SA Quantum Sensor measured at completion of the first treatment per group. We also recorded temperature and wind speed using a WeatherHawk (Logan, UT, USA) 916 weather station.

Statistical analyses

We considered each group as an experimental unit. We used a mixed linear model with group as a repeated-measures factor, Kenward-Rogers adjustment to degrees of freedom, an autoregressive correlation structure, and type III sums of squares (SAS ver. 8·2; SAS Institute, Cary, NC, USA) to evaluate differences among treatments (α = 0·05) in time of first alert per group, group alert and group flight-initiation times, as well as coefficient of variation in alert time (CV_{alert}) within group. Group alert and flight-initiation times represented the average of individual times within each group by treatment. We log-transformed CV_{alert} to normalize its distribution. Treatment served as the fixed effect, but we also investigated ambient effects. Among treatments, wind speed varied by $< 0{\cdot}1$ m s^{-1} and temperature by $< 0{\cdot}1$ °C, thus we did not include them in our final model. However, as per Blackwell *et al.* (2009a), we included ambient light intensity and the interaction of treatment and ambient light intensity in our model.

Neighbour distances were analysed with a general linear model and relative to aircraft position (take-off, aircraft over centre of enclosure), treatment, and their interaction. Group was entered as a repeated-measures factor.

Results

CONTRAST OF VISUAL STIMULI

Chromatic and achromatic contrast results indicate that Canada geese easily discriminated visually between approaching aircraft (standard-aircraft and predator model) against the visual background (Table 1). Across different ambient light conditions (sunny, partly cloudy, cloudy), chromatic contrast was higher for the standard aircraft than for the predator model (Table 1). Additionally, chromatic contrast was higher for the standard aircraft with lights on than with lights off (Table 1). This finding corroborates our assumption that, given our human perception, Canada geese would perceive aircraft with lights on as more contrasting than with lights off.

Table 1. Chromatic and achromatic contrast values under sunny, partly cloudy, and cloudy ambient light conditions for a standard fixed-wing design, radio-controlled (RC) aircraft (standard aircraft) with lights off or on, and another RC aircraft (predator model) designed to mimic a raptor. Contrast values were calculated using characteristics of the visual system of Canada geese. Units are just noticeable differences (JND; Appendix S2). JND > 3 indicate visual stimuli that can be easily discriminated from the visual background

	Standard aircraft lights off	Standard aircraft lights on	Predator model
Chromatic contrast			
Sunny	82·15	84·20	58·36
Partly cloudy	84·45	87·25	60·62
Cloudy	37·06	40·94	16·95
Achromatic contrast			
Sunny	45·44	45·69	17·58
Partly cloudy	45·78	45·99	17·96
Cloudy	58·96	59·01	31·25

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Across all ambient light conditions, achromatic contrast was higher for the standard aircraft than for the predator model (Table 1). However, the achromatic contrast values were essentially identical for the standard aircraft with lights on and off (Table 1).

AIRCRAFT APPROACHES

We completed all three aircraft approaches against 14 groups of geese over 2 days. During approaches, the geese exhibited some degree of alert behaviour prior to and during aircraft take-off. However, these behaviours (e.g. showing head up and neck extended, increased scanning, or crouching) were intermittent with foraging activity, preening, or resting (i.e. they were not maintained). Furthermore, based on head positions, the animals did not track the aircraft following take-off. Responses to approach of the standard aircraft on the final leg were indicative of a sustained alarm and similar to those given to the predator model. Also, neighbour distances changed in response to aircraft approach, further evidence that disturbance at take-off did not confound response to the approach.

Individuals within groups showed the first alert response to approach by the standard aircraft with lights on (mean ± SD seconds before aircraft was over centre of enclosure; 14·1 ± 5·5 s) approximately 4 s earlier than observed during approaches by the standard aircraft with lights off (9·7 ± 5·6 s), and approximately 6 s earlier than first alert to the predator model (7·9 ± 5·0 s), both statistically significant responses (Table 2). Group alert response to the approach by the standard aircraft with lights on (mean ± SE; 11·4 ± 4·4 s) also occurred approximately 4 s earlier than observed for approaches by the standard aircraft with lights off (7·3 ± 4·4 s), and approximately 5 s before the group alert response to the predator model (6·3 ± 4·3 s); these responses were also statistically significant (Table 2). In addition, for both the first alert and group alert response, there was an interaction of the predator model treatment and ambient light intensity (Table 2). Specifically, as ambient light intensity increased, the average alert response to approach by the predator model occurred sooner (Fig. 2). Also, the coefficient of variation in alert response to approach by the standard aircraft with lights on (mean ± SD; 31·7 ± 36·2 s), standard aircraft with lights off (44·0 ± 29·2 s), and predator model (43·2 ± 40·6 s) was not statistically different (Table 2).

As to group flight response, five to eight groups per treatment were scored as having zero flight behaviour by the time that the aircraft was over the centre of the enclosure. We could not normalize these data for comparison, but group flight-initiation times (mean ± SE) were generally similar (standard aircraft with lights on: 1·1 ± 1·8 s; standard aircraft with lights off: 1·3 ± 1·6 s; predator model: 0·7 ± 1·0 s). Examining neighbour distances, we found that geese aggregated in response to aircraft approach: neighbour distance (mean ± SE) at take-off (3·11 ± 0·21 m) exceeded that when an aircraft was over centre of enclosure (2·25 ± 0·21 m; $F_{1,65}$ = 8·21, P = 0·006). We did not find significant differences in neighbour distance among treatments ($F_{2,65}$ = 1·55; P = 0·219) or the interaction between aircraft position and treatment ($F_{2,65}$ = 2·73; P = 0·073).

Discussion

Under semi-natural conditions, Canada geese responded more quickly to the approach of a standard radio-controlled aircraft that exhibited 2-Hz, alternating, pulsed lighting than to the same aircraft with lights off, or a second aircraft that resembled a raptor (predator model). More specifically, use of aircraft lighting enhanced individual alert responses on average by 4·2 s over approaches with lights off. Using the average flight speeds, we estimated that geese responded to the standard aircraft with lights on at approximately 404 m from the enclosure centre vs. 261 m with lights off. Lighting also enhanced responses to the standard aircraft on average by 5·6 s (or 202 m) over approaches by the predator model.

We found that Canada geese were better able to visually discriminate approach by the standard aircraft compared with that of the predator model. Specifically, responses to the predator model were a function of ambient light intensity: the higher the ambient intensity, the quicker the responses. Ambient light might have increased the contrast between the predator model and sky; this was likely due to chromatic, rather than achromatic contrast, which varied little among light conditions (Table 1). Interestingly, alert responses to the standard aircraft were not significantly dependent on ambient light, which corroborates the visual contrast data suggesting that this object was more visually salient than the predator model. Importantly, our findings are in agreement with previous studies suggesting that discrimination of large objects is dependent upon chromatic information, whereas detection of smaller objects and texture requires achromatic contrast information (human, Mullen 1985; domestic chick, *Gallus gallus* L., Osorio, Miklósi & Gonda 1999; bumblebee, *Bombus terrestris* L., Spaethe, Tautz & Chittka 2001).

Canada geese are prey to large, aerial diurnal raptors (Mowbray *et al.* 2002), but their slower reaction to the predator model might be due to several nonmutually exclusive factors, other than chromatic and achromatic sensitivity. First, each experimental group was consistently exposed to the predator model last in the treatment series, and their motivation to respond to approaching objects may have been reduced by previous treatments. Second, although we attempted to standardize the approach of each aircraft, flight dynamics (e.g. speed of descent or climb) varied between standard-aircraft and predator model treatments. Third, the standard aircraft exceeded the predator model in wingspan by 1·2 m, thus presenting a larger object area for the wide visual field of the Canada goose (Fernández-Juricic *et al.* 2011b).

However, Canada geese reacted in the same general way to both the standard aircraft and predator model, which suggests that this species showed antipredator behaviour to aircraft approaches on collision course, and that groups were not habituated to treatment. This finding is important because guidance, to date, by aviation authorities does not consider how birds respond to aircraft approach or the possibility of

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Table 2. Results from a mixed linear model analysis of alert responses of groups of captive Canada geese ($N = 14$ experimental groups; $n = 4$ birds per group) to the approach of a standard fixed-wing design, radio-controlled (RC) aircraft (standard aircraft) exhibiting a 2-Hz alternating pulse of two lights positioned on the landing gear, the standard aircraft with lights off, and another RC aircraft designed to mimic a raptor (predator model). Each group was exposed to the three treatments sequentially, with a standard aircraft treatment randomly selected for the first and second approach, and the predator model used as the third treatment for all groups. Time corresponds to seconds before an aircraft was over the centre of the circular enclosure containing the group. The experiments took place in Erie county, north-central Ohio, USA, on 21 and 23 July 2009

Alert response metric*	Effect†	Time	SD	Model estimate	SE	d.f.‡	*t* value	*P*
1st Alert	Standard aircraft lights on	14·1	5·5	13·09950	4·01470	28·2	3·26	0·0029
	Standard aircraft lights off	9·7	5·6	10·67550	4·01470	28·2	3·26	0·0128
	Predator model	7·9	5·0	−2·27480	4·01470	28·2	−0·57	0·5755
	Standard aircraft lights on × ALI§	.	.	0·00081	0·00312	28·2	0·26	0·7984
	Standard aircraft lights off × ALI	.	.	−0·00078	0·00312	28·2	−0·25	0·8036
	Predator model × ALI	.	.	0·00840	0·00312	28·2	2·69	0·0119
	Differences in least squares means							
	Standard aircraft lights on vs. Standard aircraft lights off	.	.	4·34870	1·41590	23·9	3·07	0·0053
	Standard aircraft lights on vs. predator model	.	.	6·17460	1·72960	33·7	3·57	0·0011
	Standard aircraft lights off vs. predator model	.	.	1·82590	1·41590	23·9	1·29	0·2096
Group alert	Standard aircraft lights on	11·4	4·4	12·02770	3·25990	32·9	3·69	0·0008
	Standard aircraft/lights off	7·3	4·4	10·39790	3·25990	32·9	3·19	0·0031
	Predator model	6·3	4·3	−1·91130	3·25990	32·9	−0·59	0·5617
	Standard aircraft lights on × ALI	.	.	−0·00051	0·00253	32·9	−0·20	0·8427
	Standard aircraft lights off × ALI	.	.	−0·00252	0·00253	32·9	−1·00	0·3267
	Predator model × ALI	.	.	0·00679	0·00253	32·9	2·68	0·0114
	Differences in least squares means							
	Standard aircraft lights on vs. Standard aircraft/lights off	.	.	4·07310	1·32980	22·7	3·06	0·0056
	Standard aircraft lights on vs. Predator model	.	.	5·09190	1·52040	35·2	3·35	0·0019
	Standard aircraft lights off vs. Predator model	.	.	1·01870	1·32980	22·7	0·77	0·4515
Log_{10} CV alert	Standard aircraft lights on	31·7	36·2	1·39340	0·51910	33·3	2·68	0·0112
	Standard aircraft lights off	44·0	29·2	0·52100	0·51910	33·3	1·00	0·3228
	Predator model	43·2	40·6	1·28460	0·51910	33·3	2·47	0·0186
	Standard aircraft lights on × ALI	.	.	−0·00023	0·00040	33·3	−0·57	0·5703
	Standard aircraft lights off × ALI	.	.	0·00078	0·00040	33·3	1·94	0·6090
	Predator model × ALI	.	.	0·00004	0·00040	33·3	0·09	0·9266
	Differences in least squares means							
	Standard aircraft lights on vs. Standard aircraft/lights off	.	.	−0·35630	0·22140	19·0	−1·61	0·1240
	Standard aircraft lights on vs. Predator model	.	.	−0·21680	0·24830	35·3	−0·87	0·3885
	Standard aircraft lights off vs. Predator model	.	.	0·13950	0·22140	19·0	0·63	0·5361

*An alert response represented the time (seconds) required for the aircraft to reach the centre of the enclosure (see Fig. 1) from the point at which an individual showed alert behaviour. First alert response was the earliest alert response to the aircraft approach within a group by treatment. Group alert response represented the average of individual alert times within a group by treatment. Log_{10} CV alert represents the base-ten log-transformed coefficient of variation of alert response within group by treatment.
†NOINT (no intercept) option for Proc Mixed used because of over-parameterized default design matrix.
‡d.f. represents Kenward-Rogers approximation of degrees of freedom (SAS/STAT Users Guide Version 8).
§Ambient light intensity (ALI; $\mu mol\ m^{-2}\ s^{-1}$) was measured only once, upon landing of the Standard aircraft after first treatment.

exploiting avian detection and reaction to an approaching aircraft (e.g. ICAO 2009; but see NTSB 2010). Yet, a recent study found morphological evidence that birds that collided with aircraft had tried to avoid them before collision (Bernhardt *et al.* 2010). Our findings on direct aircraft approaches extend previous research showing escape behaviours in birds (Andersen, Rongstad & Mytton 1989; Bélanger & Bédard 1989; Goudie 2006) and mammals (Bleich *et al.* 1994; Born *et al.* 1999; Schnidrig-Petrig & Ingold 2001) in response to approach of aircraft. Overall, the framework of antipredator behaviour theory is clearly relevant to understanding sensory and risk factors involved in bird–aircraft interactions.

Flight responses did not vary significantly between treatment conditions. We attribute this result to the fact that the geese were flightless for at least 2 weeks before the experiment, and confined within an experimental enclosure during the aircraft approach. This combination of factors might have negated attempts at flight in response to aircraft approaches.

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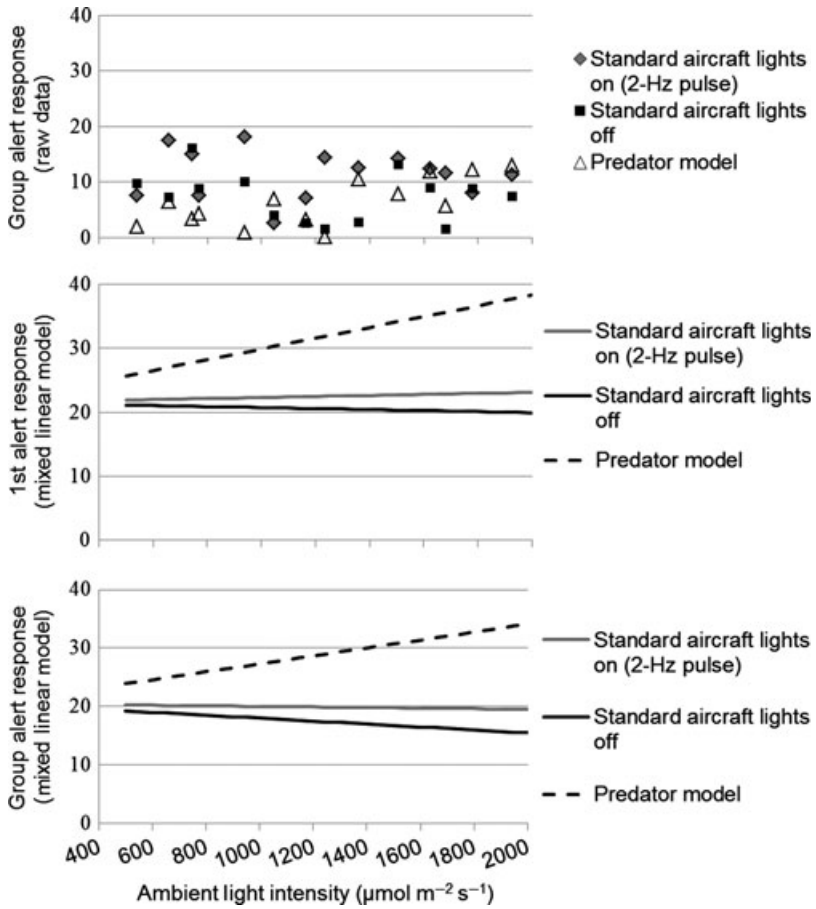

Fig. 2. Group alert response by treatment (raw data) and model estimates (mixed linear model) for first alert and group alert response per treatment (see Appendix S3) by Canada geese to the approach of a standard fixed-wing design, radio-controlled (RC) aircraft (standard aircraft) with lights on or off, and another RC aircraft designed to mimic a raptor (predator model). An alert response represented the time (seconds) required for the aircraft to reach the centre of the enclosure (see Fig. 1) from the point at which an individual showed alert behaviour. First alert response was the earliest alert response to aircraft approach within a group by treatment. Group alert response represented the average of individual alert times within a group by treatment. Greater values for alert metrics represent earlier responses.

Nevertheless, the observed aggregation of the geese in response to aircraft approach offers additional evidence that the aircraft were viewed as potential threats.

APPLIED IMPLICATIONS

Understanding animal sensory ecology and associated behaviours can aid the development of methods specifically intended to exploit certain behaviours to reduce negative human–wildlife interactions; examples include the manipulation of animal resource use and response to disturbance (see Blackwell *et al.* 2009a,b). Our results show the potential of using aircraft lighting to enhance the detection of aircraft by the Canada goose, a species involved in the highest number of strikes reported to the FAA (1990–2010) that resulted in damage to the aircraft (FAA unpublished report). Specifically, a 2-Hz alternating pulse of lights enhanced visibility of an aircraft from the perspective of the Canada goose visual system. Spectral properties of the LEDs that composed the lights for this study can be achieved using available lighting technology for commercial aircraft (e.g. high-intensity discharge lighting), and field tests with commercial carriers could quantify the effectiveness of external lights to reduce the rate of bird strikes.

Our results cannot be generalized easily, as RC aircraft are smaller and slower than civil aircraft, and our geese were not free-ranging birds in flight. Nevertheless, our integration of sensory ecology and animal behaviour in an experimental approach can clearly be used to improve the potential effectiveness of aircraft lighting in the context of bird strikes. For instance, our visual contrast models (parameterized with visual properties of the Canada goose visual system; Appendix S2) can be used to estimate chromatic and achromatic contrasts of lighting with peaks at other wavelengths to which geese are more sensitive. This approach allows the narrowing of light characteristics (e.g. wavelength, pulse frequency, lamp size) that could be tested in controlled and field conditions (e.g. low ambient light) to further enhance aircraft detection and avoidance by birds. For example, findings from the vision model developed herein for the Canada goose (Appendix S2) indicate that to further enhance visibility of aircraft to Canada geese, lighting should peak in the ultraviolet/violet range (380–400 nm; Appendix S4).

Bird strikes are a concern world-wide (Allan 2002; (ICAO 2009). At the airport level, success in reducing bird strikes involves integration of approaches (e.g. FAA 2009; Blackwell *et al*. 2009b), rather than a single method. The same need for integration holds true for the next challenge: to reduce bird strikes in airspace outside of airport property. Over 20% of bird–aircraft collisions reported to the FAA (1990–2010; http://wildlife-mitigation.tc.faa.gov/wildlife/) occurred at altitudes over 762 m above-ground level, thus outside any benefit of bird-management actions on an airport. Dolbeer (2011) specified the level of integration necessary, noting the need for increased efforts to eliminate bird attractants within 8 km of airports, use of recent advances in bird-detecting radar and bird-migration forecasting, as well as research to enhance aircraft detection and avoidance by birds. In essence, environmental policies and wildlife hazard management at the airport level fall short, even with advances in radar and migration forecasting, unless coupled with systems in place on aircraft that are designed specifically to enhance detection and avoidance of approaching aircraft by birds. We contend, therefore, that research directed at using current aircraft systems, such as lighting or possibly even fuselage paint schemes (Fernández-Juricic *et al*. 2011a), to enhance avian alert response to aircraft approach could yield quicker flight responses and a reduced frequency of bird–aircraft collisions.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Animal care and maintenance.

Appendix S2. Calculation of chromatic and achromatic contrast.

Appendix S3. Description of radio-controlled aircraft.

Appendix S4. Determination of chromatic and achromatic contrast of different LED lights based on the Canada goose vision model.

Fig. S1. Irradiance curves used for chromatic and achromatic contrast calculations based on the spectra of commercially available LEDs (CoolLED, Andover, UK).

Fig. S2. Chromatic contrast results (units, just noticeable differences, JND) for LEDs with different peak wavelengths (CoolLED, Andover, UK) under different ambient light conditions: (a) sunny, (b) partly cloudy, and (c) and cloudy.

Fig. S3. Achromatic contrast results (units, just noticeable differences, JND) for LED lights with different peak wavelengths (CoolLED, Andover, UK) under different ambient light conditions: (a) sunny, (b) partly cloudy, and (c) and cloudy.

Table S1. Parameters used to fit the irradiance curves of the LEDs to spectra provided by the product manufacturer (CoolLED, Andover, UK). Shown are peak wavelengths (λ) of LEDs and the SD used for curve fitting.

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