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The effects of radar on avian behavior: Implications for wildlife management at airports

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ABSTRACT

Airports often contain foraging, breeding, and roosting resources for wildlife. Airports also have different types of radars to assist with air traffic control, monitoring weather, and tracking wildlife that could become a risk for collision with aircraft. The effect of radar electromagnetic radiation on wildlife behavior is not well understood. The goal of this study was to determine whether bird behavior is affected by radar in two contexts: stationary radar (e.g., surveillance radar) and approaching radar (e.g., aircraft weather radar). We used brown-headed cowbirds (*Molothrus ater*) as a model species as they are common at airports. We hypothesized that radar challenges attention mechanisms and thus might distract birds from foraging or avoiding threats (i.e. aircraft). In the stationary radar context, we performed one experiment in the summer and one in the winter. In the summer, we found indication of changes in vigilance and movement behaviors during and after exposure to stationary radar. For example, movement rate increased from before to during radar exposure in the summer ($t_{101} = -3.21$, $P = 0.002$). In the winter, we also found that stationary radar increased movement behaviors. In the approaching radar context, we found that birds exposed to an approaching vehicle with radar showed earlier escape responses ($t_{56.3} = -2.66$, $P = 0.010$) or escape flights that dodged sideways more than with the radar off ($t_{41.5} = -2.67$, $P = 0.011$). Taking these findings together, we suggest that birds might avoid stationary radar units, and moving radar units (e.g., aircraft) might enhance escape responses at low vehicle speeds during taxi, but likely not at higher speeds during take-off, landing, and flight.

1. Introduction

Airports utilize a large number of sources of electromagnetic radiation, specifically in the microwave range (Joseph et al., 2012). Radar is a type of microwave that air traffic control and aircraft use for navigation, surveillance, communication, and detection of weather patterns and bird flocks (Huansheng et al., 2010; Joseph et al., 2012; Stimson, 1998). These sources of electromagnetic radiation may make airports areas with high levels of microwaves (Joseph et al., 2012), and have the potential to affect habitat use by birds and/or cause negative consequences at the individual or population levels (Kelly and Allan, 2006). However, little is known about how these microwaves might affect animals. Some studies indicate that even low doses of electromagnetic radiation can have significant effects on many aspects of an organism's ecology (reviewed in Balmori, 2009; Cucurachi et al., 2013; Fernie and Reynolds, 2005) and behavior (Tanner, 1966; Tanner et al., 1967).

Radar is associated with electric and magnetic fields that pulse on multiple time scales simultaneously (Stimson, 1998; Fig. 1a). Microwaves are only emitted for a small percentage, or duty cycle, of the total interpulse period (Fig. 1b). Airports use many X-band radars (Fig. 1a) with microwaves of a frequency that can penetrate skin and muscle tissues to a depth of ~4 mm (National Council on Radiation Protection and Measurements, 1981). This tissue penetration may allow an animal to detect these microwaves through one of two mechanisms: thermoreception (Byman et al., 1986) and auditory detection (Lin, 1978).

Microwaves have been shown to raise body temperature (Byman et al., 1986) and through thermoreception increase the incidence of thermoregulatory behaviors (e.g., gaping, wing spreading, and panting) in birds (Wasserman et al., 1985). Thermoreception of microwaves has also been hypothesized to cause changes in avoidance and dominance behaviors (Wasserman et al., 1984a,b). Pulses of microwaves generate a thermoelastic pressure

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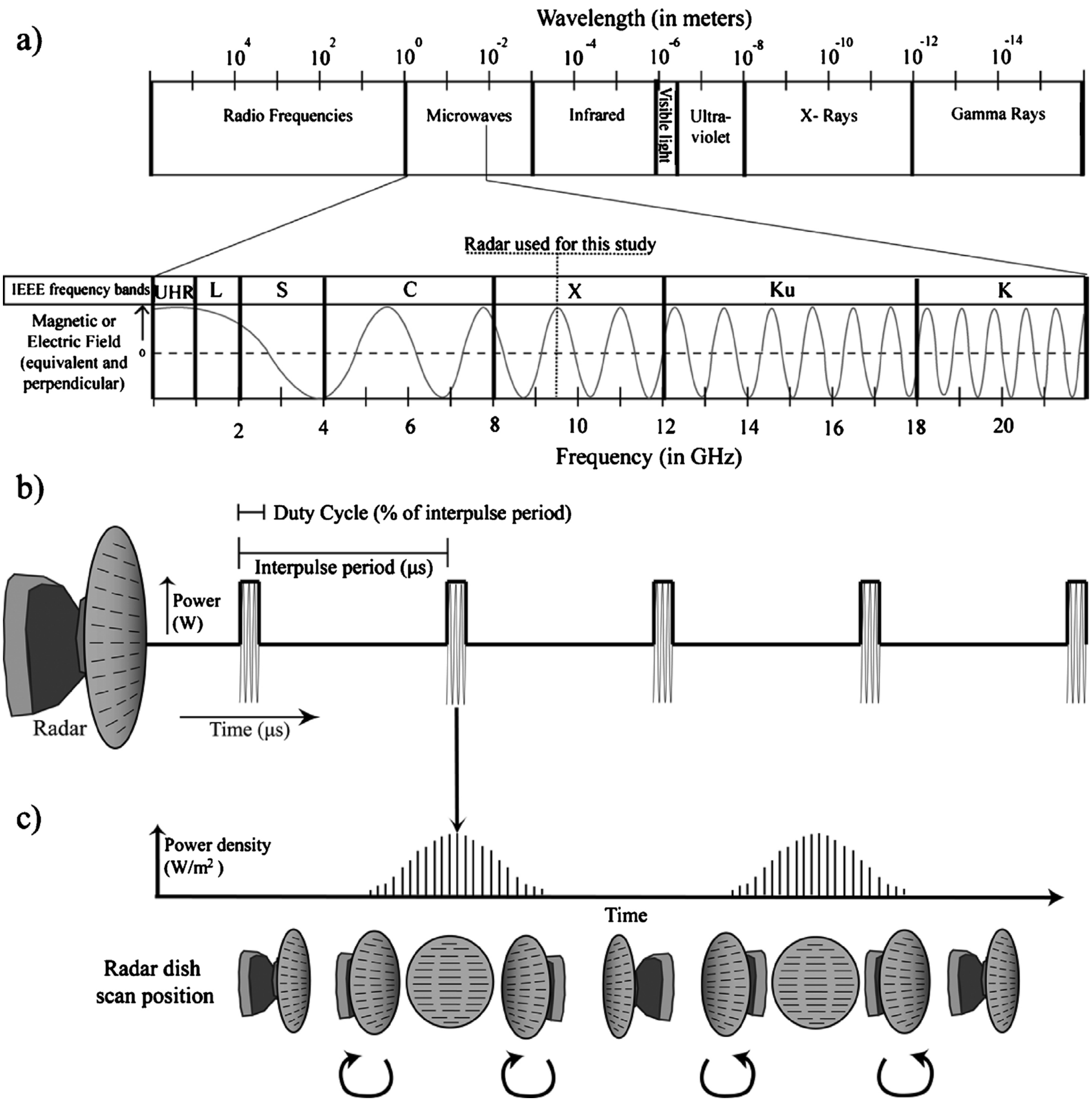

Fig. 1. Properties of radar. (a) The electromagnetic spectrum, with microwaves inset. The frequency of radar used in this study (9.3 GHz) is marked with the dotted line. Also displayed in (a) is the nature of electromagnetic waves, with equivalent and perpendicular magnetic fields, the intensity of which follow the wave pattern of the electromagnetic radiation wavelength. Adapted from Sorrentino and Bianchi (2010). Radar pulses: (b) the peak power emitted per pulse at the antenna, and (c) power density at some distance as transmitted by the antenna. Power density is modulated by the dish or antenna, which rotates to scan up to 180° around it. A single pulse from (b) is displayed as one of the vertical lines in (c). Adapted from Stimson (1998).

wave that is heard as an auditory sound (Lin, 1977), which has been shown in mammals but not in birds (Lin, 1978). In both mechanisms, the intensity of the response is dependent on the power density of the incident microwaves (Lin, 1978; Wasserman et al., 1985).

We investigated how radar affects bird behavior using brown-headed cowbirds (*Molothrus ater*) by simulating two situations in which animals are exposed to radar at airports: stationary (e.g., surveillance radar) and approaching (e.g., aircraft weather radar). Under semi-natural conditions, we investigated the foraging and vigilance behaviors of cowbirds in response to stationary radar in two experiments. In a third experiment, we assessed cowbird escape behavior in response to an approaching threat (vehicle) fitted with radar.

Assuming that birds can detect and process radar microwaves with their sensory systems, we hypothesized that radar increases sensory load and challenges attention mechanisms. Attention is limited (Dukas, 2004), and birds with difficult foraging tasks are less likely or take longer to detect other stimuli (Dukas and Kamil, 2000; Kaby and Lind, 2003). Based on this attention hypothesis, we made a general prediction: radar microwaves would reduce the ability of birds to attend to other sensory tasks. In the stationary radar context (hereafter experiment 1A and 1B), we predicted that birds would forage less during exposure to radar microwaves, as they would attend to radar to the detriment of foraging. In approaching radar context (hereafter experiment 2), we predicted that birds would alert later to and escape later from the approaching threat with radar on. Additionally, we predicted that the direction of the escape flights would be more irregular with the radar on than off, because the intermittent microwaves may cause distraction while in mid-flight. However, we also considered an alternative hypothesis for experiment 2: if radar microwaves attract more attention and/or increase alertness to the threat, then radar may enhance the detection and perception of the approaching stimulus. Hence, we alternatively predicted that birds would respond earlier to the approaching threat with radar on than one with radar off.

In experiment 2 we were able to use two different radar units with different power densities. Therefore, we hypothesized that increased power density would increase the sensory response to the radar (e.g., Wasserman et al., 1985). This enhanced response with power density could apply to both of the previously mentioned hypotheses. If radar distracts attention from the threat, then the radar with higher power density would trigger more irregular flights and delay alert and escape behaviors. If radar increases alertness or attracts attention to the threat, then the radar with the higher power density would trigger earlier alert and escape behaviors.

2. Methods

2.1. Bird capture and maintenance

All procedures were approved by Purdue Animal Care and Use Committee (protocol #1110000081) and the Institutional Animal Care and Use Committee of the United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center (QA-2136). Our study species, the brown-headed cowbird, is commonly found on airport grounds and has been involved in >130 reported bird-aircraft collisions (hereafter, bird strikes) in the past 23 years (Dolbeer et al., 2013). Species belonging to the families *Sturnidae* and *Icteridae*, which includes the brown-headed cowbird (Lowther, 1993), are the second most common avian group involved in bird strikes with civil aircraft (Dolbeer et al., 2013), and among the top five most hazardous groups to military aircraft (Zakrajsek and Bissonette, 2005).

For the stationary radar experiments, we captured 91 brown-headed cowbirds for experiment 1A (72 males and 19 females), and 41 for experiment 1B (all males) using six decoy traps located at the National Aeronautic and Space Administration's (NASA) Plum Brook Station, Erie County, OH, USA (41°22′ N, 82°41′ W). We were unable to capture an even number of males and females for experiment 1A, and we were unable to capture females for experiment 1B. Birds were then transported to and housed in outdoor aviaries (width 2 m × length 2 m × height 3 m) at Purdue University Ross Reserve, West Lafayette, IN, USA (40°24′35″ N, 87°4′2″ W), where the experiments were conducted. Birds were housed for 1.5–3 months before being used in experiments. The enclosures provided areas with shade and wind protection, and contained perches. Animals were housed in groups of 10–20 individuals, and were given equal parts of white millet, game bird chow, and sunflower seeds, and water ad libitum. Food was provided in at least 5 small dishes per enclosure, and water was provided in at least 2 large dishes which were heated to prevent freezing in the winter. Food and water were checked or changed every day, and enclosures were cleaned daily.

For the approaching radar experiment, we captured 116 brown-headed cowbirds (58 males and 58 females) using the same decoy traps in the same location. Birds captured for the approaching radar experiment were kept less than one month prior to the experiments. We housed birds in length 2.4 m × width 2.4 m × height 1.8 m enclosures at the Plum Brook Station in Erie County, OH, USA, where the experiment was conducted. Experiment 2 was conducted at a different location from experiments 1A and 1B due to space requirements, so we will not be comparing data from the two experiments. The animals used for both experiments were, however, trapped at the same location. The enclosures for experiment 2 were located inside an aviary with large, barn-style doors that were opened during the day to allow airflow and light, and with screened windows that were always open. Bird in groups of 20–50 individuals were provided metal perches, and were given white millet, black oil sunflower, and water ad libitum. Food and water were provided in at least 2 large dishes in each enclosure, and were checked or changed daily. Enclosures were cleaned daily.

2.2. Radar units

We used two X-band radar units, both loaned to us by Honeywell International Inc. The first unit was a solid state radar (RDR-4000 Weather Radar System, Honeywell International Inc., Morristown, New Jersey). This radar unit emits in the 9.33–9.38 GHz range, has a maximum duty cycle of 10%, and an average interpulse interval of 100 μs. The antenna has a gain of 35 dBi, nominal peak transmit power of 40 W, and rotates over an angle of 160° at an average rate of 58° s^{-1}. Any single point along the arc of the antenna rotation only experiences radiation from the dish for a small portion of time (Fig. 1c).

The second unit was a magnetron radar (PRIMUS 880 Digital Weather Radar System, Honeywell International Inc.) The magnetron radar emits in the 9.36–9.40 GHz frequency range. However, this unit has a lower duty cycle (0.048%) and shorter interpulse period (2 μs) than the solid state radar. The antenna of the magnetron radar has a gain of 28.5 dBi, and scans at an average rate of 58° s^{-1}. While having a peak power of 10,000 W, the magnetron radar has a power density of approximately 0.27 mW/cm^2 at a distance of 10 m, which is lower than the solid state radar (1.01 mW/cm^2 at 10 m). Overall, the magnetron radar had a higher peak power but a lower power density than the solid state radar. Nevertheless, both units are used in aircraft: the magnetron radar on smaller, business-type jets and helicopters, and the solid state radar on larger commercial airplanes (Levi Bunch, pers. comm.).

2.3. Experiments 1A and 1B: stationary radar

We conducted two stationary radar experiments (hereafter, experiments 1A and 1B), which differed mostly in the types of foraging substrate and the season conducted. In experiment 1A (performed in July 2012), we manipulated the visual saliency of the food items in relation to the visual background. The rationale was to determine if the effects of radar would be more pronounced in the foraging task that required higher attention loads (e.g., lower visual conspicuousness of food) than lower attention loads (e.g., higher visual conspicuousness of food). Because the avian visual system is different from that of humans (Cuthill, 2006), we calculated the perceived chromatic contrast (measured in Just Noticeable Differences or JND) of food in relation to the visual background from the cowbird visual perspective. One JND is a unit of distance in an abstract color space specific to a species' visual system. Lower and higher JND values indicate that an object is less or more conspicuous in relation to the visual background. We used white millet as the food item and sand substrates with different coloration. Chromatic contrast was calculated using the following parameters: (1) spectral properties of ambient light (irradiance), (2) reflectance of the white millet and sand substrates, and (3) sensitivity of the cowbird visual system (Vorobyev and Osorio, 1998).

We used a StellarNet Black Comet portable spectroradiometer (StellarNet, Tampa, Florida) to measure both irradiance and reflectance, as in Moore et al. (2012). Irradiance was measured in several light environments: sunny, cloudy, and shady conditions, as those conditions were all possible at the site of the experimental enclosure. We measured sunny conditions in an open field with <10% cloud cover, cloudy conditions in the same open field with >80% cloud cover, and shady conditions in a closed forest with <10% cloud cover and ~70% foliage cover. We measured the reflectance of the white millet and the substrates. We used three sand colors as the foraging substrates: brown (Light Brown Bottled Sand, Tree House Studio, sku# 551424), red (Red Bottled Sand, Tree House Studio, sku# 553065), and green (Green

Bottled Sand, Tree House Studio, sku# 796342). Finally, we obtained from the literature (Fernández-Juricic et al., 2013) information on cowbird peak sensitivity of visual pigments, absorbance of oil droplets, and relative densities of different photoreceptors. Chromatic contrast was calculated using Vorobyev and Osorio's physiological color opponency model (Vorobyev and Osorio, 1998) in Avicol v5 (Gomez, 2006). The chromatic contrast (in JNDs) of white millet with brown sand in the different light conditions was: sunny = 17.5, cloudy = 17.8, and shaded = 20.2. The chromatic contrast (in JNDs) of millet with red sand in the three light conditions was: sunny = 37.2, cloudy = 37.6, and shaded = 39.6. The chromatic contrast (in JNDs) of millet with green sand in the three light conditions was: sunny = 93.4, cloudy = 93.2, and shady = 93.0. Overall, from the visual perspective of cowbirds, white millet was more salient against the green than the red and the brown backgrounds.

In experiment 1B (conducted in December 2012), we used the same food item (white millet) and a single substrate due to experiment 1A findings (see below): sawdust, sifted to particulates of a similar size to sand. In both stationary radar experiments 1A and 1B, we exposed individuals to the solid state radar which was located outside a visual blind. The radar unit was placed at 5 m (power density in the direct path of the antenna was calculated to be 4.03 mW/cm^2 based on manufacturer specifications) from the enclosure holding the bird because we wanted to use a distance with high chances of detecting behavioral responses to the radar.

In both experiments, the experimental enclosure (width 1 × length 1 × height 0.75 m) was without any metal components that might reflect incident microwaves. This enclosure was in the center of a 10 m × 10 m area surrounded by a 2 m tall black cloth blind. Two Everio video cameras (GZMG750BUS, JCV Kenwood, Yokahama, Japan) filmed the enclosure, one overhead and one from the side. Another Everio camera filmed the dish of the radar. These cameras fed into a multi-channel DVR so that all inputs were recorded in the same video file.

To encourage foraging behavior, we deprived birds of food from 12 to 20 h before the trials (following Fernández-Juricic et al., 2012). We tested for differences in behaviors and body mass in birds with different food deprivation times and found no significant effects (results available upon request). Thus, we had no evidence that individuals with longer deprivation times were adversely affected. Prior to each trial, we scattered 5 g of white millet on to the substrate. At the start of each trial, a single bird was placed in the enclosure and allowed to acclimate for a period of time (2 min in experiment 1A, and 3 min in experiment 1B) after it first pecked. After acclimating, we exposed the bird to a treatment phase of 5 min, during which the radar was either on or off. Finally, there was a 5 min after-treatment phase during which the radar was off. Individuals were only tested once in the enclosure. We measured the body mass of the birds before they were placed in the enclosure. We recorded ambient temperature using a handheld Kestrel 3500 weather meter.

We recorded cowbird behaviors using JWatcher (version 1.0 Blumstein and Daniel, 2007). The two observers (experiment 1A: Melissa Hoover, experiment 1B: Eleanor Sheridan) were trained until they reached an intra- and inter-observer reliability of 95%. All behaviors were considered as mutually exclusive. We recorded the following response variables: (1) peck rate (number of times per min the bill touched the substrate), (2) head up rate (number of times per min the head of the animal moved with the bill parallel to the ground), (3) proportion of time head up, (4) movement rate (number of times per min the bird walked, ran, or flew within the enclosure), (5) proportion of time moving, and (6) maintenance rate. Maintenance rate in experiment 1A was the number of times per minute the bill touched any other part of the body (e.g. preening feathers), and in experiment 1B also included puffing up of feathers, rearranging of wings on the back and whole body shakes. Head up behavior was considered a proxy of vigilance behavior (Fernández-Juricic and Beauchamp, 2008).

We recorded these behaviors over two time scales: experiment-wide scale to assess medium-term responses to radar and 1-min scale to assess more immediate responses to radar. The experiment-wide scale considered all phases of the trial (2 or 3 min before radar exposure, 5 min during radar exposure, and 5 min after radar exposure). At the 1-min time scale, we considered the bird responses at radar onset and offset. Radar *onset* was one minute before and one minute after the radar was turned on. Radar *offset* was one minute before and one minute after the radar was turned off.

2.4. Experiment 2: approaching radar

We performed this experiment in June and July 2013, and deprived birds of food from 12 to 20 h before each trial to encourage foraging. For this experiment, we also compared the behaviors of birds with different food deprivation times and found no significant effects. Before the trials, we moved birds to a holding location near the experimental site in width 0.5 m × length 0.6 m × height 0.3 m enclosures, where we provided water ad libitum but no food (for 0:30–5:30 h). This holding location was visually obscured from all parts of the vehicle approach and was not under the influence of the experimental microwaves, which we measured with a High Frequency Analyzer (Gigahertz solutions, Fürth, Germany).

For the vehicle approach, we used a white 2011 4 × 4 supercab Ford F-150 (Ford Motor Company, Dearborn, Michigan), which was initially parked 225 m away from the experimental enclosure. The radar was installed on the roof of the truck over the cab, bolted to a wooden platform attached to a roof rack and powered by a Troy-Bilt 5550 watt portable generator (Valley City, OH) in the bed of the truck. The radar dish was shielded from the wind with a panel of fiberglass reinforced plastic, which also blocked the movements of the radar dish from being visible to the birds, making the approach of the truck visually identical for all radar treatments. The truck headlights were also blocked for all trials so that no light cue was available to the animals. For this experiment, we used two radar units: the solid state radar and the magnetron radar. The radar treatment levels were: (1) radar off (the generator on the truck was running but both radar units were off), (2) magnetron radar (with the solid state unit off and the magnetron unit on), and (3) solid state radar (with the magnetron unit off and the solid state unit on). The assignment of the radar treatments was random.

The experimental enclosure was semicircular with a radius of 2 m and a height of 1 m. The floor of the experimental enclosure was green artificial turf approximately 2.5 cm high. The mesh of the enclosure was plastic netting with a mesh of 1.3 cm^2 with a PVC frame. A food dish containing ∼0.5 L white millet and black oil sunflower seeds was 10 cm from the front edge of the enclosure in the center. The top of the back, semicircular edge of the enclosure had strands of artificial, leafy vegetation attached 10 cm below the roof of the enclosure. The vegetation covered 12–20 cm of the outer wall of the enclosure. This vegetation provided refuge for escape (similar to Morgan and Fernández-Juricic, 2007).

Two JVC Everio (GZ-MG330AU, JCV Kenwood, Yokahama, Japan) cameras filmed the behavior of the birds from the right and left sides of the experimental enclosure. Two EverFocus security cameras (EZ700W-001, Everfocus Electronics, Taipei, Taiwan) filmed the enclosure from overhead. These overhead cameras (3.3 m high) were placed 1.3 m apart to allow each camera to view the entire base of the experimental enclosure. Two additional JVC Everio cameras filmed the approach path of the truck at the start line of 210 m from the enclosure and at 30 m from the front edge of the enclosure. For diagrams of the experimental enclosure and camera locations see Appendix Fig. 1. All six cameras were recorded onto a Night

Owl H.264 DVR (Night Owl Security, Gray, Tennessee). All channels recorded at a resolution of 704 × 240 pixels and at 30 frames/s. An observer behind the screen observed the videos of the birds during each experiment.

At the start of a trial, the truck was parked behind the start line with the generator on (irrespective of the treatment) while we measured wind speed, temperature, and humidity at the rear of the enclosure. We also measured light intensity with a portable digital lux meter (401025, Extech Instruments, Nashua, New Hampshire). Afterwards, two birds (one male and one female) were released into the enclosure. We used pairs of birds for this experiment to help increase sample size and because brown-headed cowbirds are often found in flocks when foraging in fields like those near airport runways (Lowther, 1993). The birds were allowed to acclimate to the enclosure for at least 3 min without any disturbance. If the birds had been foraging for at least 30 s during those 3 min, the observer signaled to the truck driver to start the treatment exposure. If not, the birds were allowed to acclimate until they had foraged constantly for at least 30 s for up to 15 min. If the birds did not forage after 15 min, the trial was stopped and the birds were removed from the enclosure. If the birds successfully foraged, the truck driver would start the approach with a given treatment. However, to apply the radar treatments, the driver had to exit the vehicle at the start line after the birds were released in the enclosure. To eliminate differences between the treatments, the driver exited the vehicle with the same motions for all treatments, including the radar off treatment, before starting an approach. Pairs of birds were only used once and were therefore only exposed to one of the radar treatment levels.

The driver accelerated the truck to a speed of 6.7 m s^{-1} before reaching the 210 m start line and then maintained a speed of 6.765 ± 0.002 m s^{-1} until 8 m from the experimental enclosure, at which point the driver braked to stop at least 2 m from the front of the enclosure (see Appendix Fig. 1b). A High Frequency Analyzer (HFW59D, Gigahertz solutions, Fürth, Germany) was monitored by the observer behind the screen during the approach to ensure that the radar was functioning properly. If the radar turned off or stopped working before the birds completed their escape flights, that trial was not used.

We measured the following behaviors: alert distance (AD), flight initiation distance (FID), angle of diversion, vertical take-off angle, and sinuosity. We recorded all behaviors separately for each of the two birds in the experimental enclosure for each approach. We measured the time of the first frame when the animal displayed alert and flight behaviors. An alert behavior was defined as a change in behavior or the rate of a behavior from the baseline, such as moving from a head down to a head up position, stretching the neck up, crouching, and freezing. A flight was defined as a walk or run away from the approaching vehicle, or a flight recorded the moment the animal began pushing off the ground. While we attempted to maintain a constant vehicle speed for all approaches, there was some measurable variation in vehicle speed that we included in our calculations. We calculated the vehicle speed by taking the distance between the cameras filming the vehicle approach and dividing it by the time it took the vehicle to travel that distance. We determined the time at which the vehicle would have collided with the enclosure, and measured the difference between that time and the time the animal displayed an alert or flight behavior. To measure the AD and FID, we multiplied that time by the speed of the vehicle.

We measured the variables of angle of diversion, vertical take-off angle, and sinuosity using stereo triangulation based on the position of the bird bills in two calibrated cameras. This process was completed in MATLAB (R2012a) using the Calibration Toolbox for MATLAB (http://www.vision.caltech.edu/bouguetj/calib_doc/index.html, Bouguet, n.d.) and is detailed in Appendix 1. The output of this method is the three dimensional position of the bill in each frame of flight relative to a constant reference point. The start of flight was the three dimensional position of the bill of the animal in the frame before it spread its wings to fly. The small size of the enclosure seemed to encourage some animals to change direction sharply (>90°) once near a portion of the vegetative cover. We only used the flights before this change in direction, if present. If there was no sharp change in direction, we used the flight until the bird crossed the outside, bottom edge of the enclosure in the view of either overhead camera. We measured the angle of diversion from the path of the vehicle by comparing the direction of the flight to the direction of the vehicle approach (°). We measured the vertical take-off angle (°) when the animal passed 50 cm from the start of flight. A distance of 50 cm was chosen because it was within the range of distances used to measure take-off angle in other studies (Kullberg et al., 1998; Lind et al., 2002). We measured the vertical take-off angle by measuring the angle (°) of the flight compared to a line at the level of the bird bill at the start of flight, parallel to the ground. Sinuosity is a measure of the directness of the flight, and was calculated by dividing the sum of the distances traveled by the distance from the start to the end of the flight (unitless, with 1 indicating a direct flight of a straight line and values >1 indicating increasingly less direct flights). Descriptions of all the dependent variables can be found in Appendix 1.

2.5. Statistical analysis

In the stationary radar experiments, we used general linear mixed models (using SAS 9.3). We first used a full model in which we included radar exposure, ambient temperature, body mass, and, in experiment 1A, substrate color as between-subject factors. We did not include sex as a factor, because in experiment 1A the sexes were imbalanced and confounded with body mass, and in experiment 1B we were unable to catch an adequate number of females to include in the experiment. The within-subject factor was individual identity. At the experiment-wide scale, there were three levels of radar exposure: before, during, and after exposure to the radar. At the 1-min scale at radar onset, radar exposure had two levels: the minute before and the minute after the radar was turned on. At the 1-min scale at radar offset, radar exposure had two levels: the minute before and the minute after the end of the radar exposure. We also used a reduced model, from which we removed factors other than radar exposure and substrate that were not significant in the full model. We compared the fit of the full vs. the reduced models with AIC and reported results from the model with the lowest AIC values that still maintained all significant factors. For all analyses, we used the following dependent variables: peck rate, head up rate, proportion of time head up, maintenance rate, movement rate, and proportion of time moving.

In the approaching radar experiment, we used general linear mixed models (using SAS 9.3) to analyze the dependent variables: AD, FID, angle of diversion, vertical take-off angle, and sinuosity. In the full model, we included radar treatment (radar off, magnetron radar, and solid state radar) and sex as categorical factors and ambient light intensity and speed of the truck as continuous factors. We used sex, as we did not have body mass measurements but were able to capture equal numbers of males and females for experiment 2. Trial was included as a repeated-measures random factor, because in each trial two birds were exposed to the same approaching vehicle and all behaviors were recorded for both birds separately. We also used a reduced model from which we removed non-significant factors other than radar treatment. We compared the fit of the full versus the reduced models and reported the one with the lowest AIC values that still maintained all significant factors. Models with sinuosity as a dependent variable did not converge due to rounding errors with light intensity, so we scaled light intensity in that model by dividing by 1000.

For all models (both stationary and approaching radar experiments), we used the Kenward–Rodgers degrees of freedom estimation method and restricted maximum likelihood estimation method. We checked all variables for normality, and log transformed those variables that were not normal. All results presented are the untransformed least squares means ± standard error. For the independent variables of time period (before, during, and after radar exposure) and radar treatment (radar off, magnetron radar, and solid state radar), we used pairwise comparisons (*t*-tests) to determine differences between treatments. We used a value of $P = 0.05$ as our significance threshold.

3. Results

3.1. Experiments 1A and 1B: stationary radar

In experiment 1A, we found some significant changes at the experiment-wide scale (i.e., when comparing the whole periods of before, during, and after radar exposure). The head-up rate and proportion of time head-up significantly changed with radar exposure (Table 1, Fig. 2). Both head-up rate (Fig. 2a) and proportion of time head-up (Fig. 2b) decreased from before to during radar exposure (head up rate: $t_{103} = 3.07$, $P = 0.003$, proportion of time head up: $t_{103} = 2.4$, $P = 0.018$), but did not differ during and after radar exposure (head up rate: $t_{103} = 1.58$, $P = 0.116$, proportion of time head up: $t_{103} = 1.26$, $P = 0.211$) (Fig. 2a and b). Experiment-wide, radar exposure significantly influenced cowbird movement rate and proportion of time moving (Table 1, Fig. 2). Individuals had higher movement rate (Fig. 2c) and proportion of time moving (Fig. 2d) during radar exposure compared to before radar exposure (movement rate: $t_{101} = -3.21$, $P = 0.002$, proportion of time moving: $t_{103} = -4.13$, $P < 0.001$), but the variation between during and after radar exposure was not significant (movement rate: $t_{101} = -0.08$, $P = 0.934$, proportion of time moving: $t_{103} = -0.64$, $P = 0.522$) (Fig. 2c and d). Body mass had a significant effect on several behaviors experiment-wide (Table 1): proportion of time head-up increased with body mass (coefficient 0.0027 ± 0.0011, $t_{46} = 2.38$, $P = 0.022$), and movement rate decreased with body mass (coefficient -0.0035 ± 0.0013, $t_{44.3} = -2.65$, $P = 0.011$). Peck rate also decreased with body mass (coefficient -0.003 ± 0.0012, $t_{45.6} = -2.52$, $P = 0.015$). Substrate color did not have a significant effect on any behavior (Table 1).

In experiment 1A, at the 1-min time scale, at radar onset there were no significant changes in any behavior (Table 2). Additionally, substrate color did not affect any of the measured behaviors at radar onset (Table 2). Body mass and ambient temperature also did not have any significant effects, and were therefore removed from the model (Table 2). In experiment 1A at radar offset, there were also no significant changes in behavior (Table 2). Peck rate decreased with body mass at radar offset in experiment 1A (coefficient -0.005 ± 0.001, $t_{40.7} = -3.51$, $P = 0.001$) (Table 2). Substrate color did not significantly affect any behavior at radar offset (Table 2).

In experiment 1B, there was a significant decrease in peck rate experiment-wide (Table 1), but this decrease in peck rate was only significant from before (16.3 ± 1.2 pecks min^{-1}) to after (10.1 ± 1.0 pecks min^{-1}) exposure to the radar ($t_{36.4} = 2.97$, $P = 0.005$). Peck rate during radar exposure (12.1 ± 1.1 pecks min^{-1}) did not differ from either before radar exposure ($t_{36.1} = 1.95$, $P = 0.059$) or after radar exposure ($t_{36.1} = 1.04$, $P = 0.304$). We did not find significant changes experiment-wide in head-up rate, proportion of time head-up, movement rate, or proportion of time moving (Table 1). Experiment-wide, proportion of time head up significantly increased (Table 1) with body mass (coefficient 0.025 ± 0.011, $t_{17} = 2.24$, $P = 0.038$). Ambient temperature did not have a significant effect on any behavior experiment-wide and was therefore removed from the reduced models (Table 1).

In experiment 1B, on the 1-min time scale at radar onset, movement rate significantly increased (Table 2) from before (11.9 ± 1.8 movements min^{-1}) to after (22.2 ± 2.1 movements min^{-1}) radar onset. Body mass and ambient temperature did not significantly affect any behavior at radar offset in experiment 1B and were removed from the models (Table 2). Radar offset did not significantly affect any behavior in experiment 1B (Table 2). In experiment 1B, on the 1-min time scale at radar offset, peck rate decreased with body mass (coefficient -0.027 ± 0.012, $t_{17} = -2.24$, $P = 0.039$) and head up rate increased with body mass at radar offset in experiment 1B (coefficient 0.036 ± 0.016, $t_{16} = 2.31$, $P = 0.035$; Table 2). Ambient temperature did not have a significant effect on any behavior at radar offset in experiment 1B and was removed from the models (Table 2).

3.2. Experiment 2: approaching radar

We did not find significant effects of radar on alert distance (AD, Table 3), but we found significant effects of radar treatment on flight initiation distance (FID) (Table 3; Fig. 3a). Birds exposed to the solid state radar had a greater FID than birds exposed to either the magnetron radar (FID: $t_{55.6} = -2.1$, $P = 0.040$) or the radar off (FID: $t_{56.3} = -2.66$, $P = 0.010$). This means that birds exposed to the solid state radar escaped earlier to the vehicle approach than birds in either the magnetron radar or radar off treatment. Vehicle speed, light intensity, and sex did not significantly affect AD or FID, but models with some or all of these factors had the best fit (i.e., lowest AIC values, Table 3).

Radar treatment also had a significant effect on the angle of diversion (Table 3; Fig. 3b). Cowbirds exposed to the magnetron radar diverged more from the path of the truck than cowbirds in the radar off group ($t_{41.5} = -2.67$, $P = 0.011$), whereas the solid state radar did not differ from either the magnetron radar ($t_{42.0} = 1.15$, $P = 0.257$) or radar off treatments ($t_{42.2} = -1.13$, $P = 0.266$) (Fig. 3b), indicating that cowbirds in the magnetron radar treatment flew more perpendicular to the approaching truck than the radar off treatment. Light intensity also had a significant effect on the angle of diversion (Table 3), with cowbirds diverging more from the path of the vehicle when light intensity was higher (coefficient 0.0004 ± 0.0001, $t_{39.8} = 3.09$, $P = 0.004$). Sex and vehicle speed did not affect the angle of diversion significantly but models with these variables had a better fit (i.e., lower AIC values, Table 3).

Radar treatment did not have an effect on the vertical take-off angle or on the sinuosity of flights (Table 3). However, sex did have an effect on vertical take-off angle (Table 3): males took off more steeply ($59.6 \pm 2.1°$) than females ($53.5 \pm 2.0°$). Vehicle speed and light intensity did not affect take-off angle, but the model including vehicle speed had the best fit in terms of AIC values (Table 3). Sex also had an effect on flight sinuosity (Table 3), with males having more sinuous or less direct escape flights (1.20 ± 0.01) than females (1.15 ± 0.01). Vehicle speed had a significant effect on sinuosity (Table 3), with sinuosity increasing with vehicle speed (coefficient 0.141 ± 0.064, $t_{47.5} = 2.19$, $P = 0.034$).

4. Discussion

With both the stationary and approaching radar experiments, we found some behavioral responses of cowbirds that could be associated with the presence of radar. In the stationary radar experiments, we found that birds moved more and decreased vigilance behaviors when exposed to radar, although other behaviors were not significantly affected. This did not follow our prediction that birds would decrease foraging and increase vigilance in response

Table 1
General linear mixed model showing foraging and vigilance behaviors at the experiment-wide scale of both the stationary radar experiments 1A and 1B (see text for details). AIC values for models with all covariates (full model) and models with non-significant terms removed (reduced model) are shown for comparison. Bolded AIC values indicate the model used. Periods of radar exposure are before, during, and after radar exposure. Levels of substrate color are brown, green, and red. Significant values are displayed in bold.

	Full model AIC	Reduced model AIC		$F_{d,f}$	P
Experiment 1A					
Peck rate (log)	−460.5	**−470.3**	Radar exposure	$2.18_{2,103}$	0.118
			Substrate	$0.07_{2,53.9}$	0.933
			Body mass	$6.35_{1,45.6}$	**0.015**
Head up rate	2.2	**−11.7**	Radar exposure	$11.2_{2,103}$	**<0.0001**
			Substrate	$2.27_{2,61.4}$	0.112
Proportion of time head up (log)	−566.5	**−577**	Radar Exposure	$6.9_{2,103}$	**0.002**
			Substrate	$0.33_{2,61.9}$	0.720
			Body mass	$5.67_{1,46}$	**0.022**
Maintenance rate (log)	−1174	**−1204**	Radar exposure	$0.21_{2,102}$	0.809
			Substrate	$1.19_{2,48.9}$	0.313
Movement rate (log)	−489.9	**−498.6**	Radar exposure	$7.04_{2,101}$	**0.001**
			Substrate	$1.77_{2,56.2}$	0.181
			Body mass	$7.04_{1,44.3}$	**0.011**
Proportion of time moving	−536.3	**−555.9**	Radar exposure	$13.4_{2,103}$	**<0.0001**
			Substrate	$0.86_{2,60.4}$	0.430
Experiment 1B					
Peck rate (log)	−135.7	**−152.6**	Radar exposure	$4.5_{2,36.2}$	**0.018**
Head up rate	−8.1	**−17.8**	Radar exposure	$3.11_{2,36.2}$	0.057
Proportion of time head up	−55.6	**−62.8**	Radar exposure	$0.68_{2,36.1}$	0.513
			Body mass	$5.04_{1,17}$	**0.038**
Maintenance rate (log)	−428.9	**−459.2**	Radar exposure	$0.04_{2,36.7}$	0.962
Movement rate	−55.1	**−68.3**	Radar exposure	$1.96_{2,36.3}$	0.155
Proportion of time moving	−91.5	**−105.9**	Radar exposure	$2.97_{2,36.4}$	0.064

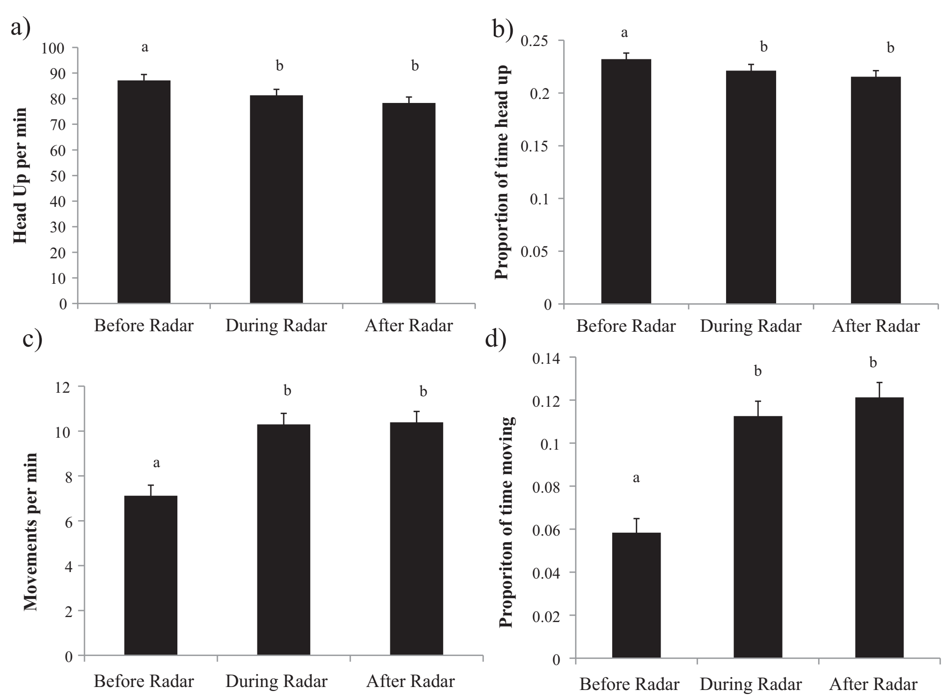

Fig. 2. Significant changes in (a) head up rate, (b) proportion of time head up, (c) movement rate, and (d) proportion of time moving at the longer time scale in the stationary radar experiment 1A. The significant changes were from before to during and after radar, with behaviors being similar during and after radar. Letter superscripts indicate statistical differences.

to radar. In the approaching radar experiment, we found that cowbirds responded earlier to approaches with the solid state (more powerful) radar, and diverged more from the path of the approaching vehicle with the magnetron radar (less powerful). This followed the predictions of our alternative hypothesis that radar increases alertness or attention to a threat.

In the stationary radar experiment 1A, we did not find effects of the substrate color on any behavioral response, which suggests

Table 2
General linear mixed model showing how radar onset and offset affect foraging and vigilance behaviors in both the stationary radar experiments 1A and 1B, at the 1-min scale (see text for details). AIC values for models with all covariates (full model) and models with non-significant terms removed (reduced model) are shown for comparison. Bolded AIC values indicate the model used. Levels of radar are before and after the radar is turned on. Levels of substrate color are brown, green, and red. Significant values are displayed in bold.

	Onset					Offset				
	Full model AIC	Reduced model AIC		$F_{d.f}$	*P*	Full model AIC	Reduced model AIC		$F_{d.f}$	*P*
Experiment 1A										
Peck rate (log)	−220.3	**−237.1**	Radar	$0.04_{1,52.1}$	0.835	−250.5	**−259.4**	Radar	$0.14_{1,50}$	0.709
			Substrate	$0.38_{2,50.2}$	0.683			Substrate	$0.49_{2,45.7}$	0.617
								Body mass	$12.3_{1,40.7}$	**0.001**
Head up rate	87.3	**75.3**	Radar	$0.78_{1,49.2}$	0.381	65.1	**52.1**	Radar	$1.14_{1,51}$	0.284
			Substrate	$1.33_{2,48.8}$	0.273			Substrate	$2.14_{2,54.6}$	0.124
Proportion of time head up	−41.3	**−55.1**	Radar	$0.05_{1,51.4}$	0.817	−47.8	**−56.4**	Radar	$1.04_{1,48.8}$	0.312
			Substrate	$0.75_{2,50.8}$	0.477			Substrate	$1.46_{2,53.5}$	0.241
Maintenance rate (log)	−635.2	**−661.9**	Radar	$0.6_{1,51.3}$	0.444	−609	**−637.7**	Radar	$1.00_{1,46.1}$	0.323
			Substrate	$0.71_{2,63.7}$	0.494			Substrate	$1.02_{2,38.4}$	0.371
Movement rate (log)	−270.7	**−288**	Radar	$0.5_{1,51.5}$	0.482	−254.6	**−271.1**	Radar	$0.14_{1,42.9}$	0.706
			Substrate	$0.26_{2,53.8}$	0.775			Substrate	$2.96_{2,47.5}$	0.062
Proportion of time moving (log)	−301.5	**−321.4**	Radar	$0.17_{1,51.3}$	0.678	−267.4	**−285.1**	Radar	$0.16_{1,48.3}$	0.688
			Substrate	$0.77_{2,51}$	0.468			Substrate	$1.65_{2,50}$	0.202
Experiment 1B										
Peck rate	8.8	**−3.6**	Radar	$0.24_{1,18}$	0.632	−4.9	**−12.2**	Radar	$0.39_{1,18}$	0.539
								Body mass	$5.02_{1,17}$	**0.039**
Head up rate	−0.6	**−13.7**	Radar	$0.41_{1,18}$	0.532	**10**	–	Radar	$0.18_{1,18}$	0.674
								Body mass	$5.32_{1,16}$	**0.035**
								Temperature	$4.3_{1,16}$	0.055
Proportion of time head up	−17.2	**−29.3**	Radar	$3.07_{1,18}$	0.097	−11.4	**−21.1**	Radar	$1.54_{1,18}$	0.230
Maintenance rate (log)	−181.4	**−205.9**	Radar	$0.16_{1,18}$	0.691	−187.1	**−212.4**	Radar	$0.02_{1,18}$	0.898
Movement rate	−40.1	**−54.1**	Radar	$6.74_{1,18}$	**0.018**	−77.3	**−93.7**	Radar	$0.47_{1,18}$	0.503
Proportion of time moving (log)	−138.2	**−158.1**	Radar	$4.19_{1,18}$	0.056	−98.4	**−116**	Radar	$1.26_{1,18}$	0.277

Table 3
General linear mixed model showing the alert distance (AD), flight initiation distance (FID), vertical take-off angle, angle of diversion, and sinuosity of cowbirds in response to an approaching vehicle with the three radar treatments: radar off, solid state radar, and magnetron radar. AIC values for models with all covariates (full model) and models with non-significant terms removed (reduced model) are shown for comparison. Bolded AIC values indicate the model used. Significant values are displayed in bold.

	Full model AIC	Reduced model AIC		$F_{d,f}$	P
Alert distance (AD)	**1037.2**	1066.3	Radar treatment	$0.61_{2,49.5}$	0.547
			Sex	$0.25_{1,50.3}$	0.620
			Vehicle speed	$0.47_{1,46.1}$	0.496
			Light intensity	$1.14_{1,47.8}$	0.291
Flight initiation distance (FID) (log)	72.4	**67.7**	Radar treatment	$3.72_{2,54.9}$	**0.031**
			Vehicle speed	$0.64_{1,55}$	0.428
			Light intensity	$0.75_{1,54.1}$	0.389
Vertical take-off angle	740.7	**732.8**	Radar treatment	$1.8_{2,45.6}$	0.176
			Sex	$6.86_{1,43.7}$	**0.012**
			Vehicle speed	$0.0_{1,47.9}$	0.998
Angle of diversion	**800.7**	808.8	Radar treatment	$3.58_{2,41.9}$	**0.037**
			Sex	$1.69_{1,40.2}$	0.201
			Vehicle speed	$0.2_{1,44.5}$	0.660
			Light intensity	$9.55_{1,39.8}$	**0.004**
Sinuosity (log)	−**164.3**	–	Radar treatment	$0.43_{2,44.6}$	0.652
			Sex	$6.11_{1,48.9}$	**0.017**
			Vehicle speed	$4.79_{1,47.5}$	**0.034**
			Light intensity	$3.99_{1,42.7}$	0.052

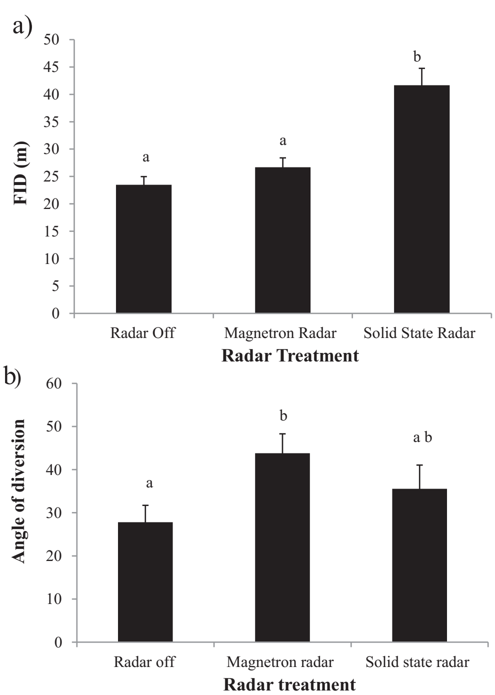

Fig. 3. FID and flight direction in response to an approaching vehicle with one of three radar treatments: radar off, magnetron radar on (low power density) and solid state radar on (high power density). (a) The flight initiation distance in response to an approaching vehicle, with larger distances indicating a flight earlier in the vehicle approach. (b) The angle of diversion from the path of the approaching vehicle, measured at the end of the initial flight to cover. Letter superscripts indicate statistical differences.

that the degree of visual conspicuousness of the food items did not influence foraging behaviors. Previous work (e.g., Siddiqi et al., 2004) has set a range (1–4 JNDs) at which items are difficult to discern from the background. In our study, the visual contrast of the seeds was much higher than 4 JNDs. It is possible that we did not find significant effects of substrate color on foraging behavior because the foraging task was not visually challenging enough.

In the stationary radar experiment 1A, we found that cowbirds scanned less and moved more during radar exposure at the experiment-wide scale, but this effect was not reversed after radar exposure. In experiment 1B, we also observed an increase in movement rate, this time at the 1-min scale at radar onset. Birds may have been moving within the enclosure to avoid the microwaves as the antenna scanned the enclosure. This finding is similar to that of Wasserman et al. (1984a), where blue jays avoided portions of enclosures with microwaves. However, this result cannot explain the continuation of higher movement rates in the period after radar exposure. A decrease in vigilance behavior could have been caused by habituation to the enclosure after the first 2 min (see Fernández-Juricic et al., 2013). Factors other than radar exposure, such as food depletion after the first couple of minutes could also have led to increased movement rates as birds searched in the enclosure for food (Krebs et al., 1974). However, no bird consumed more than 25% of the food provided in each trial. We also found that peck rate decreased with body mass, similar to previous studies (e.g.; Lewis and Dougherty, 1992; Fernández-Juricic and Beauchamp, 2008).

In the approaching radar experiment, we did not find a significant effect of either radar treatment on alert distance, maybe because birds were alert to the vehicle before we could begin recording alert behaviors or the birds were alert but we could not detect overt behaviors. Nevertheless, there was a significant effect of radar on flight initiation distance. Contrary to our predictions based on limited attention, we found that with the solid state radar birds escaped earlier, allowing birds more time to maneuvre out of the path of an approaching vehicle. This result supports our alternative hypothesis, that radar increases alertness or attracts attention to the approaching threat. Greater attention directed toward the radar could change the assessment of the threat, which is one of the behavioral steps at which an animal can modify to avoid collision with a vehicle (Lima et al., 2014). There have been many studies showing that animals can evaluate threats and change flight initiation distance accordingly (reviewed by Stankowich and Blumstein, 2005). Cowbirds and white-tailed deer (*Odocoileus virginianus*) have also been shown to modify behavioral response times in response to vehicle approaches similar to the one used in this study (Blackwell et al., 2014, 2009b; Blackwell and Bernhardt, 2004; Blackwell and Seamans, 2009; DeVault et al., 2014). Overall, if the radar treatment enhances the perceived risk of the approaching vehicle, this could lead to earlier escape responses (Ydenberg and Dill, 1986; Cooper and Blumstein, 2013).

The other significant effect of the approaching radar, the increased angle of diversion in the magnetron radar treatment, could be interpreted as the bird maneuvring to avoid a collision. Diversions from the direction of approach of a threat have also been documented in response to raptor predator models (Devereux et al., 2008; Kullberg et al., 2000; Lind et al., 2002, 2003). We propose that in our experiment where birds were in the center of a road, escape flights could vary between two extremes: birds flying away from the road (more perpendicular to the vehicle approach) and birds flying along the road in front of the vehicle (parallel to the vehicle approach) (similar to findings from Husby and Husby, 2014). For the animal to avoid a collision when flying away from the road, it would only have to travel part of the width of the vehicle (2.0 m). On the other hand, to avoid collision while flying along the road, the animal would have to rise over top of the vehicle (a 3.1 m height). Flying away from the road would have the shortest distance to travel to escape collision, whereas flying along the road would have the longest. Because birds in the magnetron radar treatment had a greater angle of diversion, they flew more perpendicular to the vehicle approach and therefore shorter distances away from the vehicle. This result could also support our alternative hypothesis that radar increases alertness or attracts attention to the threat, making the threat seem riskier, as birds chose shorter escape directions when exposed to the magnetron radar.

Although we did not find significant effects of radar on sinuosity or vertical take-off angle, we did find that males and females differed for these two variables. Males took off more steeply and flew with more sinuous flights than females. It has been hypothesized that in the context of initiating escape flights, prey should optimize acceleration (i.e., lower take-off angles) or maneuverability (i.e., steeper take-off angles) depending on predator attack speed and distance (Howland, 1974; Witter and Cuthill, 1993). This trade-off between acceleration and take-off angle has been demonstrated by Kullberg et al. (1998), and male and female cowbirds may optimize acceleration versus take-off angle differently. Our results seem to indicate that males, having greater body mass (Lowther, 1993) and likely muscle mass, are optimizing maneuverability in escape flights, and females are optimizing acceleration. This result is opposite to that of previous studies: take-off angles generally decrease with increased body mass (Kullberg et al., 1996; Lind et al., 1999; Witter et al., 1994). Our findings could instead indicate that the sexes have different escape strategies. Males seemed to be dodging and outmaneuvering the approaching threat, but females seemed be accelerating in a more direct path, possibly as if toward nearby cover (Kullberg and Lafrenz, 2007; Witter and Cuthill, 1993).

There are different ways that the two mechanisms of detecting microwaves could explain why the solid state and magnetron radars affected behaviors differently. Through the thermoreception of microwaves, the difference in power density of the two radars could be the reason the solid state radar (higher power density) increased FID while the magnetron radar (lower power density) did not. Higher power densities are more likely to raise the temperature of tissues and alter behavior (Wasserman et al., 1985). Through the hearing of microwave pulses as summarized in Lin (1978), a difference in the intensity of the sound produced could possibly explain why we observed a significant effect of the magnetron radar on angle of diversion. The two radars we used had different interpulse intervals and energy per pulse, and these differences could have produced a different intensity of sound from the magnetron radar (Lin, 1978). To our knowledge, a vital part of this mechanism, bone conduction of sound, has yet to be documented in birds (but see Schwartzkopff, 1955). In mammals, however, measurable vibrations at the round window have been produced by the bone conduction of sounds from microwave pulses (Chou et al., 1975).

4.1. Applied implications

The effects of radar on bird behavior could potentially be applied to the management of birds at airports, where electromagnetic radiation levels are high. Airports are locations where human-wildlife interactions are tightly managed (Cleary and Dolbeer, 2005; DeVault et al., 2013). Bird strikes are of conservation concern for threatened/endangered bird species (Blackwell et al., 2009a) as well as a safety and monetary concern for the aviation industry (Dolbeer et al., 2013). To mitigate this problem, many airports employ wildlife control techniques that involve removing attractive habitats for breeding or foraging, trapping and removal of wildlife, wildlife repellents, and in some cases lethal control (Cleary and Dolbeer, 2005; DeVault et al., 2013; Hesse et al., 2010). The changes in behaviors we observed could be used to inform wildlife control techniques on airports.

We found some evidence that stationary radar changes movement behaviors. These increased movements may be an indication that birds were attempting to avoid radar microwaves, as in Wasserman et al. (1984a). There are also studies on other frequencies of electromagnetic radiation over much longer time periods that showed population declines and changes in the distribution of species during the breeding season (Balmori and Hallberg, 2007; Everaert and Bauwens, 2007; Rejt et al., 2007). These avoidance behaviors in response to radar could potentially be exploited in combination with other stimuli, like visual cues, to develop deterrents for areas of airport property close to radar. However, other studies using a similar X-band radar without a visual cue have shown that radar alone does not alter the behavior of migrating birds (e.g. Bruderer et al., 1999).

In our approaching radar experiment, the increase in flight initiation distance we observed could allow birds to perform escape maneuvers more successfully in response to an aircraft (Bernhardt et al., 2010). Assuming our flight initiation distances are similar to those given to aircraft, we can argue that at taxiing aircraft speeds (approximately 3–10 $m\,s^{-1}$) birds responding to an aircraft with the solid state radar would escape 2–6 s earlier than birds responding to an aircraft with no radar, potentially leading to an increase in the number of successful escapes. However, these effects may be minimized at higher speeds. For instance, approach speeds during landing of large aircraft using solid state radars (e.g., Airbus A330, a category C aircraft) range from 62 to 73 $m\,s^{-1}$ (Federal Aviation Administration, 2014), leaving birds with 0.3 s more to escape in response to the radar. Take-off and cruising speeds are generally higher than approach speeds (ranging from 67 to over 250 $m\,s^{-1}$ depending on aircraft type), leaving birds with very little more time (from 0.3 to <0.1 s) to make successful escape maneuvers. There is limited evidence that in some circumstances birds might increase flight initiation distances with increases in vehicle speed (Legagneux and Ducatez, 2013; DeVault et al., 2014), so our estimates of how much earlier birds respond to aircraft with radar in flight may be conservative.

In conclusion, we found evidence that just one of the many types of electromagnetic radiation found at airports can change avian behavior. We also found different effects of two radar units during vehicle approach, indicating that slight differences in power density and pulse properties can potentially alter bird behavior. Our findings suggest that radar enhances some avoidance responses to approaching threats, and therefore changes how birds evaluate the risk of a threat. Overall, this provides some evidence that birds notice the presence of radar in some contexts, which has implications for wildlife management at airports.

Acknowledgments

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.applanim.2015.08.001.

References

Balmori, A., 2009. Electromagnetic pollution from phone masts. Effects on wildlife. Pathophysiology 16, 191–199, http://dx.doi.org/10.1016/j.pathophys.2009.01.007.

Balmori, A., Hallberg, Ö., 2007. The urban decline of the house sparrow (*Passer domesticus*): a possible link with electromagnetic radiation. Electromagn. Biol. Med. 26, 141–151, http://dx.doi.org/10.1080/15368370701410558.

Bernhardt, G.E., Blackwell, B.F., DeVault, T.L., Kutschbach-Brohl, L., 2010. Fatal injuries to birds from collisions with aircraft reveal anti-predator behaviours. Ibis 152, 830–834, http://dx.doi.org/10.1111/j.1474-919X.2010.01043.x.

Blackwell, B.F., Bernhardt, G.E., 2004. Efficacy of aircraft landing lights in stimulating avoidance behavior in birds. J. Wildl. Manag. 68, 725–732, 10.2193/0022-541X(2004)068[0725:EOALLI]2.0.CO;2.

Blackwell, B.F., DeVault, T.L., Fernández-Juricic, E., Dolbeer, R.A., 2009a. Wildlife collisions with aircraft: a missing component of land-use planning for airports. Landsc. Urban Plan. 93, 1–9, http://dx.doi.org/10.1016/j.landurbplan.2009.07.005.

Blackwell, B.F., Fernández-Juricic, E., Seamans, T.W., Dolan, T., 2009b. Avian visual system configuration and behavioural response to object approach. Anim. Behav. 77, 673–684, http://dx.doi.org/10.1016/j.anbehav.2008.11.017.

Blackwell, B.F., Seamans, T.W., 2009. Enhancing the perceived threat of vehicle approach to deer. J. Wildl. Manag. 73, 128–135, http://dx.doi.org/10.2193/2008-014.

Blackwell, B.F., Seamans, T.W., DeVault, T.L., 2014. White-tailed deer response to vehicle approach: evidence of unclear and present danger. PLOS ONE 9, e109988, http://dx.doi.org/10.1371/journal.pone.0109988.

Blumstein, D., Daniel, J.C., 2007. Quantifying Behavior the Jwatcher Way, illustrated edition. Sinauer Associates, Sunderland, Mass.

Bouguet, J.-Y., n.d. Camera Calibration Toolbox for Matlab. http://www.vision.caltech.edu/bouguetj/calib_doc/index.html

Bruderer, B., Peter, D., Steuri, T., 1999. Behaviour of migrating birds exposed to X-band radar and a bright light beam. J. Exp. Biol. 202, 1015–1022.

Byman, D., Demetri, E.P., Wasserman, F.E., Battista, S.P., Kunz, T.H., 1986. Thermal modelling of small birds exposed to microwave radiation (2.45 GHz CW). J. Appl. Ecol. 23, 449–459, http://dx.doi.org/10.2307/2404028.

Chou, C.K., Galambos, R., Guy, A., Lovely, R.H., 1975. Cochlear microphonics generated by microwave pulses. J. Microw. Power 10, 361–367.

Cleary, E.C., Dolbeer, R., 2005. FAA Guidance on Wildlife: A Manual for Airport Personnel, 2nd ed. The Federal Aviation Administration.

Cooper, W.E., Blumstein, D.T., 2013. Novel effects of monitoring predators on costs of fleeing and not fleeing explain flushing early in economic escape theory. Behav. Ecol. 25, 44–52, http://dx.doi.org/10.1093/beheco/art083.

Cucurachi, S., Tamis, W.L.M., Vijver, M.G., Peijnenburg, W.J.G.M., Bolte, J.F.B., de Snoo, G.R., 2013. A review of the ecological effects of radiofrequency electromagnetic fields (RF-EMF). Environ. Int. 51, 116–140, http://dx.doi.org/10.1016/j.envint.2012.10.009.

Cuthill, I.C., 2006. Color perception. In: Bird Coloration: Mechanisms and Measurements. President and Fellows of Harvard College, USA, pp. 3–40.

DeVault, T.L., Blackwell, B.F., Belant, J.L., 2013. Wildlife in Airport Environments: Preventing Animal–Aircraft Collisions Through Science-Based Management. John Hopkins University Press, Baltimore, MD.

DeVault, T.L., Blackwell, B.F., Seamans, T.W., Lima, S.L., Fernández-Juricic, E., 2014. Effects of vehicle speed on flight initiation by turkey vultures: implications for bird-vehicle collisions. PLOS ONE 9, e87944, http://dx.doi.org/10.1371/journal.pone.0087944.

Devereux, C.L., Fernàndez-Juricic, E., Krebs, J.R., Whittingham, M.J., 2008. Habitat affects escape behaviour and alarm calling in common starlings *Sturnus vulgaris*. Ibis 150, 191–198, http://dx.doi.org/10.1111/j.1474-919X.2008.00835.x.

Dolbeer, R.A., Wright, S.E., Weller, J., Begler, M.J., 2013. Wildlife strikes to civil aircraft in the United States, 1990–2012.

Dukas, R., 2004. Causes and consequences of limited attention. Brain Behav. Evol. 63, 197–210, http://dx.doi.org/10.1159/000076781.

Dukas, R., Kamil, A.C., 2000. The cost of limited attention in blue jays. Behav. Ecol. 11, 502–506, http://dx.doi.org/10.1093/beheco/11.5.502.

Everaert, J., Bauwens, D., 2007. A possible effect of electromagnetic radiation from mobile phone base stations on the number of breeding house sparrows (*Passer domesticus*). Electromagn. Biol. Med. 26, 63–72, http://dx.doi.org/10.1080/15368370701205693.

Federal Aviation Administration, 2014. Order JO 7400.2K Procedures for handling airspace matters.

Fernández-Juricic, E., Beauchamp, G., 2008. An experimental analysis of spatial position effects on foraging and vigilance in brown-headed cowbird flocks. Ethology 114, 105–114, http://dx.doi.org/10.1111/j.1439-0310.2007.01433.x.

Fernández-Juricic, E., Deisher, M., Stark, A.C., Randolet, J., 2012. Predator detection is limited in microhabitats with high light intensity: an experiment with brown-headed cowbirds. Ethology 118, 341–350, http://dx.doi.org/10.1111/j.1439-0310.2012.02020.x.

Fernández-Juricic, E., Ojeda, A., Deisher, M., Burry, B., Baumhardt, P., Stark, A., Elmore, A.G., Ensminger, A.L., 2013. Do male and female cowbirds see their world differently? Implications for sex differences in the sensory system of an avian brood parasite. PLOS ONE 8, 1–8, http://dx.doi.org/10.1371/journal.pone.0058985.

Fernie, K.J., Reynolds, S.J., 2005. The effects of electromagnetic fields from power lines on avian reproductive biology and physiology: a review. J. Toxicol. Environ. Health Part B 8, 127–140, http://dx.doi.org/10.1080/10937400590909022.

Gomez, D., 2006. AVICOL, a program to analyze sectrometric data. Free program available at http://sites.google.com/site/avicolprogram/ or from the author at dodogomez@yahoo.fr

Hesse, G., Rea, R.V., Booth, A.L., 2010. Wildlife management practices at western Canadian airports. J. Air Transp. Manag. 16, 185–190, http://dx.doi.org/10.1016/j.jairtraman.2009.11.003.

Howland, H.C., 1974. Optimal strategies for predator avoidance: the relative importance of speed and manoeuvrability. J. Theor. Biol. 47, 333–350, http://dx.doi.org/10.1016/0022-5193(74)90202-1.

Huansheng, N., Weishi, C., Xia, M., Jing, L., 2010. Bird-aircraft strike avoidance radar. IEEE Aerosp. Electron. Syst. Mag. 25, 19–28, http://dx.doi.org/10.1109/MAES.2010.5442150.

Husby, A., Husby, M., 2014. Interspecific analysis of vehicle avoidance behavior in birds. Behav. Ecol. 25, 504–508, http://dx.doi.org/10.1093/beheco/aru011.

Joseph, W., Goeminne, F., Vermeeren, G., Verloock, L., Martens, L., 2012. Occupational and public field exposure from communication, navigation, and radar systems used for air traffic control. Health Phys. 103 (December), 750–762, http://dx.doi.org/10.1097/HP.0b013e31825f78d5.

Kaby, U., Lind, J., 2003. What limits predator detection in blue tits (*Parus caeruleus*): posture, task or orientation? Behav. Ecol. Sociobiol. 54, 534–538.

Kelly, T., Allan, J., 2006. Ecological effects of aviation. In: Davenport, P.J., Davenport, J.L. (Eds.), The Ecology of Transportation: Managing Mobility for the Environment, Environmental Pollution. Springer, Netherlands, pp. 5–24.

Krebs, J.R., Ryan, J.C., Charnov, E.L., 1974. Hunting by expectation or optimal foraging? A study of patch use by chickadees. Anim. Behav. 22 (Part 4), http://dx.doi.org/10.1016/0003-3472(74)90018-9, 953-IN3.

Kullberg, C., Fransson, T., Jakobsson, S., 1996. Impaired predator evasion in fat blackcaps (*Sylvia atricapilla*). Proc. Biol. Sci. 263, 1671–1675.

Kullberg, C., Jakobsson, S., Fransson, T., 2000. High migratory fuel loads impair predator evasion in sedge warblers. The Auk 117, 1034–1038, http://dx.doi.org/10.1642/0004-8038(2000)117[1034:HMFLIP]2.0.CO;2.

Kullberg, C., Jakobsson, S., Fransson, T., 1998. Predator-induced take-off strategy in great tits (*Parus major*). Proc. R. Soc. Lond. B Biol. Sci. 265, 1659–1664.

Kullberg, C., Lafrenz, M., 2007. Escape take-off strategies in birds: the significance of protective cover. Behav. Ecol. Sociobiol. 61, 1555–1560, http://dx.doi.org/10.1007/s00265-007-0387-1.

Legagneux, P., Ducatez, S., 2013. European birds adjust their flight initiation distance to road speed limits. Biol. Lett. 9, 20130417, http://dx.doi.org/10.1098/rsbl.2013.0417.

Lewis, P., Dougherty, D.M., 1992. Pigeon performance on a variable-interval omission schedule at different levels of food deprivation. Behav. Process. 27, 27–35, http://dx.doi.org/10.1016/0376-6357(92)90037-E.

Lima, S.L., Blackwell, B.F., DeVault, T.L., Fernández-Juricic, E., 2014. Animal reactions to oncoming vehicles: a conceptual review. Biol. Rev., http://dx.doi.org/10.1111/brv.12093.

Lind, J., Fransson, T., Jakobsson, S., Kullberg, C., 1999. Reduced take-off ability in robins (*Erithacus rubecula*) due to migratory fuel load. Behav. Ecol. Sociobiol. 46, 65–70.

Lind, J., Hollén, L., Smedberg, E., Svensson, U., Vallin, A., Jakobsson, S., 2003. Detection distance influences escape behaviour in two parids, *Parus major* and *P. caeruleus*. J. Avian Biol. 34, 233–236, http://dx.doi.org/10.1034/j.1600-048X.2003.03097.x.

Lind, J., Kaby, U., Jakobsson, S., 2002. Split-second escape decisions in blue tits (*Parus caeruleus*). Naturwissenschaften 89, 420–423, http://dx.doi.org/10.1007/s00114-002-0345-8.

Lin, J.C., 1978. Microwave Auditory Effects and Applications. Thomas, Springfield, Illinois.

Lin, J.C., 1977. On microwave-induced hearing sensation. IEEE Trans. Microw. Theory Tech. 25, 605–613, http://dx.doi.org/10.1109/TMTT.1977.1129167.

Lowther, P.E., 1993. Brown-headed cowbird (*Molothrus ater*). Birds N. Am. (Online), http://dx.doi.org/10.2173/bna.47.

Moore, B.A., Baumhardt, P., Doppler, M., Randolet, J., Blackwell, B.F., DeVault, T.L., Loew, E.R., Fernández-Juricic, E., 2012. Oblique color vision in an open-habitat bird: spectral sensitivity, photoreceptor distribution and behavioral implications. J. Exp. Biol. 215, 3442–3452, http://dx.doi.org/10.1242/jeb.073957.

Morgan, T., Fernández-Juricic, E., 2007. The effects of predation risk, food abundance, and population size on group size of brown-headed cowbirds (*Molothrus ater*). Ethology 113, 1173–1184, http://dx.doi.org/10.1111/j.1439-0310.2007.01419.x.

National Council on Radiation Protection and Measurements, 1981. Radiofrequency Electromagnetic Fields Properties, Quantities and Units, Biophysical Interaction, and Measurements. NCRP, Bethesda, MD.

Rejt, L., Mazgajski, T., Kubacki, R., Kieliszek, J., Sobiczewska, E., Szmigielski, S., 2007. Influence of radar radiation on breeding biology of tits (*Parus sp.*). Electromagn. Biol. Med. 26, 235–238, http://dx.doi.org/10.1080/15368370701357841.

Schwartzkopff, J., 1955. On the hearing of birds. The Auk 72, 340–347, http://dx.doi.org/10.2307/4081446.

Siddiqi, A., Cronin, T.W., Loew, E.R., Vorobyev, M., Summers, K., 2004. Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*. J. Exp. Biol. 207, 2471–2485, http://dx.doi.org/10.1242/jeb.01047.

Sorrentino, R., Bianchi, G., 2010. Microwave and RF Engineering. Wiley, Hoboken, NJ, USA.

Stankowich, T., Blumstein, D.T., 2005. Fear in animals: a meta-analysis and review of risk assessment. Proc. R. Soc. B Biol. Sci. 272, 2627–2634, http://dx.doi.org/10.1098/rspb.2005.3251.

Stimson, G.W., 1998. Introduction to Airborne Radar, 2nd ed. SciTech Publishing Inc., Raleigh, NC.

Tanner, J.A., 1966. Effect of microwave radiation on birds. Nature 210, 636, http://dx.doi.org/10.1038/210636a0.

Tanner, J.A., Romero-Sierra, C., Davie, S.J., 1967. Non-thermal effects of microwave radiation on birds. Nature 216, 1139, http://dx.doi.org/10.1038/2161139a0.

Vorobyev, M., Osorio, D., 1998. Receptor noise as a determinant of colour thresholds. Proc. Biol. Sci. 265, 351–358, http://dx.doi.org/10.1098/rspb.1998.0302.

Wasserman, F.E., Dowd, C., Byman, D., Schlinger, B.A., Battista, S.P., Kunz, T.H., 1985. Thermoregulatory behavior of birds in response to continuous wave 2.45-GHz microwave radiation. Physiol. Zool. 58, 80–90.

Wasserman, F.E., Dowd, C., Byman, D., Schlinger, B.A., Battista, S.P., Kunz, T.H., 1984a. Aversion/attraction of blue jays to microwave irradiation. Physiol. Behav. 33, 805–807, http://dx.doi.org/10.1016/0031-9384(84)90051-9.

Wasserman, F.E., Dowd, C., Schlinger, B.A., Byman, D., Battista, S.P., Kunz, T.H., 1984b. The effects of microwave radiation on avian dominance behavior. Bioelectromagnetics 5, 331–339, http://dx.doi.org/10.1002/bem.2250050306.

Witter, M.S., Cuthill, I.C., 1993. The ecological costs of avian fat storage. Philos. Trans. Biol. Sci. 340, 73–92.

Witter, M.S., Cuthill, I.C., Bonser, R.H.C., 1994. Experimental investigations of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. Anim. Behav. 48, 201–222, http://dx.doi.org/10.1006/anbe.1994.1227.

Ydenberg, R.C., Dill, L.M., 1986. The economics of fleeing from predators. In: Rosenblatt, J.S., Beer, C., Busnel, M.-C., Slater, P.J.B. (Eds.), Advances in the Study of Behavior. Academic Press, pp. 229–249.

Zakrajsek, E.J., Bissonette, J.A., 2005. Ranking the risk of wildlife species hazardous to military aircraft. Wildl. Soc. Bull. 33, 258–264, 10.2193/0091-7648(2005)33[258:RTROWS]2.0.CO;2.