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

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THE EFFECTS OF RADAR ON AVIAN BEHAVIOR: IMPLICATIONS FOR WILDLIFE MANAGEMENT AT AIRPORTS

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ABSTRACT

Sheridan, Eleanor R. M.S., Purdue University, August 2014. The effects of radar on avian behavior: implications for wildlife management at airports. Major Professor: Esteban Fernández-Juricic.

Airports are areas with a high availability of resources for wildlife to forage, breed, and roost. Airports also have different types of radars to assist with air traffic control as well as tracking of wildlife that could become a risk for aircraft. The effect of radar electromagnetic radiation on wildlife behavior is not well understood. The goal of this study was to determine if bird behavior is affected by radar in two contexts: static radar (e.g., surveillance radar) and approaching radar (e.g., aircraft weather radar). We used brown-headed cowbirds as a model species. In the static radar context, we performed two separate studies. In the first study, we found some indication of changes in vigilance and movement behaviors during and after exposure to static radar. In the second study, we also found that static radar increased movement behaviors. In the approaching radar context, we found that birds exposed to an approaching vehicle with radar showed earlier escape responses and flights that dodged sideways more than without radar. Taking these findings together, we suggest that birds may move to avoid static radar units, and moving radar units (as in aircraft) could enhance escape responses so that birds would be more likely to escape from vehicles like aircraft at low speeds during taxi, but likely not at the higher speeds during take-off, landing, and flight.

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 intermittent microwave that both air traffic control and aircraft themselves use for navigation and surveillance (Stimson, 1998). Radar is also used for communication between air traffic control and aircraft as well as detection of weather patterns and bird flocks (Huansheng et al., 2010; Joseph et al., 2012). These sources of electromagnetic radiation make airports areas of concentrated microwaves compared to surrounding areas (Joseph et al., 2012), yet little is known about how the high levels of microwaves at airports might affect the interactions between animals and humans. The presence of high levels of electromagnetic radiation has the potential to affect how animals use airport property. This is relevant because species might choose a seemingly suitable area on or near airports to inhabit, but that area may actually have negative consequences at the individual or population levels due to the high levels of microwaves (Kelly and Allan, 2006). If that is the case, airports could actually function as ecological traps (Blackwell et al., 2013).

Radar, a common type of electromagnetic radiation used at airports, is associated with electric and magnetic fields (Figure 1a) that pulse on multiple time scales simultaneously (Stimson, 1998). Microwaves are only emitted for a small percentage, or duty cycle, of the total interpulse period (Figure 1b). The radar we used for this study and other X-band radars at airports have a frequency of about 9.3 GHz (Figure 1a). Microwaves of this frequency can penetrate skin and muscle tissues to a depth of approximately 4 mm (National Council on Radiation Protection and Measurements, 1981). This penetration of tissues may allow an animal to detect these microwaves through one of two mechanisms: (1) thermoreception, as microwaves are able to increase tissue temperatures (Byman et al., 1986), and (2) auditory detection of microwave pulses (Lin, 1978).

Thermoreception of microwaves has been shown to raise body temperature and increase the incidence of different thermoregulatory behaviors (e.g. gaping, wing spreading, and panting) in birds (Wasserman et al., 1985). Thermoreception of microwaves has also been hypothesized to cause other changes in behavior, such as avoidance of areas irradiated with microwaves, and changes in dominance hierarchies (Wasserman et al., 1984a, 1984b). The second mechanism, auditory detection of microwave pulses, has been documented in humans and several other mammal species, but not in birds (reviewed in Lin, 1978). Pulses of microwaves generate a thermoelastic pressure wave that is heard as an auditory sound (Lin, 1977). The intensity of the response to microwaves through both of these mechanisms has been shown to be dependent on the power density of the incident microwaves (Lin, 1978; Wasserman et al., 1985).

Based on the aforementioned evidence that birds may be able to detect radar, we investigated how radar affects bird behavior by simulating two situations in which animals are exposed to radar at airports: static (e.g., surveillance radar) and approaching (e.g., aircraft weather radar). Our study species, the brown-headed cowbird (Molothrus ater), is commonly found on airport grounds and has been specifically identified in over 130 reported bird strikes in the past 23 years (Dolbeer et al., 2013). All species belonging to the families Sturnidae and Icterinae, 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., 2000), and among the top five most hazardous groups to military aircraft (Zakrajsek and Bissonette, 2005). We investigated the foraging and vigilance behaviors of cowbirds in response to static radar in two experiments. We assessed cowbird escape behavior in response to an approaching threat with radar.

We assumed that the presence of radar microwaves would require sensory processing by birds through one of the two mechanisms mentioned previously (thermoreception and auditory detection). Following from this assumption, we hypothesized that radar would increase sensory load and challenge attention mechanisms.

Attention is limited, as the brain cannot process all available information (Dukas, 2004). Limited attention has been shown to affect bird behavior; for instance, blue jays were less likely to detect a peripheral visual stimulus while attending to a difficult foraging task (Dukas and Kamil 2000), and blue tits foraging on a more difficult task took longer to detect a predator (Kaby and Lind, 2003). Therefore, we predicted that, radar microwaves would reduce the ability of birds to attend to other tasks. In the static radar experiment, we predicted that birds would forage less during exposure to radar microwaves, as they would be paying attention to radar through vigilance behavior to the detriment of foraging.

Following the same hypothesis, in the approaching radar experiment, attention to the radar would distract attention from evaluating and escaping from the approaching threat. Therefore, we predicted that birds would alert to, escape later from, and have more irregular escape flights from the approaching threat with radar present than an approaching vehicle without radar. However, there is an alternative hypothesis: radar microwaves may not compromise attention mechanisms, and actually may enhance the detection and perception of the approaching stimulus. The prediction that follows from this alternative hypothesis is that birds would respond to the approaching threat with radar earlier.

Finally, in the context of different types of radar, we hypothesized that increased power density increases the response to radar, as has been previously shown with other microwaves (e.g. Wasserman et al., 1985). In the approaching radar experiment we were able to use two different radar units with different power densities, and we predicted that the radar with higher power density would have a more pronounced effect on the aforementioned behaviors.

METHODS

Bird capture and maintenance

All procedures were approved by Purdue Animal Care and Use Committee (protocol #1110000081). For the static radar experiments, we captured brown-headed cowbirds in Ohio using six decoy traps located at the National Aeronautic and Space Administration's (NASA) Plum Brook Station, Erie County, Ohio, U.S.A. (41˚22'N, 82˚41'W): 91 for experiment 1 (72 males and 19 females), and 41 for experiment 2 (all males). For the static radar experiments, we were unable to capture an even number of males and females for experiment 1, and we were unable to capture females for experiment 2. Birds were then transported to and housed in outdoor aviaries (3 x 2 x 2 m) at Purdue University Ross Reserve, in Indiana (40°24'35" N, 87°4'2"W), where the experiments were conducted. Animals were provided equal parts of white millet, game bird chow, and sunflower seeds, and water ad libitum.

For the approaching radar experiments, we captured 116 brown-headed cowbirds (58 males and 58 females) using the same decoy traps in the same location. We housed birds in 2.4 x 2.4 x 1.8 m enclosures at the Plum Brook Station Erie County, Ohio, U.S.A., where the experiment was conducted. Birds were provided white millet, black oil sunflower, and water ad libitum.

Radar units

For these experiments we used two 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.). This radar unit emits in the X-band range (9.33 - 9.38 GHz). It has a maximum duty cycle of 10%, and an average interpulse interval of 100 μs. The antenna used in this experiment had a gain of 35 dBi, and the nominal peak transmit power of 40 W. The antenna of this radar unit rotates over an angle of 160° at an average rate of 58° s^{-1}. Any one position only experiences incident radiation from the dish for a small portion of time during the antenna rotation (Figure 1c).

The second unit was a magnetron radar (PRIMUS 880 Digital Weather Radar System, Honeywell International Inc.) The magnetron radar also emits in the X-band frequency range (9.36 – 9.40 GHz), but has a lower duty cycle (0.048%) and shorter interpulse period (2 μs) than the solid state radar. The antenna of the magnetron radar had 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).

These two radar units are both used in aircraft. The magnetron radar is used on smaller, business-type jets and helicopters, while the solid state radar is used on larger commercial airplanes (Bunch pers. comm.). Given that these two radars have different properties and are used in different aircraft, we chose to use two radars in the approaching radar experiment.

Static radar experiments

We conducted two static radar experiments. In experiment 1, 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 food saliency) than lower attention loads (e.g., higher food saliency). Because the avian visual system is different from that of humans (Cuthill, 2006), we calculated the perceived chromatic contrast of food in relation to the visual background from the cowbird visual perspective. 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.

We used a StellarNet Black Comet portable spectroradiometer (StellarNet, Tampa, FL) 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 decided to have 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 data on the physiology of the cowbird visual system (peak sensitivity of visual pigments, absorbance of oil droplets, relative densities of different photoreceptors) from the literature (Fernández-Juricic et al., 2013). 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 JND's) of white millet with brown sand in the different light conditions was: sunny = 17.5, cloudy = 17.8, and shady = 20.2. The contrast (in JND's) of millet with red sand in the three light conditions was: sunny = 37.2, cloudy = 37.6, and shady = 39.6. The contrast (in JND's) 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 2, we used the same food item (white millet) and a single substrate: sawdust, sifted to particulates of a similar size to sand.

In both static radar experiments, we exposed individuals to the solid state radar which was located outside a visual blind, 5 m from the enclosure holding the bird. We calculated the power density in the direct path of the antenna at a distance of 5 m to be approximately 4.03 mW/cm^2. The unit was placed at 5 m from the animals because we wanted to use a close distance to be able to detect any effects of the radar on behavior.

In both seasons, the experimental arena consisted of a small enclosure (1 x 1 x .75 m) without any metal components that might reflect incident microwaves. This enclosure was in the center of a 10 x 10 m square area enclosed with a 2 m tall black cloth blind.

Two Everio video cameras (GZMG750BUS, JCV) filmed the arena, one overhead and one from the side. Another Everio camera filmed the dish of the radar. These cameras fed into a muti-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 hr before the trials (following Fernández-Juricic et al., 2012). Prior to each trial, we scattered 5 g of white millet on to the substrate to provide foraging material. 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 the experiment 1, 3 min in experiment 2) after it first pecked. After acclimating, we exposed the bird to a treatment phase of 5 mins, during which the radar was either on or off. Finally, there was a 5 min after-treatment phase during which the radar was off. We measured the body mass of the birds before they were placed in the arena. We recorded ambient temperature using a handheld Kestrel 3500 weather meter (0835DT).

We recorded different behaviors using JWatcher (version 1.0 Blumstein and Daniel, 2007). Individuals recording behaviors (experiment 1: Melissa Hoover, experiment 2: Eleanor Sheridan) trained until they reached an intra- and interobserver reliability of 95%. We recorded the following response variables: peck rate, head up rate, proportion of time head up, maintenance rate, movement rate, and proportion of time moving (definitions in Table 1). We recorded these behaviors over two time scales. The experiment-wide scale included 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-minute time scale, we included the effects of radar exposure at radar onset and offset. Radar onset was measured one minute before and one minute after the radar turned on, and radar offset was measured one minute before and one minute after the radar turned off. We used the experiment-wide scale to search for longer-term effects of radar, and we used the 1-minute scale to search for more immediate effects of the beginning and end of radar exposure.

Approaching radar experiment

We preformed this experiment in June and July 2013, and deprived birds of food from 12 to 20 hr before each trial to encourage foraging. Before the trials, we moved birds to a holding location near the experimental site in 0.3 x 0.5 x 0.6 m enclosures, where we provided water ad libitum but no food (for 0:30 to 5:30 hr). 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 (HFW59D)

For the vehicle approach, we used a 2011 4x4 supercab Ford F-150, 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 5,550 watt portable generator (01919-1) in the bed of the truck. The radar dish was shielded from the wind with a panel of fiberglass reinforced plastic, which does not block microwaves; this shield 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: radar off, in which the generator of the truck was on and both radar units were off, magnetron radar (lower power density) with the solid state radar off, and solid state radar (higher power density) with the magnetron radar off. The assignment of the radar treatments was random.

The experimental arena (shown in Figure 2a) was semicircular with a radius of 2 m and a height of 1 m. The floor of the experimental arena was AstroTurf carpet approximately 2.5 cm high. The mesh of the enclosure was built of plastic deer netting with a mesh of 1.3 cm squares 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 arena in the center. The top of the back, semicircular edge of the arena had strands of artificial, leafy vegetation attached 10 cm below the roof of the arena. The vegetation covered 12 – 20 cm of the outer wall of the enclosure. This vegetation provided refuge (similar to Morgan and Fernández-Juricic, 2007), and the birds were able to grasp and land on the artificial vegetation through the mesh of the enclosure.

Two JVC Everio (GZ-MG330AU) cameras filmed the behavior of the two birds from the right and left sides of the arena (C1 & C2 in Fig. 2a). Two EverFocus security cameras (EZ700W-001) filmed the enclosure from overhead (C3 & C4 in Fig. 2a). These overhead cameras were placed 1.3 m apart to allow each camera to view the entire base of arena. Two additional JVC Everio cameras filmed the approach path of the truck at the start line of 210 m from the arena and at 30 m from the front edge of the arena (See Figure 2b). All six cameras were recorded onto a Night Owl H.264 DVR. All channels recorded at a resolution of 704x240 pixels and at 30 frames per s. The DVR was located 30 m to one side of the arena, behind a screen. 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 arena using a portable Kestrel 3500 weather meter (0835DT). We also measured light intensity with a portable digital lux meter (Extech Instruments, 401025). Afterwards, two birds (one male and one female) were released in the enclosure. The birds were allowed to acclimate to the arena for at least 3 mins 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 mins. If the birds did not forage, 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. To apply the radar treatments, the driver had to exit the vehicle. 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.

The truck would accelerate to a speed of 6.7 m s^{-1} before reaching the start line that was 210 m from the experimental arena. The truck would then maintain a speed of 6.765 ± 0.002 m s-1 until it was 8 m from the experimental arena, at which point it would brake and stop at least 2 m from the front of the arena. A High Frequency Analyzer

(HFW59D) 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), time to collision (TTC) at alert, flight initiation distance (FID), time to collision (TTC) at flight, angle of diversion, vertical take-off angle, and sinuosity (Table 2). We recorded all behaviors separately for each of the two birds in the experimental arena for each approach. We measured the time of the first frame of alert and flight behaviors (cameras C1 & C2 in Fig. 2a). An alert behavior was defined as a change in behavior or the rate of a behavior from the baseline. Changes indicative of an alert included moving from a head down position 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. We calculated the vehicle speed by taking the distance between the cameras in Fig. 2b and dividing 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 determine time to collision (TTC). To measure the alert distance (AD) and flight initiation distance (FID) we multiplied the time to collision by the speed of the vehicle. We searched the videos for alert and flight behaviors for 95% of the vehicle approach, from when the truck reached the start line to after the truck had passed the brake line (Figure 2b).

We measured the variables of angle of diversion, vertical take-off angle, and sinuosity using stereo triangulation based on the position of the bird beaks in two calibrated cameras (C3 & C4 in Fig. 2a). This process was completed in MATLAB (R2012a) using the Calibration Toolbox for MATLAB (http://www.vision.caltech.edu/bouguetj/calib_doc/index.html, Bouguet) and is detailed in Appendix 1. The output of this method is the three dimensional position of the bird beak in each frame of flight relative to a constant reference point. The start of flight was the three dimensional position of the beak 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 either overhead camera (C3 & C4 in Fig. 2a). We measured the angle of diversion (see Figure 3a) from the path of the vehicle, by comparing the direction of the flight to the direction of the vehicle approach (in degrees). We measured the vertical take-off angle when the animal passed 50 cm from the start of flight (Figure 3b). 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's beak at the start of flight, parallel to the ground (Figure 3b). 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 greater than 1 indicating increasing less direct flights).

Statistical analysis

In the static radar experiments, we used repeated-measures general linear mixed models (using SAS 9.3). We included, radar exposure, ambient temperature, body mass, and, in experiment 1, substrate color as between-subject factors. We did not include sex as a factor, as in experiment 1 the sexes were imbalanced and confounded with body mass, and in experiment 2 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-minute scale at radar onset, radar exposure had two levels: the minute before and after radar turned on. At the 1-minute scale at radar offset, radar exposure had two levels: the minute before and after the end of radar. For all analyses, we used the following dependent variables (Table 1): peck rate, head up rate, proportion of time head up, maintenance rate, movement rate, and proportion of time moving. We checked all variables for normality, and log transformed those variables that were not normal (See Tables 3-5).

In the approaching radar experiment, we used general linear mixed models (using SAS 9.3) to analyze the dependent variables listed in Table 2: AD, TTC at alert, FID, TTC at flight, angle of diversion, vertical take-off angle, and sinuosity. We included radar treatment (radar off, magnetron radar, and solid state radar) and sex as categorical factors and ambient light intensity and the 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 this experiment. Trial was included as a repeated-measures random factor, because for each trial, two birds were exposed to the same approaching vehicle, and all behaviors were recorded for both birds separately. Variables were log transformed if they were not normally distributed (FID, TTC at flight, and sinuosity). 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 1,000.

For all models (both static and approaching radar experiments) we used the Kenward-Rodgers degrees of freedom estimation method and restricted maximum likelihood estimation method. 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.

RESULTS

Static radar experiments

In experiment 1, at the experiment-wide scale, the head up rate and proportion of time head up significantly changed with radar exposure (Table 3). Both head up rate and proportion of time head up decreased from before to during radar exposure (head up rate: $t_{102} = 3.08$, $P = 0.003$, proportion of time head up: $t_{100} = 2.35$, $P = 0.021$), but did not differ during and after radar exposure (head up rate: $t_{102} = 3.59$, $P = 0.115$, proportion of time head up: $t_{100} = 1.20$, $P = 0.232$) (Fig. 4a & 4b). Experiment-wide, radar exposure significantly influenced cowbird movement rate and proportion of time moving (Table 3). Individuals had higher movement rate and proportion of time moving during radar exposure compared to before radar exposure (movement rate: $t_{101} = -3.10$, $P = 0.003$, proportion of time moving: $t_{102} = -4.12$, $P < 0.001$), but the variation between during and after radar exposure was not significant (movement rate: $t_{101} = -0.08$, $P = 0.933$, proportion of time moving: $t_{102} = -0.64$, $P = 0.524$) (Figure 4c & 4d). Body mass had a significant effect on several behaviors experiment-wide (Table 3): peck rate decreased with body mass (coefficient -0.008 ± 0.003, $t_{45.2} = -2.54$, $P = 0.015$), proportion of time head up increased with body mass (coefficient 0.011 ± 0.005, $t_{45.7} = 2.37$, $P = 0.022$), and movement rate decreased with body mass (coefficient -0.008 ± 0.004, $t_{44.9} = -2.02$, $P = 0.050$). Substrate color and ambient temperature did not have a significant effect on any behavior experiment-wide in experiment 1 (Table 3).

At the 1-minute time scale in experiment 1, at radar onset, there were no significant changes in behaviors (Table 4). Additionally, substrate color, ambient temperature and body mass did not affect significantly any of the measured behaviors at radar onset (Table 4). In experiment 1 at radar offset, there were also no significant changes in behavior (Table 5). Peck rate decreased with body mass at radar offset in experiment 1 (coefficient -0.010 ± 0.004, t39.8 = -2.93, P = 0.006) (Table 5). Substrate color and ambient temperature did not significantly affect any behavior at radar offset (Table 5).

In experiment 2, there was a significant decrease in peck rate experiment-wide (Table 3), but this decrease in peck rate was only significant from before (19.8 ± 3.6 pecks min^{-1}) to after (12.0 ± 3.0 pecks min^{-1}) exposure to the radar ($t_{36.6} = 2.95$, P = 0.006). Peck rate during radar exposure (14.4 ± 3.0 pecks min^{-1}) did not differ from either before radar exposure ($t_{36.1} = 1.94$, P = 0.60) or after radar exposure ($t_{36.1} = 1.04$, P = 0.307). 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 3). Experiment-wide, proportion of time head up significantly increased (Table 3) with body mass (coefficient 0.026 ± 0.012, $t_{16} = 2.18$, P = 0.044). Ambient temperature did not have an effect on any behavior experiment-wide in experiment 2 (Table 3).

At radar onset, on the 1-minute time scale in experiment 2, movement rate significantly increased (Table 4) from before (4.8 ± 1.8 movements min^{-1}) to after (8.4 ± 1.8 movements min^{-1}) radar onset. Body mass and ambient temperature did not significantly affect any behavior at radar offset in experiment 2 (Table 4). Radar offset did not significantly affect any behavior in experiment 2 (Table 5). At radar offset in experiment 2 (Table 5), peck rate decreased with body mass (coefficient -0.027 ± 0.012, $t_{16} = -2.15$, P = 0.048) and head up rate increased with body mass at radar offset in experiment 2 (coefficient 0.036 ± 0.015, $t_{16} = 2.31$, P = 0.035). Ambient temperature did not have a significant effect on any behavior at radar offset in experiment 2 (Table 5).

Approaching radar experiment

We did not find significant effects of radar on alert distance or time to collision at alert (Table 6). We found significant effects of radar treatment on flight initiation distance and time to collision at flight (Table 6; Fig. 5a). Birds exposed to the solid state radar had a greater FID and greater TTC at flight than birds exposed to either the magnetron radar (FID: $t_{55.7} = -2.42$, P = 0.019, TTC at flight: $t_{55.7} = -2.42$, P = 0.019) or the radar off (FID: $t_{56.3} = -3.30$, P = 0.002, TTC at flight: $t_{56.3} = -3.30$, P = 0.002). 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, TTC at alert, FID, or TTC at flight (Table 6).

Radar treatment also had a significant effect on the angle of diversion (Table 6; Fig. 5b). Cowbirds exposed to the magnetron radar diverged more from the path of the truck than cowbirds in the radar off group ($t_{41.5} = -2.67$, $P = 0.011$), while the solid state radar did not differ from either the magnetron radar ($t_{42.0} = 1.15$, $P = 0.257$) or radar off treatments ($t_{42.2} = -1.13$, $P = 0.266$), 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 6), 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 (Table 6).

Radar treatment did not have an effect on the vertical take-off angle or on the sinuosity of flights (Table 6). Sex did have an effect on vertical take-off angle (Table 6): males took off more steeply (60.1 ± 2.1°) than females (53.8 ± 2.0°). Vehicle speed and light intensity did not affect take-off angle (Table 6). Sex also had an effect on flight sinuosity (Table 6), with males having more sinuous escape flights (1.20 ± 0.01) than females (1.15 ± 0.01), meaning that males had less direct flights. Vehicle speed and light intensity had a significant effect on sinuosity (Table 6), with sinuosity increasing with light intensity (coefficient 0.0009 ± 0.0004, $t_{42.4} = 2.32$, $P = 0.025$), and sinuosity increasing with vehicle speed (coefficient 0.132 ± 0.064, $t_{48.3} = 2.08$, $P = 0.043$).

DISCUSSION

With both the static and approaching radar experiments, we found some effects on cowbird behavior that could be associated with the presence of radar. In the static radar experiments, we found that birds moved more and decreased vigilance behaviors when exposed to radar, although other behaviors were not significantly affected. In the approaching radar experiment, we found that cowbirds responded earlier to approaches with the solid state radar, and diverged more from the path of the approaching vehicle with the magnetron radar.

In static radar experiment 1 we did not find effects of the substrate color on any behavioral response, which suggests that the degree of visual saliency of the food items were not associated with foraging behaviors. Visual saliency is measured in just noticeable differences (JND's), and previous work has (e.g. Siddiqi et al., 2004) has set a range (1 – 4 JND's) at which items are difficult to discern from the background. In our study, the food item contrast with the substrates was much higher than 4 JND's; it ranged from 17.5 to 93.4 JND's. Therefore, the food items were probably not difficult to discern on any substrate color. It is possible that we did not find significant effects of substrate color on foraging behavior because the foraging task was not challenging.

In experiment 1, we did find that cowbirds scanned less and moved more during radar exposure, but this effect was not reversed after radar exposure. In experiment 2, we also observed an increase in movement rate, this time at the 1-minute scale at radar onset. Birds may have been moving within the enclosure to avoid the microwaves as the antenna scanned the enclosure. This is similar to Wasserman et al. (1984a), where blue jays avoided portions of enclosures with microwaves. However this cannot explain the continuation of higher movement rates after radar exposure. A decrease in vigilance behavior could have been caused by habituation to the enclosure after the first 2 mins (see Fernández-Juricic et al., 2013). Factors other than radar, such as food depletion after the first couple minutes could also have led to increased movement rates (Stephens and Krebs 1986). However the birds were likely not becoming satiated throughout the trial (e.g. DeMarse et al., 1999), as they did not peck less over time, and no bird consumed more than 25% of the food provided in each trial.

In the approaching radar experiment, we predicted that the radar would distract attention from assessment of the approaching threat and delay alert behaviors. We did not find a significant effect of either radar treatment on alert distance or TTC at alert. While radar may have had no effect on alert behavior, it is also possible that the birds were alert to the vehicle before we could begin recording alert behaviors or that the birds were alert but we could not detect those behaviors. There were significant effects of radar on flight initiation distance and time to collision at flight. Contrary to our predictions based on limited attention (Dukas, 2004), we found that with the solid state radar birds escaped earlier, allowing birds more time to maneuver out of the path of an approaching vehicle. This result supports our alternative hypothesis, that radar attracts attention to the approaching threat. This could change evaluation of the threat, which is one of the behavioral steps at which an animal can fail to avoid collision with a vehicle (Lima et al., 2014). There have been many studies showing that animals can evaluate threats and modify flight initiation distance accordingly (reviewed by Stankowich and Blumstein, 2005). Cowbirds and white-tailed deer have also been shown to modify behavioral response times in response to properties of vehicle approaches similar to the one used in this study (Blackwell and Bernhardt, 2004; Blackwell and Seamans, 2009; Blackwell et al., 2009; DeVault et al., 2014). If the radar treatment enhances the perceived risk of the approaching vehicle, this could lead to an earlier escape (Ydenberg and Dill, 1986; Cooper and Blumstein, 2013).

The other significant effect of approaching radar, the increased angle of diversion in the magnetron radar treatment, could also be interpreted as the bird maneuvering to avoid a collision. Diversions from the direction of approach of a threat have also been documented in response to raptor predator models (Kullberg et al., 2000; Lind et al., 2002, 2003; Devereux et al., 2008), providing some evolutionary basis for this behavior.

We propose that in our experiment where birds were in the center of the 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 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, while flying along the road would have the longest. Therefore, 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 attracts attention to the threat, making the threat seem riskier, as birds chose shorter escape directions when exposed to the magnetron radar.

While 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 are optimizing maneuverability in escape flights, and females are optimizing acceleration. This result is opposite that of trends in previous work. Take-off angles generally decrease with increased body mass (Witter et al., 1994; Kullberg et al., 1996; Lind et al., 1999), and male cowbirds tend to have greater body mass than females (Lowther, 1993). 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 towards nearby cover (Witter and Cuthill, 1993; Kullberg and Lafrenz, 2007).

We found that the solid state and magnetron radar affected different behaviors. There are several ways that the two mechanisms of detecting microwaves could explain why the 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 and TTC at flight 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 sound in the magnetron radar (Lin, 1978). To our knowledge a vital part of this mechanism, bone conduction of sound, has not been 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).

Applied Implications

The effects of radar on behavior we found can 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). Bird collisions with aircraft (a.k.a. bird strikes) are of conservation concern for some bird species as well as 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; 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 static 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 have shown changes in the distribution of species during the breeding season (Everaert and Bauwens, 2007; Rejt et al., 2007). Further information on this avoidance behavior could allow wildlife managers at airports to focus efforts to deter birds from areas of the airport with low densities of electromagnetic radiation, if birds are already avoiding areas near radar units with high densities of electromagnetic radiation.

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). To get a rough idea how our results could apply to moving aircraft, we will assume flight initiation distance is the same in response to aircraft. 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. An escape 2 - 6 s earlier has the potential to increase the number of successful escapes. However, during the flight of an aircraft, the speeds are much higher and the increased reaction time due to radar would be less. Approach speeds for landing are usually the slowest part of a flight, and the approach speeds of a large aircraft that could be using the RDR-4000 solid state radar (e.g. the Airbus A330, a category C aircraft) range from 62 – 73 m s^{-1} (Federal Aviation Administration, 2014). At these higher speeds, birds responding to aircraft with radar would escape only 0.3 s earlier than to the aircraft without radar. In the other parts of a flight, take-off and cruising, speeds are generally higher than approach speeds (ranging from 67 to over 250 m s^{-1} depending on aircraft type). Birds would have from 0.3 to less than 0.1 s to make escape maneuvers in those portions of the flight, which may not be enough time to allow them a successful avoidance. There is some evidence that birds increase flight initiation distances with increases in vehicle speed, contrary to our assumption (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. How birds might respond to radar at higher speeds, similar to aircraft in flight, is difficult to determine, and requires further study.

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 approaching radars units, indicating that slight differences in power density and pulse properties can potentially alter bird behavior. These results did not support our hypothesis that radar microwaves compromise attention mechanisms. Instead, our findings suggest that radar attracts attention 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.

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TABLES

Table 1

Definitions of behaviors recorded for the static radar experiments.

Behavior	**Definition**
Peck rate	The number of times per minute the beak touched the substrate
Head up rate	The number of times per minute the head of the animal moved (roll, pitch or yaw) when the beak was parallel with the ground
Proportion of time head up	The proportion of time spent with head in the up position, where the beak was parallel to the ground
Maintenance rate	Experiment 1: the number of times per minute the beak touched any other part of the body (e.g. preening feathers) Experiment 2: the number of times per minute animals performed any of the following maintenance behaviors: beak touching any other part of the body (e.g. preening feathers), puffing up of feathers, rearranging of wings on the back, or a whole body shake.
Movement rate	The number of times per minute the animal walked or ran on the ground, or flew within the enclosure.
Proportion of time moving	The proportion of time the animal spent walking, running or flying.

Table 2

Definitions of behaviors recorded for the approaching radar experiment.

Behavior	**Definition**
Alert Distance (AD)	The distance of the vehicle to the experimental arena when the animal displayed an alert behavior. Alert behaviors were a change in behavior or rate of behavior from the baseline, and included moving from a head down position to a head up position, stretching the neck up, crouching, and freezing (ceasing all movement for a short period of time)
Time to collision (TTC) at alert	The time before the vehicle would collide with the experimental arena when the animal displayed an alert behavior (described above)
Flight initiation distance (FID)	The distance of the vehicle to the experimental arena when the animal displayed a flight behavior. Flight behaviors were recorded at the start of a walk or run to away from the approaching vehicle and when the animal began pushing off the ground at the start of a flight
Time to collision (TTC) at flight	The time before the vehicle would collide with the experimental arena when the animal displayed a flight behavior (described above)
Angle of diversion	The angle between the animal's flight direction (measured at the end of the initial flight to cover) and the direction of the vehicle. The vehicle always approached the arena at the same angle, perpendicular to the front edge. The animal could go left, right, or parallel to the approaching vehicle. See Fig. 3a
Vertical take-off angle	The angle at which the animal took off (measured when the animal had flown 50 cm). This was measured by calculating the distance the animal rose above the ground and comparing that with the distance traveled along the ground. See Fig 3b
Sinuosity	The directness of the flight (unitless, with 1 indicating a flight of a straight line, and values >1 indicating increasingly less direct flights). Calculated by dividing the sum of the distances traveled in each frame by the distance from the start to the end of the flight.

Table 3

General linear mixed model showing foraging and vigilance behaviors at the longer time scale of both the static radar experiments. Periods of radar exposure are before, during, and after radar exposure. Levels of substrate color are brown, green, and red.

	Experiment 1			**Experiment 2**		
	F	**d.f.**	**P**	**F**	**d.f.**	**P**
Peck rate (log)						
Radar exposure	2.20	2, 102	0.117	4.46	2, 36.2	**0.019**
Substrate color	0.06	2, 52.8	0.945	-	-	-
Body mass	6.47	1, 45.2	**0.015**	1.17	1, 16	0.295
Temperature	0.39	1, 66.6	0.537	0.35	1, 16	0.561
Head up rate						
Radar exposure	11.3	2, 102	**<0.001**	3.14	2, 36.2	0.055
Substrate color	1.95	2, 59.9	0.151	-	-	-
Body mass	0.15	1, 47.3	0.697	3.67	1, 16	0.074
Temperature	0.43	1, 89.8	0.513	0.89	1, 16	0.359
Proportion of time head up (log)						
Radar exposure	6.90	2, 101	**0.002**	0.68	2, 36.1	0.512
Substrate color	0.33	2, 59.6	0.718	-	-	-
Body mass	5.22	1, 45.9	**0.027**	4.76	1, 16	**0.044**
Temperature	0.03	1, 94.4	0.866	0.02	1, 16	0.899
Maintenance rate (log exp. 1 only)						
Radar exposure	0.21	2, 101	0.810	0.04	2, 36.7	0.961
Substrate color	1.35	2, 46.5	0.269	-	-	-
Body mass	1.19	1, 40.1	0.282	0.01	1, 16	0.923
Temperature	2.15	1, 52.4	0.148	1.25	1, 16	0.281
Movement rate (log exp. 1 only)						
Radar exposure	6.92	2, 101	**0.002**	2.01	2, 36.3	0.149
Substrate color	1.80	2, 54.6	0.176	-	-	-
Body mass	4.59	1, 44.7	**0.038**	2.72	1, 16	0.119
Temperature	1.42	1, 76.1	0.237	0.66	1, 16	0.427
Proportion of time moving (log exp. 1 only)						
Radar exposure	13.33	2, 102	**<0.001**	3.05	2, 36.5	0.060
Substrate color	1.03	2, 58.4	0.365	-	-	-
Body mass	0.65	1, 47.0	0.425	3.41	1, 16	0.084
Temperature	0.96	1, 84.5	0.329	0.74	1, 16	0.401

Table 4

General linear mixed model showing how radar onset affects foraging and vigilance behaviors in both the static radar experiments, at the shorter time scale. Levels of radar exposure are before and after the radar turns on. Levels of substrate color are brown, green, and red.

	Experiment 1			**Experiment 2**		
	F	**d.f.**	**P**	**F**	**d.f.**	**P**
Peck rate (log exp. 1 only)						
Radar exposure	0.05	1, 48.3	0.829	0.24	1, 18	0.632
Substrate color	0.27	2, 45.8	0.764	-	-	-
Body mass	2.26	1, 39.8	0.141	0.27	1, 16	0.609
Temperature	2.33	1, 56.6	0.132	0.70	1, 16	0.414
Head up rate						
Radar exposure	0.78	1, 49.5	0.379	0.41	1, 18	0.532
Substrate color	1.16	2, 47.9	0.322	-	-	-
Body mass	0.94	1, 41.3	0.338	0.18	1, 16	0.677
Temperature	0.11	1, 60.1	0.744	0.01	1, 16	0.914
Proportion of time head up (log)						
Radar exposure	0.06	1, 48.9	0.815	3.07	1, 18	0.097
Substrate color	0.83	2, 47.3	0.441	-	-	-
Body mass	2.19	1, 40.8	0.147	2.08	1, 16	0.169
Temperature	0.68	2, 59.3	0.412	0.06	1, 16	0.814
Maintenance rate (log)						
Radar exposure	0.59	1, 50.8	0.447	0.16	1, 18	0.691
Substrate color	0.20	2, 61.5	0.463	-	-	-
Body mass	0.20	1, 46.5	0.653	0.84	1, 16	0.372
Temperature	0.90	1, 92.0	0.345	1.45	1, 16	0.246
Movement rate (log exp. 1 only)						
Radar exposure	0.50	1, 51.0	0.483	6.74	1, 18	**0.018**
Substrate color	0.52	2, 51.6	0.597	-	-	-
Body mass	3.35	1, 43.7	0.074	0.96	1, 16	0.341
Temperature	0.08	1, 67.0	0.782	1.58	1, 16	0.226
Proportion of time moving (log)						
Radar exposure	0.17	1, 51.1	0.679	4.19	1, 18	0.056
Substrate color	1.06	2, 49.3	0.356	-	-	-
Body mass	1.78	1, 42.8	0.189	0.95	1, 16	0.344
Temperature	0.10	1, 61.0	0.753	1.89	1, 16	0.188

Table 5

General linear mixed model showing how radar offset affects foraging and vigilance behaviors in both the static radar experiments, at the shorter time scale. Levels of radar exposure are before and after the radar turns off. Levels of substrate color are brown, green, and red.

	Experiment 1			**Experiment 2**		
	F	**d.f.**	**P**	**F**	**d.f.**	**P**
Peck rate (log exp. 1 only)						
Radar exposure	0.14	2, 49.7	0.708	0.39	1, 18	0.539
Substrate color	0.41	2, 45.1	0.666	-	-	-
Body mass	8.57	1, 39.8	**0.006**	4.61	1, 16	**0.048**
Temperature	0.80	1, 53.3	0.375	0.06	1, 16	0.809
Head up rate						
Radar exposure	1.18	1, 50.1	0.282	0.18	1, 18	0.674
Substrate color	2.02	2, 52.9	0.142	-	-	-
Body mass	0.01	1, 43.5	0.937	5.32	1, 16	**0.035**
Temperature	0.30	1, 72.4	0.588	4.30	1, 16	0.055
Proportion of time head up (log)						
Radar exposure	1.07	1, 49.7	0.307	1.54	1, 18	0.230
Substrate color	1.66	2, 52.3	0.201	-	-	-
Body mass	1.69	1, 43.1	0.201	3.82	1, 16	0.068
Temperature	3.16	1, 71.7	0.080	0.52	1, 16	0.483
Maintenance rate (log)						
Radar exposure	1.00	1, 47.1	0.322	0.02	1, 18	0.898
Substrate color	1.13	2, 38.2	0.335	-	-	-
Body mass	0.03	1, 32.2	0.874	0.28	1, 16	0.602
Temperature	0.49	1, 45.1	0.489	0.20	1, 16	0.662
Movement rate (log)						
Radar exposure	0.14	1, 43.9	0.707	0.47	1, 18	0.503
Substrate color	3.09	2, 46.6	0.055	-	-	-
Body mass	0.04	1, 37.5	0.840	1.36	1, 16	0.261
Temperature	2.86	1, 67.2	0.096	0.53	1, 16	0.478
Proportion of time moving (log)						
Radar exposure	0.16	1, 48.6	0.690	1.26	1, 18	0.277
Substrate color	1.89	2, 48.5	0.162	-	-	-
Body mass	0.29	1, 41.1	0.595	1.18	1, 16	0.293
Temperature	2.97	1, 63.1	0.090	0.76	1, 16	0.397

Table 6

General linear mixed model showing the AD, TTC at alert, FID, TTC at flight, 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. Significant values are displayed in bold.

	F	**d.f.**	**P**
Alert distance (AD)			
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
Time to collision at alert			
Radar treatment	0.63	2, 49.3	0.535
Sex	0.26	1, 50.3	0.612
Vehicle speed	0.02	1, 45.9	0.901
Light intensity	1.15	1, 47.6	0.288
Flight initiation distance (FID) (log)			
Radar treatment	3.72	2, 54.9	**0.031**
Sex	0.0	1, 53.1	0.979
Vehicle speed	0.63	1, 55.0	0.430
Light intensity	0.76	1, 54.2	0.389
Time to collision at flight (log)			
Radar treatment	3.72	2, 54.9	**0.031**
Sex	0.0	1, 53.1	0.979
Vehicle speed	0.34	1, 55.0	0.560
Light intensity	0.75	1, 54.2	0.389
Vertical take-off angle			
Radar treatment	1.15	2, 43.5	0.328
Sex	7.32	1, 43.3	**0.010**
Vehicle speed	0.01	1, 46.2	0.939
Light intensity	0.25	1, 41.7	0.623
Angle of diversion			
Radar treatment	3.58	2, 41.9	**0.037**
Sex	1.69	1, 40.2	0.201
Vehicle speed	0.20	1, 44.5	0.660
Light intensity	9.55	1, 39.8	**0.004**
Sinuosity (log)			
Radar treatment	0.39	2, 44.8	0.676
Sex	5.23	1, 49.4	**0.027**

Vehicle speed	4.32	1, 48.3	**0.043**
Light intensity	5.38	1, 42.4	**0.025**

FIGURES

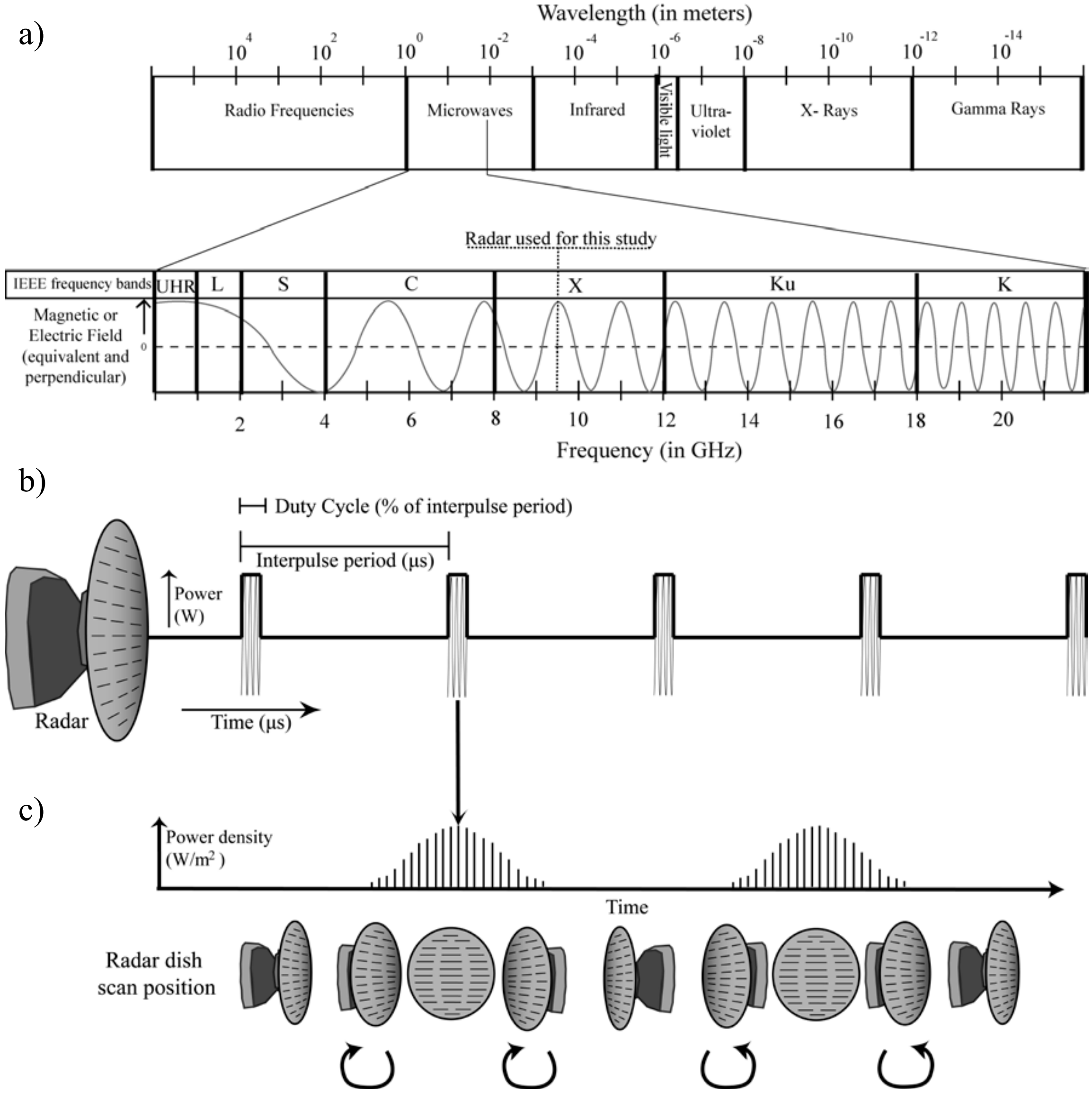

Figure 1

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 & 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)

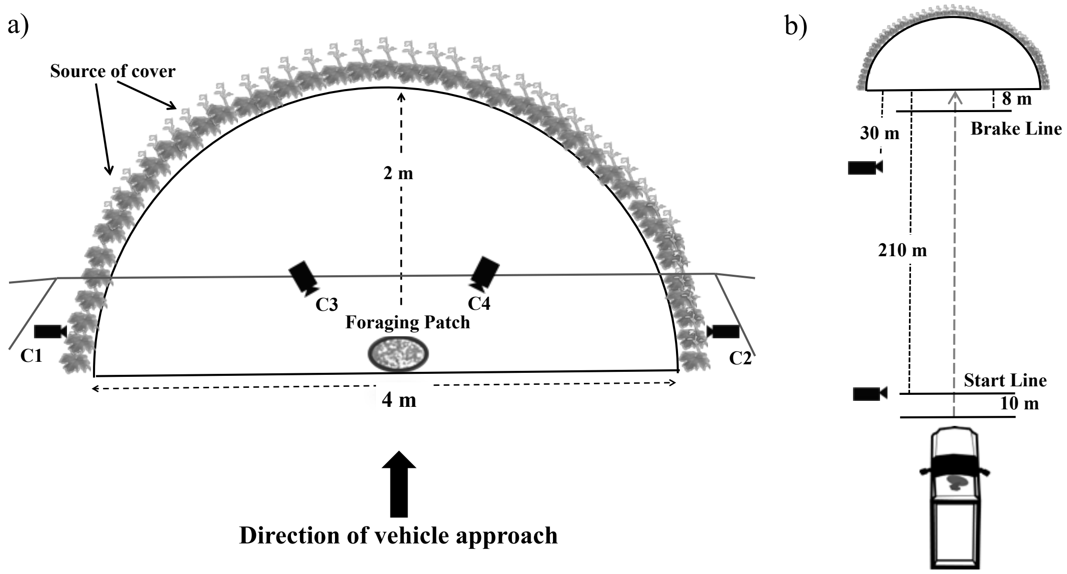

Figure 2

Experimental set up for approaching radar experiment. (a) Overhead view of the experimental arena. The arena was a semicircle of radius 2 m and height of 1 m. Sources of cover were in the form of artificial vegetation near the top of the 1 m tall wall. Cameras 1 and 2 (C1 & C2) filmed the arena from the sides, with the foraging patch in view of each camera. Cameras 3 and 4 (C3 & C4) were on a PVC frame over the top of the arena. These cameras had the entire base of the arena in view. The direction of the vehicle's approach is marked. (b) Layout of the vehicle's approach and the cameras filming the approach. The vehicle accelerated to a speed of 6.7 m s^{-1} before reaching the Start Line (210 m from the arena). Cameras filmed the moment the vehicle crossed the Start line and reached distance of 30 m from the arena. The timing of when the vehicle reached these two cameras was used to calculate vehicle speed as well as position. The vehicle began braking 8 m from the experimental arena.

Figure 3

Diagram demonstrating how (a) the angle of diversion and (b) the vertical take-off angle were measured. (a) We used the path of the vehicle beginning at the bird's position at the start of flight, which was perpendicular to the front edge of the experimental arena. We measured the bird's direction of flight, at the end of flight, and we took the absolute difference, in degrees, from the path of the vehicle. (b) We measured the direction of flight after the bird had flown a distance of 50 cm from the start of flight and measure the angle compared to a line parallel to the ground at the level of the bird's beak at the start of the flight.

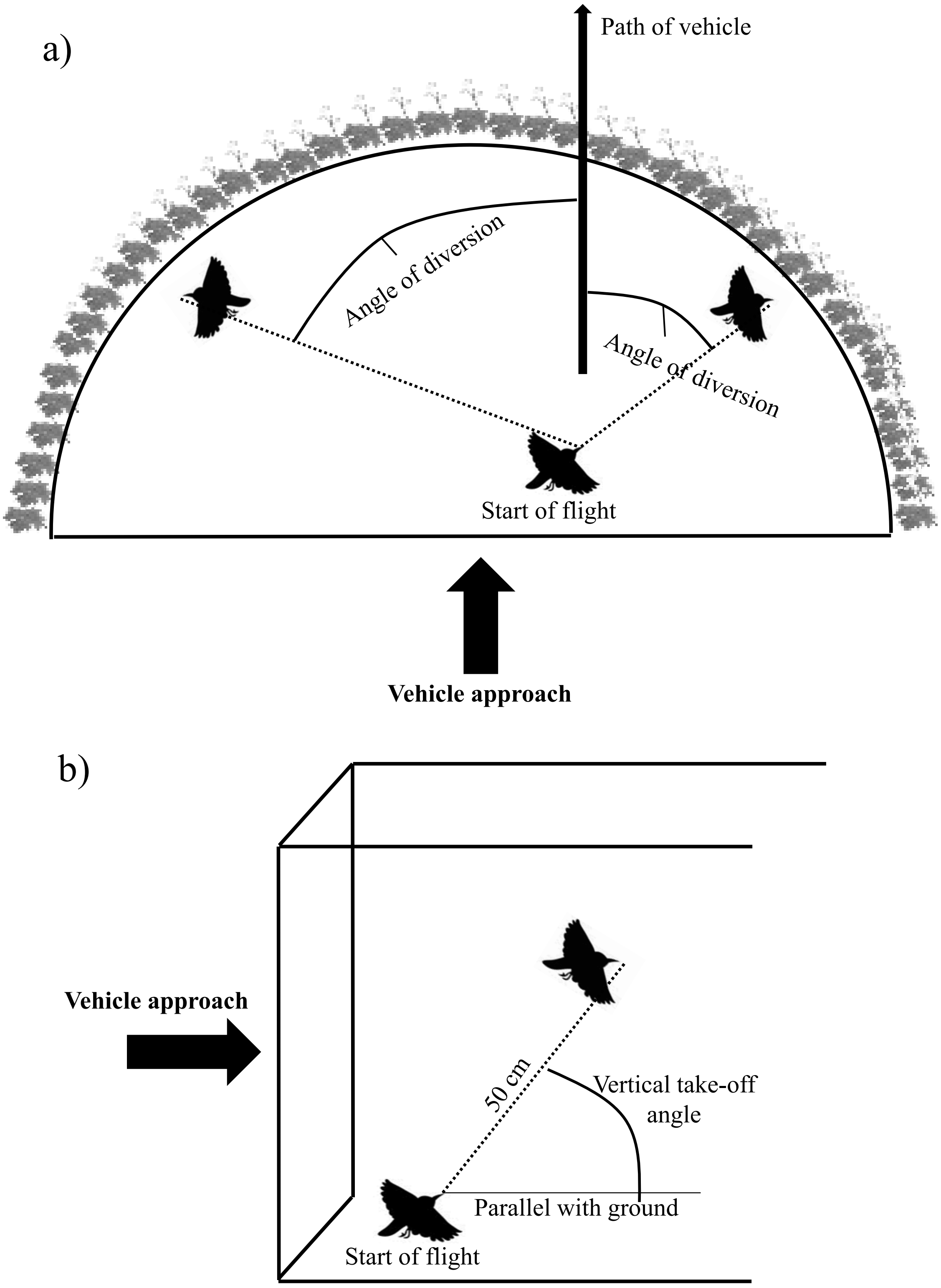
a)
Path of vehicle
Angle of diversion
Angle of diversion
Start of flight
Vehicle approach
b)
Vehicle approach
50 cm
Vertical take-off angle
Parallel with ground
Start of flight

Figure 3

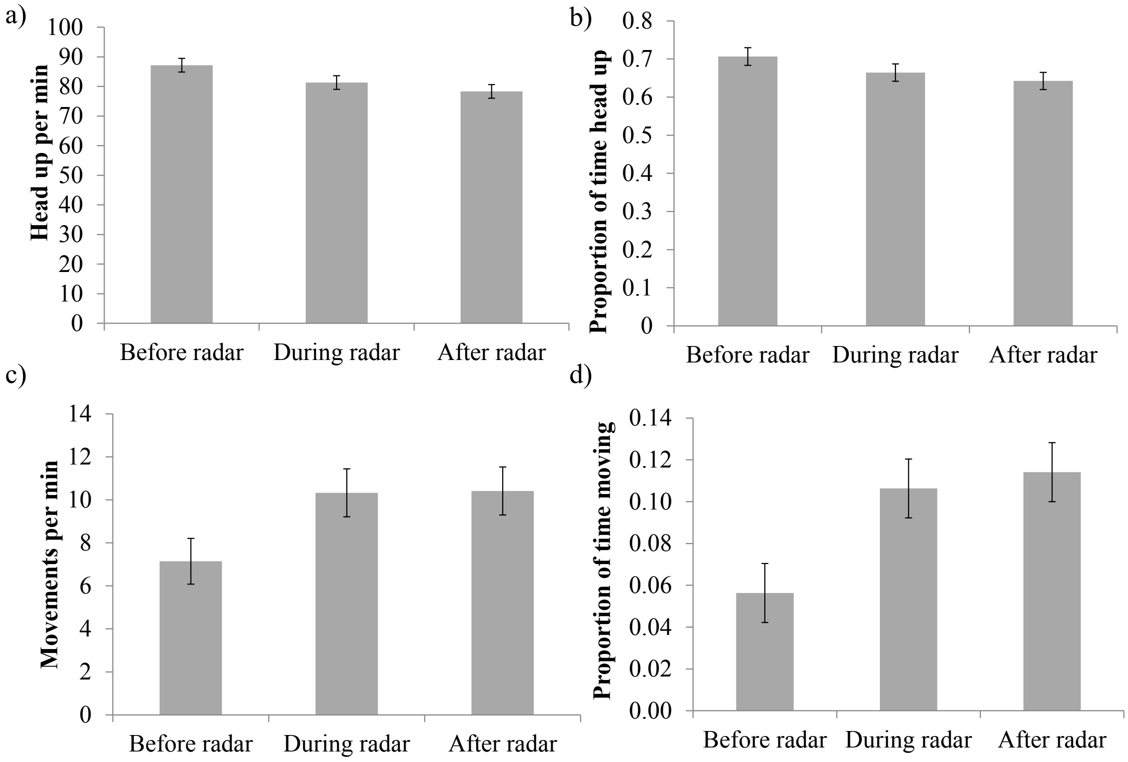

Figure 4

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 static radar experiment 1. The significant changes were from before to during and after radar, with behaviors being similar during and after radar. All behaviors are defined in Table 1.

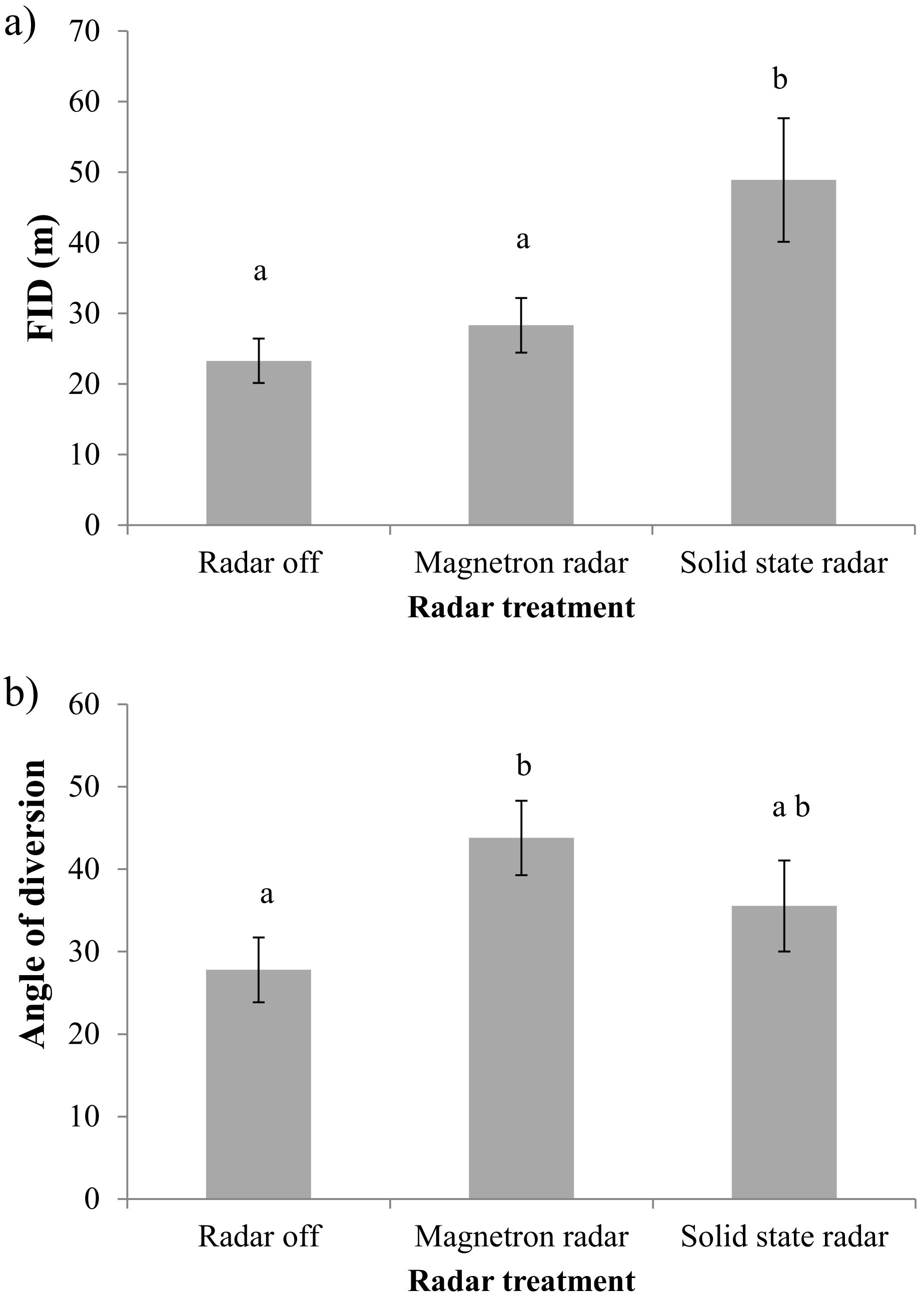

Figure 5

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.

APPENDIX

APPENDIX

Camera Calibration

Each day the experimenter calibrated the overhead cameras using a checkerboard placed in many different positions and angles within the arena. The checkerboard had squares of 12 cm sides, and was 5 squares long on each side. At all times the entire checkerboard was in view of both overhead cameras (C3 and C4 in Figure 2a). From the left and right overhead cameras, we took the two synchronized videos and cut them into a series of individual frames and then exported those frames as images using Virtual Dub (Avery Lee, Version 1.9.11). These pairs of images were of the board in the same location at the same time, as seen in each of the two cameras. At least 40 pairs of images were used for each day's calibration. This procedure was performed each day because the cameras were taken down at the end of each day. This might have moved the cameras' angle or position between days, but not during a day.

We imported these image pairs into MATLAB, using the Image names button in the Camera calibration tool window. This process was done separately for the right and left cameras. Then we used the Extract grid corners button, which required the input of the image file names, the number of images, the pixel size for the program to search for a corner (we used either 1 or 2 pixels), and whether to use the automatic square counting mechanism. Once that information has been input, the Extract grid corners tool displays each image individually and requires the user to click on the outside corners of the grid. The Extract grid corners tool then fills in the likely locations of each of the internal corners. If those corners were not correct, we made an initial guess for distortion to ensure the corners were located correctly. The program then extracts the corners, and moves on to the next image. After extracting the corners of the grid in at least 40 images, we used the Calibration button of the Camera calibration tool to calculate the properties of the camera given the corners extracted from the images. This procedure generates a file containing information such as the focal length, skew, and distortion of the camera. Before saving these results, the reprojection error in pixels can be displayed using the Analyze error button. If this error was greater than 3 pixels in any direction, we determined which images were generating the error, and re-extracted the corners of the grid in those images. Detailed instructions and example files to perform this procedure can be found at: http://www.vision.caltech.edu/bouguetj/calib_doc/htmls/example.html. This program is based on the following references: Brown, 1971, 1966; Clarke and Fryer, 1998; Fryer and Brown, 1986; Heikkila and Silvén, 1997; Sturm and Maybank, 1999; Tsai, 1987; Zhang, 1999.

Stereo triangulation

We performed the above calibration process for both the right and left cameras, using the pairs of images of the grid. We then used the Stereo Camera Calibration Toolbox to combine the left and right calibration parameters and determine the layout of the two cameras. To do this we used the Load left and right calibration files button, and input the calibration files from the above section from both cameras. For this to function properly the calibration files must be based on the same number of images, all in pairs. Then we used the Run stereo calibration button to generate a new stereo calibration file that contained the previously-generated intrinsic parameters of the left and right camera (e.g focal length) as well as extrinsic parameters of the stereo rig (i.e. the rotation and translation vectors between the two cameras). This file can be visually inspected for accuracy using the Show Extrinsics of stereo rig button to display the position of the two cameras and the positions of the board in all the pairs of images relative to the two cameras. We inspected the extrinsics of the stereo rig to ensure that all of the grids fell within the boundaries of the semicircular arena. Generating the extrinsic parameters of stereo rig was based on Rodrigues' formula (Rodrigues, 1840).

Once the stereo calibration file was saved, we used the tool stereo_triangulation. The inputs required for this are a 2xN matrix of the pixel coordinates of the birds' beak's location in each frame of the flight in both the left and right camera and the output of the stereo calibration. The output of this tool is a 3xN matrix of the three-dimensional position of the beak in each frame of the flight, relative to a constant reference point (set as the left overhead camera, C3 in Fig. 2a). To correct for the angle of the reference camera relative to the experimental arena, each day we also found the three dimensional position of vertical and horizontal reference segments (the outside edges of the arena). These reference points were used to correct angles measured between the three-dimensional positions of the birds' beaks, so that the vertical angle was relative to the ground, and the difference from the path of the vehicle was relative to the vehicle's path and not the position of the reference camera.

The error of this method was calculated by placing an object at 8 known positions within the arena, simulating a bird's flight. The distances and angles between these 8 positions were measured using both the Calibration Toolbox and the known positions. We found a range of error in the Calibration Toolbox of 0.4 – 11 cm, with an average error of 6.6 ± 0.5 cm.

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