Lights tuned to the avian eye result in early detection and escape from an approaching aircraft

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1. Summary

Collisions between birds and aircraft are a global problem. We identified different behavioral parameters affecting the probability of escape to an approaching aircraft, which is a function of the probability that the animal initiates an escape response (*probability of reaction*) and the probability of having enough time to escape (*probability of sufficient time*). Lights of high chromatic contrast tuned to the avian eye have been proposed as a solution to mitigate collisions. We approached Canada geese with a drone to estimate how aircraft lighting and changes in altitude, mimicking the flight phase where most strikes occur, affect parameters associated with the probability of escape. Onboard lights increased parameters associated with the probability of reaction at farther distances by promoting longer detection distances, which enabled the animal to initiate each stage of its escape response sooner leading to longer flight initiation distances irrespective of altitude changes. Additionally, onboard lights increased parameters associated with the probability of sufficient time where longer detection distances allowed animals to escape away from (as opposed to towards) the approaching drone. Our findings have implications for the development of light technology to deter birds away from approaching vehicles, and other anthropogenic structures (wind turbines, solar facilities).

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2. Introduction

Most bird populations are declining globally, and the third largest source of avian mortality is bird-vehicle collisions [1,2]. Globally, a subset of those bird-vehicle collisions is caused by aircraft (hereafter, bird strikes), which also bring economic burden and safety risks for the aviation industry [3,4]. Additionally, the increase in low- altitude air operations (e.g., unoccupied aircraft systems, advanced air mobility, electrical vertical take-off and landing aircrafts) is expected to further exacerbate the bird strike problem [5,6].

One proposal to mitigate bird strikes is the use of onboard lighting to enhance detection and provide more time for the animal to initiate an escape response [7,8]. Light stimuli of high chromatic contrast to the visual system of the target species can increase detection distance due to an increase in visual conspicuousness [9] and potentially minimize the negative effects of high-speed aircraft approaches [10]. For onboard lighting to be effective, lights should facilitate avoidance responses regardless of aircraft movement as most collisions between birds and aircraft occur when the aircraft is descending in altitude (i.e., approach phase & landing phase) [3]. However, vehicle approach experiments assessing bird responses to onboard lighting have not manipulated systematically change in altitude [9,10].

Behavioral responses to an approaching vehicle determine whether a collision occurs [11-13], such as escape behavior, which refers to a sequence or combination of behaviors beginning with detection, followed by attention allocation and threat assessment, and ending in movement away from the threat [14,15]. However, our understanding of these behaviors in the context of high-speed vehicles is limited as most studies have been focused on the distance from the threat where the animal initiates escape (flight-initiation distance, [16]).

To avoid a collision with a fixed-vehicle trajectory, the animal must first detect and initiate a response, and that response must be sufficiently quick to clear the trajectory of the vehicle before it arrives at the location of the animal [11, 17]. The *probability of escaping* (which varies between 0, a collision does occur, and 1, a collision does not occur) is the product of the probability that the animal initiates an escape response (hereafter, *probability of reaction*), as a function of distance, and the probability of having enough time to escape given the distance at which the escape response occurred (hereafter, *probability of sufficient time*). In this study, we identified nine parameters commonly attributed to affecting the probability of escaping, and we classified them into two categories: probability of reaction (visual attention distance, detection latency, alert distance, pre-escape distance, threat display distance, flight-initiation distance, and latency to flee), and probability of sufficient time (escape speed, take-off latency, probability of away trajectory, Table 1).

The aim of the present study was to assess whether onboard lighting technology tuned to the visual system of the viewer could improve the probability of escape (via the parameters associated with the probability of reaction and the probability of sufficient time) in wild birds at different aircraft flight phases under controlled semi-natural conditions. We approached Canada geese (*Branta canadensis*) with an unoccupied aircraft system (hereafter, UAS) varying its degree of visual conspicuousness (lights-off, lights-on steady, lights-on pulsing), starting from different approach altitudes (level approach, descent approach) to measure the aforementioned parameters (Table 1).

We selected Canada geese as our study species because they are routinely a source of damaging and costly bird strikes [18,19] due to their size and flocking behavior. Canada goose population numbers have increased in urban areas where aircraft operations occur [18]. Therefore, understanding the escape responses of Canada geese to approaching aircraft might offer insights on how to mitigate collisions for other large bodied and social birds globally. Furthermore, visual system of Canada geese has been characterized [20,21], and they show avoidance responses to specific wavelengths [22], enabling us to test a specific light wavelength that could be successful at avoiding moving aircraft. Our findings can be applied to reduce the frequency of civil and military aircraft as well as improving the success of UAS technology in a hazing context.

We tested two hypotheses relative to light and approach type treatments. First, we hypothesized that light stimuli tuned to the visual system of the viewer improves the conspicuousness of the approaching vehicle, facilitating detection at longer distances, leading to having more time to initiate each subsequent stage of the escape response [8]. We predicted that animals in response to the light-on treatments (light-on steady and light-on pulsing) relative to the light-off treatment would have longer visual attention distances, alert distances, pre-escape distances, threat display distances, flight-initiation distances, shorter detection latency, and shorter latencies to flee. Additionally, we predicted that geese would have a combination of relatively shorter take-off latencies, faster-escape speed, and be more likely to flee away from (rather than towards) the UAS (i.e., the probability of away trajectory; see below).

Second, we hypothesized level approaches are perceived as riskier compared to descending approaches because the visual angle projected onto the retina for a descending approach is smaller upon initial detection due to a greater viewing distance [23,24] (Sun & Frost, 1998, Broom & Ruxton, 2005). Animals rely on the visual angle projected by the approaching object to assess distance away and therefore risk; where larger visual angles are associated with closer threats and thus greater risk [23,25]. Consequently, we predicted that animals reacting in response to the level approach would have longer visual attention distances, alert distances, pre-escape distances, threat display distances, flight-initiation distances, but shorter detection latencies and latencies to flee relative to the descent approach. Additionally, because of the higher perceived risk associated with the level approach, we predicted that animals would have a combination of relatively shorter take-off latencies, faster escape speeds, and be more likely to flee away from (instead of towards) the UAS (i.e., probability of away trajectory; see below). We did not have an a-priori prediction for the interaction between light and approach type.

3. Methods

Overview

We conducted our study under semi-natural conditions at the north end of Purdue University Agronomy Center for Research and Education (*A.C.R.E*) (40° 29' 34.947"N, -86° 59' 51.1152"W). Our study took place over the course of 55 days from June 20th to August 17th in 2023 and comprised 23 trial days. We ran trials between 0630 and 1300 hrs.

Animal Husbandry

We collected 190 Canada geese from Marion County, Evansville, and Scherville, IN, in collaboration with Indiana Department of Natural Resources Nuisance Waterfowl Control Operator Program [26]. Each goose was identified with a randomized combination of colored leg bands. We housed geese between two separate facilities: a facility at the Ross Biological Reserve (6.71 m wide x 10.67 m long and 3.66 m tall) and a facility at Animal Sciences Research and Education Center (7.62 m wide x 30.48 m long x 2.44 m tall). At both facilities, animals were provided water and food (cracked corn and Purina™ gamebird maintenance chow) *ad libitum*. We also provided a wide array of enrichment for the birds including pools of water, strings attached to the walls and ceilings to serve as pecking distractors, and straw bales for bedding material. In the event of serious injury or illness (i.e., 24 hours or more of inactivity) animals were sedated with isoflurane and euthanized via lethal injection (1ml/ 4.5kg of Beuthanasia) or cervical dislocation. No animals were euthanized because of this experiment. At the conclusion of this experiment individuals were retained for use in future behavioral experiments. All experimental procedures and husbandry requirements were approved by the Institutional Animal Care and Use Committee at Purdue University and overseen by Purdue Laboratory Animal Program Veterinary Staff (Purdue IACUC# 1401001019).

Experimental Arena

We released a single goose per trial into a rectangular shaped open-air arena, similar to a roadway or runway (3.66 m wide x 33.15 m long) and expanded into a hexagonal shaped sub-section (6.09 m long and 4.88 m at its widest) at the eastern end (Fig. 1). The height of the north and south sides of the arena was 1.82 m, whereas the west and east sides were respectively 0.76 m and 1.22 m tall. The sides of the arena were comprised of 1.27 cm heavy duty deer fencing (*i.e.,* black square netting) staked to the ground and fixed to 2.13 m tall posts. The west side was shortest in height to allow for the UAS to enter the arena at a lower altitude, which was approximately goose height; but a wall was still present to prevent geese from immediately fleeing the arena during the UAS launch and beginning approach. The eastern side was shorter relative to the north and south sides, simultaneously minimizing chances of geese leaving the arena, but also allowing the UAS to exit easily by gaining altitude at the eastern end. We built the arena on a grass strip in between two agricultural fields to both the north and south.

At 15.24 m into the arena, we constructed 3.05 m long x 0.46 m wide x 1.83 m tall trapezoid-shaped observation blinds, made of DuraWeb Geotextile landscape fabric, attached to the netting of the arena (Fig. 1). Both the western and eastern walls of the observation blind were placed at a slant (approximately 45°) so the observers could not be seen by the goose. The UAS launch point was behind a blind 160 m away from the western wall of the experimental arena (Fig. 1). We selected that distance because an opaque object the size of the width between the rotors of the UAS (347.5 mm) was not theoretically resolvable to the Canada goose visual system based on visual acuity estimates [20, 27, 28]. The UAS launch point and pilot (RL, FAA Certificate Number: 4780039, Part-107, https://www.ecfr.gov/current/title-14/chapter-I/subchapter-F/part-107) were hidden behind a 3.05 m wide x 2.13 m tall blind made from DuraWeb Geotextile landscape fabric and secured with posts. To standardize the launch of the UAS, we built a 0.41 m tall x 2.44 m wide platform out of cinderblocks and plywood sheathing that was located directly behind the pilot's blind.

Each trial was recorded from the perspective of 6 different, GoPro Hero 10 cameras filming at 60 frames per sec as well as the camera onboard the UAS also recording at 60 frames per sec. Cameras 1 and 6 were placed atop a 3.05 m tall and 3.81 cm diameter PVC pipe, positioned on both ends of the rectangular section of the arena (Fig. 1). Camera 1 was placed on the south side of the arena while camera 6 was located on the north side. We placed two identical PVC pipes, 3.05 m tall with a 3.81 cm diameter PVC pipes without cameras opposite of cameras 1 and 6 to the north and south respectively to make the arena symmetrical (Fig. 1). Cameras 3 and 4 were placed 6.10 m away from cameras 1 and 6, respectively, farther into the arena and on top of 2.13 m tall posts (Fig 1). Camera 3 was located on the south side of the arena, while camera 4 was placed on the north side. Finally, cameras 2 and 5 were an additional 3.05 m into the experimental arena placed at a height of 0.76 m, approximately goose height. Camera 2 was placed on the north side, whereas camera 5 was placed on the south side of the arena (Fig 1). All cameras were slanted inward towards the middle of the arena.

Behavioral Experiment

On each trial day, we gathered geese from their housing enclosure, clipped their flight feathers (to prevent the animal from taking off and leaving the arena before the UAS approach started), measured their body mass, and placed each individual in a 76.2 cm long x 48.26 cm wide x 53.34 cm tall carrying crate (*Top Paw*® Single Door Folding Wire Dog Crate) for transportation to the site of the experiment. We trimmed the flight feathers with heavy-duty 22.86 cm scissors that were sanitized with ethanol after each use. Anytime geese were being held within the carrier crates, they were given access to water *ad libtum*. While geese were waiting to receive a trial, we placed them in a shaded area to minimize the chances of thermal stress, and 95.5 m away from the east end of the arena to avoid visual access to the experimental arena.

We tested a single individual at a time. Before a trial began, we carried the animal in a completely covered crate to keep the animal calm and prevent the animal from seeing the arena prior to a trial. We randomized the release direction evenly between the north and south sides of the arena (94 trials released from the north, 89 trials released from the south; the different numbers were the result of some trials being excluded from the study as explained below). The goose was released into the arena through a 96.52 cm wide by 40.64 cm tall opening from behind the middle of the observer blind (Fig. 1). After the animal left or was prompted out of the carrier crate, cloth would fall in front of the opening so that the observers were no longer visible. We monitored the behavior of the animal through small gaps in the blind.

Each goose was given a maximum of 15 min to settle before a trial was conducted. Once we determined that the goose was not showing aggressive behavior (i.e., the animal was not actively pacing, hissing, running, or head bobbing), and the animal was facing a westward direction, the observer signalled to the UAS pilot to launch the UAS. A trial began after the UAS was launched and was no longer concealed behind the blind.

We used a DJI Mavic 3 classic multi-rotor style UAS in our approaches, controlled with the DJI smart remote controller with the anti-collision lights completely covered (Dia-Jiang Innovations, Shenzhen, China). At the beginning of each trial, after ascending to the appropriate altitude and initiating forward motion, the pilot steadily increased speed until the UAS was moving at approximately 7 m/s, which was determined to be the fastest speed the pilot could maintain to fly safely through the arena. The pilot controlled the UAS from a live video feed from the DJI onboard camera at the front of the UAS that in real time reported back both UAS altitude and speed. Additionally, visual observers directly monitored the UAS during its approach through small gaps in the observation blinds. Once the UAS was inside of the arena, it continued moving forward along a straight-fixed path trajectory regardless of the animal's location within the arena. The UAS continued to move forward until it completed transit through the arena, and it then gained altitude at the very end (i.e., the eastern side) to safely exit the arena. The UAS would only deviate from a straight-path trajectory when the pilot perceived it was necessary to avoid a collision with the goose. Out of 183 trials, only 2 UAS-goose collisions occurred. In both circumstances, the UAS came into contact with the primary feathers of the animal, which were thoroughly examined afterwards; no injuries occurred. At the conclusion of each trial, the UAS was flown back to its initial launch point, and the goose was recaptured and placed back in its carrier.

We simultaneously manipulated the light stimulus onboard the UAS (hereafter, light treatment) and the starting altitude of the UAS approach towards the goose (hereafter, approach type treatment), which resulted in six unique treatment combinations. Light treatment had three levels: light-off, light-on steady, and light-on pulsing (at 2 Hz). The light stimuli attached onboard the UAS were two Lume Cube RGB Panel Pro 2.0 (15.24 cm wide by 7.97 cm tall) connected with a threaded rod and attached to the UAS with a Hanatora Camera Expansion Mount Holder for the Mavic 3 classic. Each LED panel comprised 204 LEDs and emitted 595 lumens (approximately 931.63 W/m^2 per our measurements; supplementary Fig. 1). The lumen measurement is based on the manufacture's product specifications. Both LED panels were operated with the Lume Cube control app set to display a blue color at 100% brightness. The peak wavelength output for the blue light color was 457 nm. We used this wavelength of light because in a prior study blue wavelengths incited a consistent avoidance response by Canada geese upon repeated exposures [22]. We also selected to test both a light steady and light pulsing treatment because previous studies had demonstrated the effects of both treatments on increasing the distance the animal first reacts [9,10].

The approach type treatment had two levels: level approach and descending approach. For a levelled approach, the UAS would ascend above the pilot's blind, then descend to 1 m above the ground and begin approaching the arena; the pilot maintained an altitude of 1 m for the duration of the approach (i.e., a glide slope of 0°). For a descending approach the UAS first ascended to an altitude of 8.38 m, then steadily decreased in altitude as it approached the beginning of the arena to mimic a 3° glide slope (i.e., typical landing approach of commercial aircraft) until it reached the beginning of the arena (i.e., the west side, Fig. 1) [29].

We measured several potential covariates: temperature (C), wind speed (m/s), sound intensity (db), and irradiance ($\mu W/cm^2/nm$). Temperature, wind speed, and irradiance were measured at approximately goose height and at the location in the arena where the animal-initiated escape. Sound intensity was measured from camera position 3 within the arena per trial. Temperature and wind speed were measured with a Kestrel 3500. We did not conduct a trial if the wind speed exceeded 3 m/s. We measured sound intensity by recording the decibel level 2 secs after the UAS entered the experimental arena, using the audio files of the video recordings of camera 3. We extracted the audio files with Adobe Audition, then measured the decibel level of each audio file with Praat speech analysis software. All audio files and images of the spectrogram for those 2 secs can be found in supplementary material 3. We estimated UAS approach speed for a given trial as the average vertical-movement-adjusted-approach speed at the instance (i.e., over a 200 msec period) of each behavioral response (visual attention, alert, pre-escape, threat, flight-initiation) (supplementary materials 1). For trials 1 thorough 117 we measured absolute irradiance with an Ocean Optics, Inc. (Orlando, FL, USA) Flame-S-UV-VIS spectrometer and a P400-2-SR optical fiber with CC-3 cosine corrector attached; however, due to equipment failure, we resorted to measuring absolute irradiance with our Ocean Insight Optics Inc. Jaz spectroradiometer, with the same optical configuration as the previous spectrometer, for trials 131 to 183.

We measured irradiance by taking 2 vector irradiance measurements with the sensor pointed in each cardinal direction and 2 additional measurements with the sensor facing directly up to the sky. To summarize the irradiance spectra per trial, we then interpolated the spectral data to the nearest whole nanometer and averaged $\mu W/cm^2/nm$ to produce a single value for each 1-nm interval for irradiance. Each measurement ranged from 300 nm to 700 nm based on the spectrum of light visible to the avian visual system [30]. All recorded irradiance spectra can be found in (supplementary material 3). To analyze the effects of irradiance for each trial, we summed $\mu W/cm^2$ for all wavelengths from 300 nm to 700 (the irradiance total, $\mu W/cm^2$) as a radiometric measure of light intensity. We opted for a radiometric measure of light intensity as it is more biologically meaningful, as photometric measurements are biased by estimates of human visual perception [31].

Our study included 190 individuals gathered in the summer of 2023. Our sample size was limited primarily by the capacity of our aviaries needed to maintain high standards of animal husbandry. We did not consider 7 trials due to interference that occurred during trials (i.e., animals never settling, cars driving by unexpectedly, and low-flying hawks). The final sample size for our statistical analyses was 183 individuals.

Video Analysis

We analyzed videos frame by frame with Adobe Premiere Pro. All 7 cameras (i.e., the 6 placed in the experimental arena and the camera onboard the UAS) were synchronized to the nearest frame using the AtomicClock: NTP Time app, whereby prior to the start of each trial time we displayed time in h:min:sec:msec to each camera.

Prior to video analysis, we developed an ethogram of behaviors based on the existing literature of Canada goose behavior, escape behavior, and the initial observations from the pilot and observations during trials [9,13,15,32-34]. The ethogram consisted of 20 relevant aspects related to 5 distinct behaviors: visual attention, alert, threat-display, pre-escape, and flight-initiation (supplementary Table 1). Importantly, the vantage of pilot from video control of the UAS and our placement of 6 cameras in the arena allowed us to discern between responses to the approaching UAS and potential effects of stimuli from outside the arena.

Four behavioral categories occurred sequentially (visual attention, alert, pre-escape, and flight-initiation). While threat display behavior typically occurred after alert and before flight-initiation, the animal could adopt a threat display either before or after pre-escape behavior; therefore, we considered the behavior separate from the sequence of the other four behaviors. Not all animals necessarily showed each behavior in the sequence (27.33% percent of birds did not show all four behaviors). We measured each behavior in the context of distance away from the UAS at the first frame the animal started showing a specific behavioral category (supplementary Table 1). Again, every behavior was corroborated with multiple camera viewpoints to ensure the animals behavior was in response to the UAS.

We estimated the distance between the UAS and the goose with the UAS's GPS tracking data and estimates of the animal's location within the arena based on the video footage and landmarks within the arena (supplementary material 1b). We measured the difference in time between behaviors by using the difference in frame number multiplied by the frame rate to convert the measure to seconds (i.e., 1 sec/60 frames). Escape speed was measured as the distance between the location of the animal when it initiated escape and the location where escape ended (i.e., the animal slowed or stopped its movement) divided by the temporal difference between escape initiation and the end of escape [35,36]. In the event the animal ran into the side walls of the arena, we used that first frame the animal touched the arena netting as the termination of escape.

Detection latency was defined as the amount of time that passed between the first frame in which the UAS was visible to the first frame in which the animal displayed a behavioral response (either visual attention or alert behavior; [37,38]. We defined latency to flee as the amount of time between the first behavioral response to the UAS (see Detection latency, above) to the final behavioral response (i.e., typically pre-escape distance or flight-initiation distance) [39,40]. Take-off latency was defined as the temporal difference between flight initiation and the last frame the animal was touching its previous location (i.e., before leaving the ground; [41,42]).

Finally, we estimated the probability of away trajectory from a binary variable (0= the animal fled towards the UAS, 1= the animal fled away from the UAS) [43,44]. We defined towards versus away responses based on estimates of the linear escape angle between the animal's previous location and the location where escape ended and relative to the location of the approaching UAS. Escape angle measurements were limited to between 0 and 180° [45]. With the UAS at 0°, we defined a towards response as an escape angle between 0 and 90°, whereas an away response was defined as any escape angle greater than 90°. All images used to make the escape angle estimates can be found on (supplementary material 3).

Statistical Methods

We first assessed the correlations between confounding variables (time of the trial, temperature, wind speed, sound intensity, irradiance, UAS speed, and goose body mass) to minimize multicollinearity issues [46]. There were large correlations (i.e., $r > 0.50$) between trial time and irradiance ($r = 0.52$), and temperature ($r = 0.54$); and irradiance and temperature ($r = 0.67$). Additionally, there was a large correlation between wind speed and sound intensity ($r = 0.58$).

Several studies have demonstrated that ambient light intensity affects the perception of lighting in geese [9,22]. Due to the strong correlation between irradiance, trial time, and temperature we chose to retain irradiance and omit temperature and time of day because of the known influence of ambient light [9,23]. Ambient sound intensity has also been shown to affect detection and escape behavior in response to an approaching vehicle [10,47]. However, we chose to keep wind speed and remove sound intensity in our analysis for two reasons. First, our sound meter was at a fixed location within the arena, whereas the location of the animal was variable due to its movement and the size of the arena. As a result, our measure of sound intensity was not indicative of the perceived sound intensity at the location of the animal. Second, because we used the same model of UAS between trials the variation in sound between trials was likely the result of prevailing wind conditions [48].

Our intention with including wind speed as a covariate was solely to control for its potential confounding effects rather than making any type of conclusions about the effects of wind or background noise.

To test our predictions, we used general linear models to analyze the effects of light treatment and approach type treatment on our nine continuous dependent variables (Table 2), and a generalized linear model to analyze the probability of away trajectory (i.e., a binary variable). Due to the sequential nature of visual attention distance, alert distance, pre-escape distance, and flight-initiation distance, we also ran a general linear mixed model to evaluate whether the distances at which animals engaged in each behavioral stage were different and to examine how much variation among stages was due to between-individual differences.

All general linear models and the single generalized linear model included three categorical variables (light treatment, approach type treatment, approach speed), three continuous variables (wind speed, goose weight, irradiance) and three different interaction effects (light treatment and approach type treatment, light treatment and approach speed, and approach type treatment and approach speed). We measured approach speed as a continuous variable; however, after plotting speed against each of the dependent variables, we noticed that the relationships were profoundly non-linear, violating the linearity assumption of general linear models [49]. We decided to transform approach speed into a categorical variable to improve model fit, following this criterion: speeds less than or equal to the mean observed UAS speeds (5.52 m/s) were categorized as slow speeds (0.27 m/sec to 5.52 m/sec), whereas those greater than the mean, as fast speeds (5.52 m/sec to 8.09 m/sec). We also included body mass as a potential confounding factor in escape behavior [50]. To meet the normality of residuals and homoscedasticity assumptions of general linear models, we log-transformed threat display distance, pre-escape distance, flight-initiation distance, and take-off latency.

Unfortunately, trials 118-130 were missing irradiance data due to equipment failure in the field. To avoid information loss in the models due to pairwise deletion, we used predictive mean matching to impute the values with the *mice* package [51]. We used temperature and time of day, given their strong correlations with irradiance, to find trials with similar values where we had irradiance measurements. This process generated a candidate pool of potential irradiance values for each trial with missing irradiance data. To summarize the pool of candidate values, we averaged 50 random values drawn from each candidate pool as an estimate of the average potential candidate value. We then substituted these values for the missing irradiance data. We ran our final statistical analysis with and without the imputed values to ensure they were qualitatively similar with regards to significant effects. Herein, we present the results with the imputed values (Table 2) and note in our results where the results were not qualitatively similar. All model results without the imputed values are reported in supplementary table 2. The average pool of potential candidate values can be found in supplementary material 3.

We used the *stats* package to run both our general and generalized linear models [52]. We determined significance for each independent variable with type 3 sum of squares analysis from the *psych* package for all models [53]. Additionally, we also estimated the partial omega-squared for each independent variable as a measure of effect size. We evaluated the homogeneity of variance and normality of error assumptions for each model with the *performance* package in R [54]. We also used the *performance* package to implement a consensus-based approach to detect outliers [54]. We used both Cook's distance and the minimum covariance determinant to check for outliers and only chose to remove observations if an observation was deemed an outlier by both metrics; however, no outlier was identified. Whenever light treatment was significant for a given dependent variable, we utilized t-tests via the *emmeans* package [55] for pairwise comparisons among the three categories.

We also calculated the arithmetic means for each light treatment for all dependent variables and estimated the differences between the means of the light-on steady or light-on pulsing treatments and the mean of the light-off treatment as a measure of raw effect size (Table 3). We then used a bootstrap simulation with the *Durga* package to estimate the bootstrapped confidence intervals (presented in brackets) around the differences in the means between light treatments [56]. We opted to use the arithmetic means (rather than the predicted means of the models) to inform managers of the biologically realistic effect sizes that could be used when applying our findings to potential management strategies.

We ran a general linear mixed model, using the *afex* package, with behavioral category (i.e., distance away from the UAS for each of the four behavioral responses in the sequence) as the main, independent, fixed factor [57]. Our model considered 732 observations belonging to 183 individuals. The model also included three other fixed main factors (light treatment, approach type treatment, approach speed), and three two-way interactions (behavioral category and light treatment, behavioral category and approach type treatment, behavioral category and approach speed). The Kenward Rogers approximation was used to evaluate the significance of each independent variable for the fixed effect structure with the bound optimization quadratic approximation. The random effect structure included behavioral category as a within-subject factor and individual ID as a random factor, with random intercepts and random slopes, and with their correlations removed to allow for model convergence. To reduce the chances of singular fits we simplified the fixed structure by removing all two-way interactions [58,59] using the *nmkbw* optimizer.

We then estimated the marginal R^2 (variance attributed to just fixed effects) and conditional R^2 (variance attributed to both fixed and random effects) for our mixed model. We used the difference between the marginal and conditional R^2 estimates as a proxy of how much variation in behavioral response distance is accounted for by the random effects [60,61]. We also estimated repeatability as the population variance associated with between-individual differences in random intercepts and random slopes [61]. The repeatabilities of the random slopes provided an estimate of the between-individual variation in the rate of change between the following stages (rather than the variation within each stage): from visual attention distance to alert distance, from alert distance to pre-escape distance, and from pre-escape distance to flight initiation distance. We then ran correlations between the repeatabilities of the intercepts and the repeatabilities of the three aforementioned slopes to determine if individuals that became aware farther away from the UAS would also tend to show positive or negative trends with changes in the different stages. Following

Baker et al. (2018)[62], we categorized repeatability values ≤ 1 to 20 % as low individual variation, > 20% or ≤ 40% as moderate and any score > 40% as high [63].

We used R programming [52] to conduct all statistical analyses and to create our figures. Specifically, all our code was run in R version 4.3.2 except for the single general linear mixed model and data imputation which was run in R version 4.2.1 due to update incompatibilities. All data and code used for this study is available on Open Science Framework (https://osf.io/q57vx/?view_only=cff9808fd73d4493b400bc20fe42aa86).

4. Results

Herein, we report significant ($P < 0.05$) and non-significant ($P \geq 0.05$) effects for each of our models. Arithmetic means and the 95% confidence intervals are presented in brackets for both light and approach type treatments. Table 3 reports effect sizes for the light effects. Additionally, we report the results of the Tukey pairwise comparison tests for light treatment and the interactions of other factors with light treatment when significant.

Visual attention distance

Visual attention distance was significantly affected by light treatment (Table 2), whereby the light-on pulsing treatment (172.24 m [165.34, 177.31]) led to significantly longer visual attention distances compared to the light-off treatment (149.40 m [137.16, 159.68]) ($t_{155} = 2.57$, $P = 0.030$), but without significant changes between the light-on pulsing and light-on steady (164.47 m [153.71, 172.12]) ($t_{155} = 1.426$, $P = 0.330$) and the light-on steady and light-off treatments ($t_{155} = 1.13$, $P = 0.495$)(Table 3). Approach type treatment did not significantly affect visual attention distance (level, 160.56 m [152.31, 166.98]; descending, 163.06 m [152.74, 170.97]) nor was the interaction between light and approach type treatments significant (Table 2).

Approach speed significantly affected visual attention distance (Table 2). When approached at slower speeds (177.69 m [171.69, 180.55]), geese initiated their visual attention response to the

UAS 32.23 m farther compared to a faster approach speed (145.46 m [135.78, 154.19]) (Table 3). Further, the effect of light treatment was modulated by approach speed, as the interaction between both factors was significant (Table2, Fig. 2a). Specifically, visual attention distances at slow relative to fast approach speeds were significantly higher for the light-off (t_{155} = 6.20, P < 0.001) and light-on steady (t_{155} = 2.84, P = 0.005) treatments, but not for the light-on pulsing treatment (t_{155} = 1.66, P = 0.10) (Fig. 2a). All other effects were not significant (Table 2).

Alert distance

Alert distance was not significantly affected by light treatment (Table 2) (light-off, 123.23 m [107.18, 137.08]; light-on steady, 140.49 m [127.81, 151.21]; light-on pulsing, 142.67 m [129.48, 154.48]) (Table 3). When the imputed values for irradiance were removed, light treatment became significant (supplementary Table 2). Additionally, both approach type treatments (level, 133.16 m [122.25, 142.69]; descending, 137.45 m [125.60, 148.07]) and the interaction between light and approach type treatment were not significant (Table 2). Alert distance was significantly affected by approach speed (Table 2). When approached at slower speeds (171.82 m [165.93, 176.05]), geese adopted an alert response to the UAS 71.96 m farther away compared to a faster approach speed (99.86 m [90.37, 109.62]). All other effects were not significant (Table 2).

Pre-escape distance

Pre-escape distance was not significantly affected by light treatment (light-off, 73.00 m [58.30, 89.30]; light-on steady, 87.19 m [72.09, 102.55]; light-on pulsing, 92.18 m [76.42, 110.70]) (Table 3), approach type treatment (level, 79.87 m [69.52, 92.39]; descending, 88.77 m [75.13, 102.43]), nor the interaction between light and approach type treatment (Table 2). Approach speed significantly affected pre-escape distances (Table 2). When approached at slower speeds geese began preparing to escape 50.97 m farther from the UAS (108.87 m [94.64, 122.02]) compared to faster approach speeds (57.90 m [49.79, 67.13]). However, when the imputed values for irradiance were removed, approach speed no longer significantly affected pre-escape distance (supplementary table 2). Wind speed significantly affected pre-escape distance, whereby geese had shorter pre-escape distances with faster wind speeds (β= -0.300,SE=0.094, based on log transformed pre-escape distance). All other effects were not significant (Table 2).

Threat display distance

Threat display distance was not significantly affected by light treatment (light-off, 15.59 m [13.27, 19.42]; light-on steady, 14.51 m [11.02, 30.09]; light-on pulsing, 14.43 m [12.75, 17.24]) (Table 3), approach type (level, 11.26 m [10.08, 12.79]; descending,17.54 m [15.06, 22.86]), or the interaction between light and approach type treatment (Table 2). Wind speed significantly affected threat display distance, whereby geese had shorter threat display distances with faster wind speeds (β= -0.181, SE= 0.067, based on log transformed threat distance model). All other effects were not significant (Table 2).

Flight-initiation distance

Flight-initiation distance was significantly affected by light treatment (Table 2), whereby the light-on steady (22.68 m [16.87, 32.69]) and light-on pulsing (22.85 m [17.25, 33.68]) treatments led to longer flight-initiation distances than the light-off treatment (12.94 m [11.00, 15.63]) (Table 2 and 3). However, no pairwise comparison was significantly different (light-on pulsing and light-off, t_{165} = 1.50, P = 0.295; light-on steady and light-off, t_{165} = 1.41, P = 0.340; light-on pulsing and light-on steady, t_{165} = 0.09, P = 0.996). The difference in findings might be related to the *t*-statistic only considering the means between groups, as opposed to the *F*-statistic considering the ratio of the variances.

Approach type treatment did not have a significant effect on flight-initiation distance (level, 18.54 m [15.28, 24.38]; descending, 20.34 [15.49, 29.46]) (Table 2). However, the interaction between light and approach type treatment was significant. For the level UAS approach there were no significant differences between light treatments (light-on pulsing vs. light-off, t_{165} = -0.43, P = 0.90; light-on steady vs. light-off, t_{165} = -0.81, P = 0.700; light-on pulsing vs. light-on steady, t_{165} = 0.38,

P = 0.925). But for a descending UAS approach, geese had longer flight-initiation distances with light-on steady (t_{165} = 2.73, P = 0.019) and light-on pulsing (t_{165} = 2.49, P = 0.037) treatments compared to the light-off treatment, and without significant differences between light-on pulsing and light-on steady treatments (t_{165} = -0.24, P = 0.970) (Fig. 2b). All other effects were not significant (Table 2).

Detection latency

Detection latency (i.e., time between UAS becoming visible to first behavioral response) was significantly affected by light treatment (Table 2). Geese reacted to the UAS sooner after it first became visible for both the light-on steady (6.91 sec [5.27, 9.05]) and light-on pulsing (5.89 sec [4.49, 8.02]) treatments compared to the light-off treatment (11.61 sec [9.10, 14.31]) (Table 3). Detection latency in the light-on pulsing treatment was significantly faster than in the light-off treatment (t_{170} = -2.64, P = 0.025), but there were no significant differences between the light-on steady and light-off (t_{170} = -1.73, P = 0.199) or the light-on pulsing and light-on steady (t_{170} = -0.92, P = 0.628) treatments. Both approach types (level, 7.80 sec [6.28, 9.43]; descending, 8.62 sec [6.70, 10.70]) and the interaction between light and approach type did not significantly affect detection latency (Table 2).

Approach speed significantly affected detection latency, where geese reacted 9.98 sec sooner when approached at slower speeds (3.13 sec [2.48, 4.23]) compared to faster speeds (13.11 sec [11.27, 15.15]). The interaction between light treatment and approach speed was also significant. For each light treatment the differences between slow and fast approach speeds were significant. However, those differences were the greatest for the light-off treatment (light-off fast vs. light-off slow, t_{170} = -7.32, P < 0.001) in that detection latency was longest for the light-off treatment when approached at a fast speed. However, the differences in latency between slow and fast approach speed decreased due to a decrease in detection latency in response to the light-on steady (light-on steady fast vs. light-on steady slow, t_{170} = -4.62, P < 0.0001) and light-on pulsing (light-on pulsing fast vs. light-on pulsing slow, $t_{170} = -3.32$, $P = 0.001$) treatments. All other effects were not significant (Table 2).

Latency to flee

Latency to flee (i.e., time to initiate escape after the first behavioral response) was significantly affected by light treatment (Table 2), whereby geese were slower to initiate escape after first reacting to the light-on pulsing treatment (28.91 sec [26.35, 31.29]) compared to the light-on steady (25.77 sec [23.19, 27.88]) and the light-off treatments (23.67 sec [20.79, 26.46]) (Table 2 and 3). However, the pairwise comparisons between these light treatments were not significant (light-on pulsing vs. light-off, $t_{170} = 1.94$, $P = 0.13$; light-on steady vs. light-off, $t_{170} = -0.20$, $P = 0.98$; light-on pulsing vs. light-on steady, $t_{170} = 2.14$, $P = 0.09$), possibly due to the aforementioned limitations with the *t*-statistic. We did not find a significant effect of approach type (level, 24.42 sec [22.51, 26.23]; descending, 27.79 sec [25.30, 30.06]), and the interaction between light and approach type was also not significant (Table 2).

Approach speed significantly affected latency to flee (Table 2); when approached at slower speeds (30.86 sec [28.68, 32.53]) geese took 9.44 sec longer to initiate an escape response compared to faster approach speeds (21.42 sec [19.41, 23.35]). The interaction between light treatment and approach speed was also significant (Table 2), where geese generally took longer to flee after detection for slow compared to fast approach speeds, but the differences between speeds were more pronounced in the light-off treatment ($t_{170} = 6.07$, $P < 0.001$) relative to the light-on steady ($t_{170} = 3.17$, $P = 0.002$) and light-on pulsing ($t_{170} = 2.93$, $P = 0.004$) treatments (Fig. 2d). All other effects were not significant (Table 2).

Escape speed

Escape speed (i.e., movement speed after escape) was not significantly affected by light treatment (light-off, 3.12 m/sec [2.79, 3.52]; light-on steady, 3.10 m/sec [2.67, 3.62]; light-on pulsing, 2.50 m/sec [2.13, 2.95]) (Table 3), approach type treatment (level, 3.05 m/sec [2.71, 3.44]; descending, 2.77 m/sec [2.48, 3.12]), nor the interaction between light treatment and approach type treatment (Table 2). All other effects in the model were not significant (Table 2).

Take-off latency

Take-off latency (i.e., time interval between the initiation and movement) was significantly affected by light treatment (Table 2). Geese were slower to take-off for both the light-on pulsing (526.49 msec [448.70, 640.75]) and light-on steady treatments (595.32 msec [479.77, 819.39]) compared to the light-off treatment (475.56 msec [405.39, 565.21]) (Table 3), yet all the pairwise comparisons yielded non-significant results (light-on steady and light-off, $t_{160} = 0.91$, $P = 0.638$; light-on pulsing and light-off, $t_{160} = 0.71$, $P = 0.756$; light-on pulsing and light-on steady, $t_{160} = -0.19$, $P = 0.981$).

Take-off latency was significantly affected by approach type, whereby geese were slower to take-off for a level UAS approach (568.70 msec [495.37, 675.44]) compared to a descending UAS approach (491.16 msec [416.87, 644.93]) (Table 2). After removing the imputed values approach type was no longer significant (supplementary table 2). Importantly, when the imputed values were removed approach type was no longer significant. The interaction between light and approach type treatment was not significant nor were any other independent factors (Table 2).

Probability of away trajectory

The probability of away trajectory from the UAS was significantly affected by light treatment, where geese were more likely to flee away from (instead of towards) the UAS in response to the light-on steady (29.82% [20.86.71, 38.79]) and light-on pulsing (31.48% [22.38, 40.58]) treatments compared to the light-off treatment (22.95% [14.71, 31.19]) (Table 2 and 3). However, the pairwise comparisons did not yield significant differences between light treatments (light-on pulsing vs. light-off, $z = -1.87$, $P = 0.148$; light-on steady vs. light-off, $z = -1.73$, $P = 0.194$; light-on pulsing vs. light-on steady, $z = -0.16$, $P = 0.986$). The probability of away trajectory was also significantly affected by approach type treatment, whereby geese were more likely to flee away from (instead of towards) the

UAS during a level approach (34.83% [25.49, 44.17]) compared to a descending approach (20.48% [12.57, 28.39]) (Table 2).

The interaction between light and approach type treatment was also significant (Table 2; Fig. 2e); whereby when the UAS approached at a level altitude, there were no significant differences between light treatments (light-on pulsing vs. light-off, $z = 1.07$, $P = 0.526$; light-on steady vs. light-off, $z = 0.54$, $P = 0.852$; light-on pulsing vs. light-on steady, $z = 0.55$, $P = 0.848$). However, for a descending UAS approach, the probability of fleeing away (instead of towards) was higher with the light-on pulsing compared to the light-off treatment ($z = -2.61$, $P = 0.025$), but no significant differences were found between the light-on steady and light-off ($z = -2.19$, $P = 0.073$) and light-on pulsing and light-on steady treatments ($z = -0.72$, $P = 0.755$). All other variables were not significant (Table 2).

Differences in distance between behavioral stages

When considering the sequence of behavioral categories studied (visual attention distance, alert distance, pre-escape distance, and flight initiation distance), we found that distance at which animals reacted varied significantly depending on the behavior ($F_{3, 232} = 601.99$, $P < 0.001$). Specifically, visual attention distance (161.77 m [155.38, 166.56]) was longer than alert distance (135.25 m [127.42, 143.15]), alert distance was longer than pre-escape distance (84.08 m [74.86, 93.42]), and pre-escape distance which was longer than flight-initiation distance (19.40 m [16.17, 23.64]). Considering all behavioral categories together, light treatment ($F_{2, 177} = 2.88$, $P = 0.059$; lights-off, 90.02 m [80.23, 98.18]; lights-on steady, 106.84 m [97.64, 117.02]; lights-on pulsing, 104.09 m [95.06, 113.25]) and approach type ($F_{1,177} = 2.50$, $P = 0.116$; level, 97.84 m [90.13, 105.80]; descending, 102.72 m [95.03, 111.07]) were not significant. Yet, approach speed was significant ($F_{1,177} = 97.94$, $P < 0.001$; slow, 120.74 m [112.96, 128.93]; fast, 79.69 m [73.44, 86.11]).

The fixed effects in our mixed model explained 69.8% of the variation (R^2 marginal), whereas the combination of both fixed and random effects explained 83.6% of the variation (R^2 conditional). The mixed model allowed us to explore the proportion of the variance in the random effects due to between-individual variation. Variance associated with baseline differences between individuals in visual attention distance (i.e., repeatability of the random intercepts) was 23.9%. The percentages of population variance associated with between-individual differences in their transition from visual attention distance to alert distance was functionally 0%, from alert distance to pre-escape distance was 14.6%, and from pre-escape distance to flight initiation distance was 15.1% (i.e., repeatability of the random slopes between behavioral categories).

We assessed if there was an association between the between-individual variation in visual attention distance and the rates of change between behavioral stages in the sequence (i.e., individuals with long visual attention distances – intercepts –have longer or shorter rates of change – slopes – between stages in the behavioral sequence). We found a low positive association between the visual attention distance intercepts and the slopes from visual attention distance to alert distance (Pearson's correlation $r = 0.09$, Fig. 3a), and between the visual attention distance intercepts and the slopes from alert distance to pre-escape distance (Pearson's correlation $r = 0.28$; Fig. 3b). However, we found a moderate positive association and between the visual attention distance intercepts and the slopes from pre-escape distance to flight initiation distance (Pearson's correlation $r = 0.43$; Fig. 3c). Overall, individuals that turned their visual attention to the UAS farther away tended to become alert, show pre-escape distance, and more pronouncedly escape farther away.

5. Discussion

The main findings of our study suggest that a UAS fitted with lights tuned to the eyes of Canada geese (457 nm) increased the probability of reaction to the UAS approach by increasing the distance at which birds first reacted (i.e., visual attention distance), leading animals to initiate each stage of their escape sequence relatively sooner, ultimately resulting in an increase in flight-initiation distance. Light-on treatments also increased the probability of sufficient time by increasing the probability of away trajectory from the UAS but decreased the probability of sufficient time by slowing down take-off latencies (Table 2, Fig. 2e). The effects of light treatment on visual attention distance, detection latency, and latency to flee were modulated by approach speed [10], whereas the effects of light treatment on flight-initiation distance and the probability of away trajectory were modulated by approach type (Fig. 2b & 2e). Finally, Canada geese maintained similar alert distances, threat display distances, pre-escape distances, and escape speeds irrespective of our light and approach type treatments.

The UAS fitted with lights-on steady and pulsing increased visual attention distance by 10.08% and 15.29%, respectively, compared to the light-off treatment (Table 3). For reference, Blackwell et al. (2012) [9] found that on average the first alert response in a group of Canada geese (i.e., comparable to our visual attention distance) increased by 45.35% in response to a remote-controlled aircraft with lights-on pulsing compared to a light-off treatment. Additionally, Blackwell et al. (2009)[64] found that the first alert response in a group of brown-headed cowbirds approached by a truck fitted with a light increased by 3.77% and 29.24% in response to light-on pulsing (2 Hz) and the light-on steady treatments, respectively, compared to the light-off treatment. Yet, the same study [64] found the opposite response in mourning doves, where the average first alert distance in a group decreased by 8.33% and 7.69% in response to a light-on pulsing and light-on steady treatment, respectively, compared to a light-off treatment. While generally, lights tuned to the eyes of the target species improves detection [65], the trend and its magnitude are not the same for all species, which highlights the importance of how species-specific differences in physiology [47,64], sociality [66], experience [67-69], and habitat usage [12,70,71] influence vehicle escape responses.

The increase in visual attention distance in response to the light-on treatments allowed more time to initiate each subsequent behavior (cascade-effect). This increase translated into a large relative increase in flight-initiation distance of 76.56 % for the light-on pulsing treatment and 75.27% for the light-on steady treatment, compared to the light-off treatment (Table 3). Further, our findings on the positive correlations between random intercepts of visual attention distance and the random slopes of the transitions across behaviors suggest that individuals with longer visual attention distances also had longer alert, pre-escape, and flight-initiation distances, as has been found in other species [72]. This result suggests that lights increase the probability of escaping, where an increase in detection leads to an increase in the probability of reaction at longer distances (i.e., flight initiation distance). Figure 4 illustrates how the increase in visual attention distance cascaded throughout the escape sequence increasing the probability of reaction. For the light-on treatments, the distribution of visual attention distances (VAD) was highly concentrated at farther distances with a slight left skew (reversed x-axis), suggesting that geese in response to the light-on treatments drew their attention to the UAS at greater distances compared to the light-off treatment where visual attention distances were more likely to occur at a variety of both longer and shorter distances (Fig. 4). The distribution for both alert distances (AD) and pre-escape distances (PD) showed a trend towards being slightly more concentrated at longer distances for the light-on treatments compared to the light-off treatment (Fig. 4), despite the model results being non-significant (Table 3). Lastly, the distributions of flight initiation distances (FID) were generally right skewed for the light-on treatments, yet the distribution for the light-off treatment was exclusively concentrated at shorter distances (Fig. 4). The shift in distributions supports the idea that geese began every single stage of their escape sequence relatively sooner in response to the light-on treatments resulting in an increase in the probability of reaction at a farther distance.

Light treatment affected the probability of sufficient time in two different ways. First the probability of away trajectory increased by 29.93% and second, take-off latencies were 37.16% longer in response to the light-on treatments (Table 3). Commonly, prey animals when approached directly by a threat adjust their escape trajectory to out-maneuver the approaching threat [43,73]. Generally, away responses are more likely to result in the animal successfully avoiding an approaching threat [74,75]. High-speed take-offs across short distances when escaping can be metabolically costly [76]. Animals can decrease take-off latency to an increase in predation risk (i.e., take-off velocity) [42,77], but perhaps at the cost of an increased risk of starvation [78,79], suggesting animals should only adjust take-off latency when necessary. The extra time afforded by being aware of the UAS sooner likely enabled geese to execute a more informed escape response, where they increased the probability of away trajectories. Simultaneously, geese increased take-off latencies (i.e., a delay in escape) because they were most likely not forced into escaping at the last second when attempting to avoid a collision [39,80]. Our result suggests that geese relied on changes in escape trajectory (i.e., probability of away trajectory) to increase the probability of sufficient time and only adjusted take-off latency to reduce the probability of sufficient time when necessary. Level approaches increased the probability of away trajectory from the UAS by 70.06% and take-off latency by 15.79% (Table 3), which might be attributed to differences in risk perception due to changes in visual angle projected onto the retina between level and descending approaches at the moment of initial detection. Animals commonly use the visual angle subtended onto the retina to determine the size and distance to an object and the rate of change in visual angle (i.e., looming) to determine when a collision might occur [23, 81]. A UAS without lights approaching from the same horizontal distance but descending from a higher altitude would initially project a smaller visual angle due to the greater viewing distance relative to the visual angle of a level UAS approach. Likely, geese more readily recognized the risk associated with a larger initial visual angle and began to escape sooner resulting in an adjusted escape direction to flee away from the UAS [36], which simultaneously allowed for increased latency in take-offs. This emphasizes that geese relied on changes in escape trajectory (i.e., probability of away trajectory) and only adjusted take-off latency when necessary to increase the probability of sufficient time.

For the light-off treatment, geese had longer visual attention distances and briefer detection latencies when the UAS was moving at a slow compared to a fast approach speed. This decrease in latency to detect is likely the result of slow speeds providing more time for the animal to react to the approaching UAS at a given location within the visual scene and process the threat at further distances relative to a faster approach speed (Fig. 2a) [16]. However, for the light-on treatments, and particularly in the light-on pulsing treatment, the differences between approach speeds for both visual attention distance and detection latency were reduced (Fig. 2a). This finding suggests that light-on treatments mitigated the negative consequences of approach speed, likely due to an increase in visual conspicuousness that was more likely to enhance visual attention soon after the UAS first became visible and at longer distances [82,83]. Doppler et al. (2015)[10] found a similar trend in brown-headed cowbirds, whereby their alert responses to an approaching RC aircraft were attenuated by a light-on pulsing treatment and eliminated by a light-on steady treatment. The result suggests that in response to the light-on treatments geese were aware of the approaching UAS sooner even if it had already began approaching at a faster speed, which enabled geese to increase the probability of reaction at longer distances.

Latency to flee (i.e., time elapsed from first observed behavioral response to when the animal-initiated escape) was modulated by the interaction between light treatment and approach speed. For the light-off treatment, geese had briefer latencies to flee when the UAS was approaching at a fast compared to a slow speed (Fig. 2d). Faster approach speeds are associated with greater perceived risk, less time to process and respond, and thus briefer latencies [50]. However, during the light-on treatments, primarily the light-on pulsing treatment, escape latencies were longer and the differences in latency to flee between fast and slow approach speeds were smaller, albeit still significantly different between speeds (Fig. 2d). Interestingly though, geese in response to the light-on treatments showed longer visual attention distances and longer flight-initiation distances, despite longer latencies to flee (Table 3). We would expect latency to flee to vary if either variable alone changed (i.e., an increase in visual attention distance results in an increase in escape latency, an increase in flight-initiation distance results in a decrease in escape latency). However, what we found is that both visual attention distance and flight-initiation distance increased simultaneously, but at different magnitudes, resulting in a net increase in latency to flee. Specifically, the light-on treatments led to a larger increase in visual attention distance (18.96 m) compared to flight-initiation distance (9.83m) (Table 3). This finding suggests that geese might lengthen the latency to flee to further assess risk about the approaching threat, resulting in a delayed escape [17,39]. In essence, earlier visual detection allows for longer periods to process the threat before initiating escape, but also showing longer flight-initiation distances. Generally, longer escape latencies will reduce the probability of escaping because the more time that elapses prior to the animal initiating escape (i.e., a decrease in the probability of reaction) results in the threat getting that much closer decreasing the probability of sufficient time. However, escape latency must be understood within the context of when the animal first became aware of the approaching threat because if the animal detected the threat at a longer distance than a relatively longer escape latencies might have an inconsequential effect on the probability of sufficient time, compared to if the threat was detected at a shorter distance.

The effects of light treatment on flight-initiation distance and the probability of away trajectory from the UAS were modulated by approach type. During level approaches, the differences between light-off and both light-on treatments were minimal (Fig. 2b & 2e). But during descending approaches, geese increased both flight-initiation distance and the probability of away trajectory from the UAS in response to the light-on treatments compared to the light-off treatment (Fig. 2b & 2e). During a descending approach and light-off treatment, the UAS generated a smaller visual angle which might have limited detection. However, for descending approaches coupled with the light-on treatments, detection of the approaching object was no longer limited to just the angular size of the UAS, as the light provided additional visual cues, such as a light intensity and chromatic contrast [10,84]. As such, lighting facilitated greater awareness of the UAS, prompting the animal to initiate its escape sequence sooner resulting in an increase in the probability of escaping through increasing the probability of reaction.

Commonly, differences in escape behavior are attributed to between-individual variation [85,86]. For a stimulus to be an effective tool to mitigate collisions it ought to consistently elicit similar escape behaviors regardless of the individual [87,88]. We found that between-individual differences (i.e., repeatability of the random intercepts) accounted for a low to moderate (23.9%) level of variation in visual attention behavior. These levels of between-individual differences appear to be typical for birds (mean ± SD repeatabilities, 22.5 ± 13.4%: *Molothrus ater*, 27% [68]; *Aptenodytes patagonicus,* 10%, [89]; *Anser anser*, 45%, [90]; *Tringa totanus*, 21%, [91]; *Aphelocoma coerulescens*, 24%, [92]; *Petrochelidon pyrrhonota*, 8%, [93]). The implication is that we would expect light stimuli onboard an approaching aircraft to elicit relatively consistent changes in goose behavior regardless of the individual.

Our results have four implications for the use of lighting technology as means of reducing bird-aircraft collisions, collisions with anthropogenic structures, and also in potential hazing applications. First, an increase in detection as the result of onboard lighting can offset the negative consequence of approach speed. Aircraft speed is a major contributing factor in the context of bird-aircraft collisions [3,94]. Bird escape responses appear inadequate when approached at extremely fast approach speeds because typically the animal has little time remaining to clear the vehicles trajectory after threat detection occurs [11,17]. Our study is the second (see Doppler et al., 2015 [10]) to find that onboard lights can mitigate or offset the negative consequences of fast aircraft approach speeds.

Second, onboard lighting resulted in longer escape and higher probability of away trajectory when the aircraft was descending. Our results are similar to what others have found: descending aircraft without lights-on are less likely to prompt the initiation of escape [95,96]. However, with lights onboard, goose escape behavior was similar for both level and descending approaches. Lights might be particularly effective at helping birds initiate the proper response to aircraft changing altitude during different flight phases, which might be particularly beneficial for rotorcraft that drastically change altitude.

Third, the intensity of our light stimuli was equivalent to a 75-watt light bulb, yielding an increase in Canada goose detection and escape responses to a small approaching UAS. For perspective, the typical landing light onboard an approaching aircraft potentially produces 634 times more light than the LED panel used in our study (https://www.oxleygroup.com/product/par-64-led-replacement-landing-light). This vast difference suggests that integrating wavelengths of high visual contrast with the existing intensity of aviation lights in use could further increase the detection and escape responses, but additional testing is needed.

Fourth, UAS and onboard lighting systems paired together could increase the range at which UAS operations disturb or influence the behavior of a target species. Hazing operations involving UASs often take place at lower altitudes, which can be dangerous for both wildlife (i.e., a higher risk of collision with the UAS) and equipment (i.e., more obstacles to avoid). Based on our results, we suggest that fitting a UAS with lights tuned to the avian eye can enhance its ability to elicit escape responses when approaching from a relatively higher altitude and descending upon the animal, in turn reducing the chances of causing harm to the animals and equipment. Additionally, this technology could be applied to deter bird from wind turbines, buildings, and powerlines, which are structures that birds collide with [97-99].

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Ethical Statement

All experimental procedures and husbandry requirements were approved by the Institutional Animal Care and Use Committee at Purdue University and overseen by Purdue Laboratory Animal Program Veterinary Staff (Purdue IACUC# 1401001019). (See methods)

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Data Accessibility

All data, files, and code used in this study are available at https://osf.io/q57vx/?view_only=cff9808fd73d4493b400bc20fe42aa86

Literature Cited

1. Loss, S. R., Will, T., & Marra, P. P. (2015). Direct mortality of birds from anthropogenic causes. *Annual Review of Ecology, Evolution, and Systematics* **46**(1), 99-120. (https://doi.org/10.1146/annurev-ecolsys-112414-054133)
2. Lees, A. C., Haskell, L., Allinson, T., Bezeng, S. B., Burfield, I. J., Renjifo, L. M., Rosenberg, K. V., Viswanathan, & A., Butchart, S. H. (2022). State of the world's birds. *Annual Review of Environment and Resources* **47**(1), 231-260. (https://doi.org/10.1146/annurev-environ-112420-014642)
3. Dolbeer, R. A., Begier, M. J., Miller, P. R., Weller, J. R., & Anderson, A. L. (2023). Wildlife Strikes to Civil Aircraft in the United States, 1990–2022. *Federal Aviation Administration National Wildlife Strike Database,* **Serial Report 29,** 1-126**.** (https://www.faa.gov/airports/airport_safety/wildlife/wildlife_strikes_civil_aircraft_united_states_1990_2022)
4. Bovo, A. A., Abra, F. D., Medolago, C. A., Munhoes, L. P., & Prist, P. R. (2024). Traffic in thesky: ranking the hazard bird species to aircraft-collision in Brazil. *Ornithology Research*, **32(1)**, 11-22. (https://doi.org/10.1007/s43388-023-00165-x)
5. Mulero-Pázmány, M., Jenni-Eiermann, S., Strebel, N., Sattler, T., Negro, J. J., & Tablado, Z. (2017). Unmanned aircraft systems as a new source of disturbance for wildlife: A systematic review. *Plos One*, **12(6),** e0178448. (https://doi.org/10.1371/journal.pone.0178448)
6. Federal Aviation Administration. (2024). Federal Aviation Administration Aerospace Forecasts Fiscal Years 2024–2044. *United States Department of Transportation,* 11-38. (https://www.faa.gov/data_research/aviation/aerospace_forecasts)

7. Larkin, R. P., Torre-Bueno, J. R., Griffin, D. R., & Walcott, C. (1975). Reactions of migrating birds to lights and aircraft. *Proceedings of the National Academy of Sciences*, **72(6),** 1994-1996. (https://doi.org/10.1073/pnas.72.6.1994)

8. Blackwell, B. F., & Fernandez-Juricic, E. (2013). Behavior and physiology in the development and application of visual deterrents at airports. DeVault, T.L., Blackwell, B.F. & Belant, J.L., *Wildlife in airport environments: preventing animal–aircraft collisions through science-based management* (11-22), *John Hopkins University Press*.

9. Blackwell, B. F., DeVault, T. L., Seamans, T. W., Lima, S. L., Baumhardt, P., & Fernández-Juricic, E. (2012). Exploiting avian vision with aircraft lighting to reduce bird strikes. *Journal of Applied Ecology*, **49(4)**, 758-766. (https://doi.org/10.1111/j.1365-2664.2012.02165.x)

10. Doppler, M. S., Blackwell, B. F., DeVault, T. L., & Fernández-Juricic, E. (2015). Cowbird responses to aircraft with lights tuned to their eyes: Implications for bird–aircraft collisions. *The Condor*, **117(2)**, 165-177. (https://doi.org/10.1650/CONDOR-14-157.1)

11. DeVault, T. L., Blackwell, B. F., Seamans, T. W., Lima, S. L., & Fernández-Juricic, E. (2015). Speed kills: ineffective avian escape responses to oncoming vehicles. *Proceedings of the Royal Society B: Biological Sciences*, **282 (1801).** (https://doi.org/10.1098/rspb.2014.2188)

12. Brieger, F., Kämmerle, J. L., Hagen, R., & Suchant, R. (2022). Behavioural reactions to oncoming vehicles as a crucial aspect of wildlife-vehicle collision risk in three common wildlife species. *Accident Analysis & Prevention*, **168 (106564),** 1-11. (https://doi.org/10.1016/j.aap.2021.106564)

13. Lima, S. L., Blackwell, B. F., DeVault, T. L., & Fernández-Juricic, E. (2015). Animal reactions to oncoming vehicles: a conceptual review. *Biological Reviews*, **90(1),** 60-76. (https://doi.org/10.1111/brv.12093)

14. Branco, T., & Redgrave, P. (2020). The neural basis of escape behavior in vertebrates. *Annual Review of Neuroscience*, **43(1),** 417-439. (https://doi.org/10.1146/annurev-neuro-100219-122527)

15. Evans, D. A., Stempel, A. V., Vale, R., & Branco, T. (2019). Cognitive control of escape behaviour. *Trends in Cognitive Sciences*, **23(4),** 334-348. (https://doi.org/10.1016/j.tics.2019.01.012)

16. Lunn, R. B., Blackwell, B. F., DeVault, T. L., & Fernández-Juricic, E. (2022). Can we use antipredator behavior theory to predict wildlife responses to high-speed vehicles? *Plos One*, **17(5)**, e0267774. (https://doi.org/10.1371/journal.pone.0267774

17. Guenin, S., Pakula, C. J., Skaggs, J., Fernández-Juricic, E., & DeVault, T. L. (2024). Inefficacy of mallard flight responses to approaching vehicles. *PeerJ*, **12**, e18124. (https://doi.org/10.7717/peerj.18124)

18. Dolbeer, R. A., Seubert, J. L., & Begier, M. J. (2014). Population trends of resident and migratory Canada geese in relation to strikes with civil aircraft. *Human-Wildlife Interactions*, **8(1),** 88-99. (https://www.jstor.org/stable/24874889)

19. DeVault, T. L., Blackwell, B. F., Seamans, T. W., Begier, M. J., Kougher, J. D., Washburn, J. E., Miller, P. R., & Dolbeer, R. A. (2018). Estimating interspecific economic risk of bird strikes with aircraft. *Wildlife Society Bulletin*, **42(1)**, 94-101. (https://doi.org/10.1002/wsb.859)

20. Fernández-Juricic, E., Moore, B. A., Doppler, M., Freeman, J., Blackwell, B. F., Lima, S. L., & DeVault, T. L. (2011). Testing the terrain hypothesis: Canada geese see their world laterally and obliquely. *Brain Behavior and Evolution*, **77(3),** 147-158. (https://doi.org/10.1159/000326053)

21. 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. *Journal of Experimental Biology*, **215(19)**, 3442-3452. (https://doi.org/10.1242/jeb.073957)

22. Lunn, R., Baumhardt, P. E., Blackwell, B. F., Freyssinier, J. P., & Fernández-Juricic, E. (2023). Light wavelength and pulsing frequency affect avoidance responses of Canada geese. *PeerJ*, **11,** e16379. (https://doi.org/10.7717/peerj.16379)

23. Sun, H., & Frost, B. J. (1998). Computation of different optical variables of looming objects in pigeon nucleus rotundus neurons. *Nature Neuroscience*, **1(4)**, 296-303. (https://doi.org/10.1038/1110)

24. Broom, M., & Ruxton, G. D. (2005). You can run—or you can hide: optimal strategies for cryptic prey against pursuit predators. *Behavioral Ecology*, **16(3)**, 534-540. (https://doi.org/10.1093/beheco/ari024)

25. Ydenberg, R. C., & Dill, L. M. (1986). The economics of fleeing from predators. *Advances in the Study of Behavior,* **16,** *229-249*. (https://doi.org/10.1016/S0065-3454(08)60192-8)

26. Indiana Department of Natural Resources. Canada geese management. (https://www.in.gov/dnr/fish-and-wildlife/hunting-and-trapping/canada-geese-management/)

27. Pettigrew, J. D., Dreher, B., Hopkins, C. S., McCall, M. J., & Brown, M. (1988). Peak density and distribution of ganglion cells in the retinae of microchiropteran bats: Implications for visual acuity (Part 2 of 2). *Brain, Behavior and Evolution*, **32(1)**, 48-56. (https://doi.org/10.1159/000316042)

28. Tyrrell, L. P., Moore, B. A., Loftis, C., & Fernández-Juricic, E. (2013). Looking above the prairie: localized and upward acute vision in a native grassland bird. *Scientific Reports*, **3(1),** 3231. (https://doi.org/10.1038/srep03231)

29. Federal Aviation Administration. (2024). United States Standard for Terminal Instrument Procedures. *United States Department of Transportation*. **Order 8260.3G,** 1-564. (https://www.faa.gov/regulations_policies/orders_notices/index.cfm/go/document.information/documentID/1042947)

30. Hart, N. S. (2001). The visual ecology of avian photoreceptors. *Progress in Retinal and Eye Research*, **20(5)**, 675-703. (https://doi.org/10.1016/S1350-9462(01)00009-X)

31. Johnsen, S. (2012). *The optics of life: a biologist's guide to light in nature*. Princeton: Princeton University Press.

32. Raveling, D. G. (1969). Preflight and flight behavior of Canada geese. *The Auk*, **86(4)**, 671-681. (https://doi.org/10.2307/4083454).

33. Raveling, D. G. (1970). Dominance relationships and agonistic behavior of Canada geese in winter. *Behaviour*, **37(3-4),** 291-318. (https://doi.org/10.1163/156853970X00394).

34. Akesson, T. R., & Raveling, D. G. (1982). Behaviors associated with seasonal reproduction and long-term monogamy in Canada geese. *The Condor*, **84(2),** 188-196. (https://doi.org/10.2307/1367669).

35. Domenici, P., & Blake, R. W. (1991). The kinematics and performance of the escape response in the angelfish (*Pterophyllum eimekei*). *Journal of Experimental Biology*, **156(1)**, 187-205. (https://doi.org/10.1242/jeb.156.1.187)

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

37. Devereux, C. L., Whittingham, M. J., Fernández-Juricic, E., Vickery, J. A., & Krebs, J. R. (2006). Predator detection and avoidance by starlings under differing scenarios of predation risk. *Behavioral Ecology*, **17(2)**, 303-309. (https://doi.org/10.1093/beheco/arj032)

38. Jones, K. A., Krebs, J. R., & Whittingham, M. J. (2009). Heavier birds react faster to predators: individual differences in the detection of stalking and ambush predators. *Behavioral Ecology and Sociobiology*, **63,** 1319-1329. (https://doi.org/10.1007/s00265-009-0778-6)

39. Cresswell, Butler, Whittingham, & Quinn. (2009). Very short delays prior to escape from potential predators may function efficiently as adaptive risk-assessment periods. *Behaviour*, **146(6),** 795-813. (https://doi.org/10.1163/156853909X446217)

40. Mobbs, D., Headley, D. B., Ding, W., & Dayan, P. (2020). Space, time, and fear: survival computations along defensive circuits. *Trends in Cognitive Sciences*, **24(3),** 228-241.(https://doi.org/10.1016/j.tics.2019.12.016)

41. Provini, P., Tobalske, B. W., Crandell, K. E., & Abourachid, A. (2012). Transition from leg to wing forces during take-off in birds. *Journal of Experimental Biology*, *215*(23), 4115-4124. (https://doi.org/10.1242/jeb.074484)

42. Von Reyn, C. R., Breads, P., Peek, M. Y., Zheng, G. Z., Williamson, W. R., Yee, A. L., Leonardo, A., & Card, G. M. (2014). A spike-timing mechanism for action selection. *Nature Neuroscience*, **17(7),** 962-970. (https://doi.org/10.1038/nn.3741)

43. Domenici, P., & Blake, R. W. (1993). Escape trajectories in angelfish (*Pterophyllum eimekei*). *Journal of Experimental Biology*, *177*(1), 253-272. (https://doi.org/10.1242/jeb.177.1.253)

44. Kawabata, Y., Akada, H., Shimatani, K. I., Nishihara, G. N., Kimura, H., Nishiumi, N., & Domenici, P. (2023). Multiple preferred escape trajectories are explained by a geometric model incorporating prey's turn and predator attack endpoint. *eLife*, **12**, e77699. (https://doi.org/10.7554/eLife.77699)

45. Domenici, P., Blagburn, J. M., & Bacon, J. P. (2011a). Animal escapology I: theoretical issues and emerging trends in escape trajectories. *Journal of Experimental Biology*, **214(15),** 2463-2473.(https://doi.org/10.1242/jeb.029652)

46. Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, **36(1),** 27–46. (https://doi.org/10.1111/j.1600-0587.2012.07348.x)

47. Backs, J. A., Nychka, J. A., & Clair, C. C. S. (2022). Low audibility of trains may contribute to increased collisions with wildlife. *Transportation Research Interdisciplinary Perspectives*, **13**(100516). (https://doi.org/10.1016/j.trip.2021.100516)

48. Kapoor, R., Kloet, N., Gardi, A., Mohamed, A., & Sabatini, R. (2021). Sound propagation modelling for manned and unmanned aircraft noise assessment and mitigation: A review. *Atmosphere*, **12(11)**, 1424. (https://doi.org/10.3390/atmos12111424)

49. Poole, M. A., & O'Farrell, P. N. (1971). The assumptions of the linear regression model. *Transactions of the Institute of British Geographers*, **52**,145-158. (https://doi.org/10.2307/621706)

50. Stankowich, T., & Blumstein, D. T. (2005). Fear in animals: a meta-analysis and review of risk assessment. *Proceedings of the Royal Society B: Biological Sciences*, **272(1581)**, 2627-2634. (https://doi.org/10.1098/rspb.2005.3251)

51. Van Buuren, S., & Groothuis-Oudshoorn, K. (2011). mice: Multivariate imputation by chained equations in R. *Journal of Statistical Software*, **45(3),** 1-67. (https://doi.org/10.18637/jss.v045.i03)

52. R Core Team (2024). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

53. Revelle, W. (2020). psych: Procedures for psychological, psychometric, and personality research. *R package version*, *2* **(9).** (10.32614/CRAN.package.psych)

54. Lüdecke et al., (2021). performance: An R Package for Assessment, Comparison and Testing of Statistical Models. *Journal of Open Source Software*, **6(60)**, 3139. (https://doi.org/10.21105/joss.03139)

55. Lenth, R. (2022). *emmeans: Estimated marginal means, aka least-squares means. R package version 1.7. 2*. (https://CRAN.R-project.org/package=emmeans)

56. Khan, M. K., & McLean, D. J. (2024). Durga: An R package for effect size estimation and visualization. *Journal of Evolutionary Biology*, **37(8)**, 986-993. (https://doi.org/10.1093/jeb/voae073)

57. Singmann, H., Bolker, B., Westfall, J., Aust, F., & Ben-Shachar, M. S. (2016). afex: Analysis of Factorial Experiments. *R package version 0.16,1*. (https://CRAN.R-project.org/package=afex)

58. Singmann, H., & Kellen, D. (2019). An introduction to mixed models for experimental psychology. Spieler, D., Schumacher, E., *New methods in cognitive psychology* (pp. 4-31). Routledge.

59. Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, **24(3)**, 127-135. (https://doi.org/10.1016/j.tree.2008.10.008)

60. Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, **4(2),** 133-142. (https://doi.org/10.1111/j.2041-210x.2012.00261.x)

61. Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*, **8(11),** 1639-1644.(https://doi.org/10.1111/2041-210X.12797)

62. Baker, M. R., Goodman, A. C., Santo, J. B., & Wong, R. Y. (2018). Repeatability and reliability of exploratory behavior in proactive and reactive zebrafish, *Danio rerio*. *Scientific Reports*, **8(1),** 12114. (https://doi.org/10.1038/s41598-018-30630-3)

63. Wolak, M. E., Fairbairn, D. J., & Paulsen, Y. R. (2012). Guidelines for estimating repeatability. *Methods in Ecology and Evolution*, **3(1),** 129-137. (https://doi.org/10.1111/j.2041-210X.2011.00125.x)

64. Blackwell, B. F., Fernandez-Juricic, E., Seamans, T. W., & Dolan, T. (2009). Avian visual system configuration and behavioural response to object approach. *Animal Behaviour*, **77(3),** 673-684. (https://doi.org/10.1016/j.anbehav.2008.11.017)

65. Fernández-Juricic, E. (2016). The role of animal sensory perception in behavior-based management. Berger-Tal, O., Saltz, D., *Conservation behavior: applying behavioral ecology to wildlife conservation and management* (149-174), *Cambridge University Press*.

66. Blackwell, B. F., Seamans, T. W., DeVault, T. L., Lima, S. L., Pfeiffer, M. B., & Fernández-Juricic, E. (2019). Social information affects Canada goose alert and escape responses to vehicle approach: implications for animal–vehicle collisions. *PeerJ*, **7**, e8164. (https://doi.org/10.7717/peerj.8164)

67. Legagneux, P., & Ducatez, S. (2013). European birds adjust their flight initiation distance to road speed limits. *Biology Letters*, **9(5),** 20130417. (https://doi.org/10.1098/rsbl.2013.0417)

68. DeVault, T. L., Seamans, T. W., Blackwell, B. F., Lima, S. L., Martinez, M. A., & Fernández-Juricic, E. (2017). Can experience reduce collisions between birds and vehicles? *Journal of Zoology*, **301(1),** 17-22. (https://doi.org/10.1111/jzo.12385)

69. Dhiab, O., D'Amico, M., Boukhriss, J., & Selmi, S. (2024). Risk-taking behavior in birds foraging along interurban roads. *Journal of Ethology*, **42(3)**, 209-216. (https://doi.org/10.1007/s10164-024-00822-8)

70. 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(10)**, e109988. (https://doi.org/10.1371/journal.pone.0109988)

71. Blais, B. R., Shaw, C. J., Brocka, C. W., Johnson, S. L., & Lauger, K. K. (2024). Anthropogenic, environmental and temporal associations with vertebrate road mortality in a wildland–urban interface of a biodiverse desert ecoregion. *Royal Society Open Science*, **11(7),** 240439. (https://doi.org/10.1098/rsos.240439)

72. Samia, D. S., Nomura, F., & Blumstein, D. T. (2013). Do animals generally flush early and avoid the rush? A meta-analysis. *Biology Letters*, **9(2)**, 20130016. (https://doi.org/10.1098/rsbl.2013.0016)

73. Howland, H. C. (1974). Optimal strategies for predator avoidance: the relative importance of speed and maneuverability. *Journal of Theoretical Biology*, **47(2)**, 333-350. (https://doi.org/10.1016/0022-5193(74)90202-1)

74. Shifferman, E., & Eilam, D. (2004). Movement and direction of movement of a simulated prey affect the success rate in barn owl Tyto alba attack. *Journal of Avian Biology*, **35(2)**, 111-116. (https://doi.org/10.1111/j.0908-8857.2004.03257.x)

75. Walker, J. A., Ghalambor, C. K., Griset, O. L., McKenney, D., & Reznick, D. N. (2005). Do faster starts increase the probability of evading predators? *Functional Ecology*, **19(5),** 808-815. (https://doi.org/10.1111/j.1365-2435.2005.01033.x)

76. Nudds, R. L., & Bryant, D. M. (2000). The energetic cost of short flights in birds. *Journal of Experimental Biology*, **203(10),** 1561-1572. (https://doi.org/10.1242/jeb.203.10.1561)

77. McFarlane, L., Altringham, J. D., & Askew, G. N. (2016). Intra-specific variation in wing morphology and its impact on take-off performance in blue tits (*Cyanistes caeruleus*) during escape flights. *Journal of Experimental Biology*, **219(9),** 1369-1377. (https://doi.org/10.1242/jeb.126888)

78. Zimmer, C., Boos, M., Poulin, N., Gosler, A., Petit, O., & Robin, J. P. (2011). Evidence of the trade-off between starvation and predation risks in ducks. *Plos One*, **6(7),** e22352. (https://doi.org/10.1371/journal.pone.0022352)

79. Kou, G., Wang, Y., Ge, S., Yin, Y., Sun, Y., & Li, D. (2023). Moderate mass loss enhances flight performance via alteration of flight kinematics and postures in a passerine bird. *Journal of Experimental Biology*, **226(24),** jeb245862. (https://doi.org/10.1242/jeb.245862)

80. Tätte, K., Ibáñez-Álamo, J. D., Markó, G., Mänd, R., & Møller, A. P. (2019). Antipredator function of vigilance re-examined: vigilant birds delay escape. *Animal Behaviour*, **156**, 97-110. (https://doi.org/10.1016/j.anbehav.2019.08.010)
81. Dunn, T. W., Gebhardt, C., Naumann, E. A., Riegler, C., Ahrens, M. B., Engert, F., & Del Bene, F. (2016). Neural circuits underlying visually evoked escapes in larval zebrafish. *Neuron*, **89(3)**, 613-628. (https://www.cell.com/neuron/fulltext/S0896-6273(15)01123-X)
82. Blough, D. S. (2002). Measuring the search image: Expectation, detection and recognition in pigeon visual search. *Journal of Experimental Psychology: Animal Behavior Processes*, **28(4)**, 397. (https://doi.org/10.1037/0097-7403.28.4.397)
83. Kurylo, D. D., Chung, C., Yeturo, S., Lanza, J., Gorskaya, A., & Bukhari, F. (2015). Effects of contrast, spatial frequency, and stimulus duration on reaction time in rats. *Vision Research*, **106,** 20-26. (https://doi.org/10.1016/j.visres.2014.10.031)
84. Heap, L. A., Vanwalleghem, G., Thompson, A. W., Favre-Bulle, I. A., & Scott, E. K. (2018). Luminance changes drive directional startle through a thalamic pathway. *Neuron*, **99(2)**, 293-301.(https://doi.org/10.1016/j.neuron.2018.06.013)
85. Carrete, M., & Tella, J. L. (2013). High individual consistency in fear of humans throughout the adult lifespan of rural and urban burrowing owls. *Scientific Reports*, **3(1)**, 3524. (https://doi.org/10.1038/srep03524)
86. Sih, A., Mathot, K. J., Moiron, M., Montiglio, P. O., Wolf, M., & Dingemanse, N. J. (2015). Animal personality and state–behaviour feedbacks: a review and guide for empiricists. *Trends in Ecology & Evolution*, **30(1),** 50-60. (https://doi.org/10.1016/j.tree.2014.11.004)
87. Rankin, C. H., Abrams, T., Barry, R. J., Bhatnagar, S., Clayton, D. F., Colombo, J., Coppola, G., Geyer., M. A., Glanzman, D. L., Marsland, S., McSweeney, F. K., Wilson, D. A., Chun-Fang, W., & Thompson, R. F. (2009). Habituation revisited: an updated and revised description of the behavioral characteristics of habituation. *Neurobiology of Learning and Memory*, **92(2),** 135-138. (https://doi.org/10.1016/j.nlm.2008.09.012)
88. Blumstein, D. T. (2016). Habituation and sensitization: new thoughts about old ideas. *Animal Behaviour*, **120**, 255-262. (https://doi.org/10.1016/j.anbehav.2016.05.012)
89. Hammer, T. L., Bize, P., Saraux, C., Gineste, B., Robin, J. P., Groscolas, R., & Viblanc, V. A. (2022). Repeatability of alert and flight initiation distances in king penguins: Effects of colony, approach speed, and weather. *Ethology*, **128(4)**, 303-316.(https://doi.org/10.1111/eth.13264**)**
90. Kralj-Fišer, S., Weiß, B. M., & Kotrschal, K. (2010). Behavioural and physiological correlates of personality in greylag geese (*Anser anser*). *Journal of Ethology*, **28(2)**, 363-370. (https://doi.org/10.1007/s10164-009-0197-1)
91. Couchoux, C., & Cresswell, W. (2012). Personality constraints versus flexible antipredation behaviors: how important is boldness in risk management of redshanks (*Tringa totanus*) foraging in a natural system? *Behavioral Ecology*, **23(2),** 290-301. (https://doi.org/10.1093/beheco/arr185)
92. Beauchamp, G., & Barve, S. (2024). Gazing strategies among sentinels of a cooperative breeder are repeatable but unrelated to survival. *Biology*, **13(6)**, 458. (https://doi.org/10.3390/biology13060458)
93. Roche, E. A., & Brown, C. R. (2013). Among-individual variation in vigilance at the nest in colonial cliff swallows. *The Wilson Journal of Ornithology*, **125(4),** 685-695. (https://doi.org/10.1676/12-196.1)
94. Dolbeer, R. A., Begier, M. J., & Wright, S. E. (2008). Animal ambush: the challenge of managing wildlife hazards at general aviation airports. *Proceedings of the Corporate Aviation Safety Seminar,* **53***, 1-17.*
95. Vas, E., Lescroël, A., Duriez, O., Boguszewski, G., & Grémillet, D. (2015). Approaching birds with drones: first experiments and ethical guidelines. *Biology Letters*, **11(2)**, 20140754. (https://doi.org/10.1098/rsbl.2014.0754)
96. Pfeiffer, M. B., Hoblet, J. L., Fernández-Juricic, E., & Blackwell, B. F. (2024). Preliminary effects of UAS angle of approach on escape responses of a large-bodied raptor. *Unpublished.*
97. May, R., Reitan, O., Bevanger, K., Lorentsen, S. H., & Nygård, T. (2015). Mitigating wind-turbine induced avian mortality: Sensory, aerodynamic and cognitive constraints and options. *Renewable and Sustainable Energy Reviews*, **42**, 170-181. (https://doi.org/10.1016/j.rser.2014.10.002)
98. Masden, E. A., & Cook, A. S. C. P. (2016). Avian collision risk models for wind energy impact assessments. *Environmental Impact Assessment Review*, **56**, 43-49. (https://doi.org/10.1016/j.eiar.2015.09.001)

99. Cook, A. S., Salkanovic, E., Masden, E., Lee, H. E., & Kiilerich, A. H. (2025). A critical appraisal of 40 years of avian collision risk modelling: How have we got here and where do we go next? *Environmental Impact Assessment Review*, **110**, 107717. (https://doi.org/10.1016/j.eiar.2024.107717)

100. Dawkins, M. S. (2002). What are birds looking at? Head movements and eye use in chickens. *Animal Behaviour*, **63(5),** 991-998. (https://doi.org/10.1006/anbe.2002.1999)

101. Fernández-Juricic, E., & Kowalski, V. (2011). Where does a flock end from an information perspective? A comparative experiment with live and robotic birds. *Behavioral Ecology*, *22*(6), 1304-1311. (https://doi.org/10.1093/beheco/arr132)

102. Moore, B. A., Tyrrell, L. P., Pita, D., Bininda-Emonds, O. R., & Fernández-Juricic, E. (2017). Does retinal configuration make the head and eyes of foveate birds move? *Scientific Reports*, **7(1),** 38406. (https://doi.org/10.1038/srep38406)

103. Fernández-Juricic, E., Jimenez, M. D., & Lucas, E. (2001). Alert distance as an alternative measure of bird tolerance to human disturbance: implications for park design. *Environmental Conservation*, **28(3),** 263-269. (https://doi.org/10.1017/S0376892901000273)

104. Fernández-Juricic, E., Jimenez, M. D., & Lucas, E. (2002). Factors affecting intra-and inter-specific variations in the difference between alert distances and flight distances for birds in forested habitats. *Canadian Journal of Zoology*, **80(7)**, 1212-1220. (https://doi.org/10.1139/z02-104)

105. Card, G., & Dickinson, M. H. (2008). Visually mediated motor planning in the escape response of Drosophila. *Current Biology*, **18(17),** 1300-1307. (https://doi.org/10.1016/j.cub.2008.07.094)

106. Turesson, H., Satta, A., & Domenici, P. (2009). Preparing for escape: anti-predator posture and fast-start performance in gobies. *Journal of Experimental Biology*, **212(18),** 2925-2933.(https://doi.org/10.1242/jeb.032953)

107. Van den Hout, P. J., Mathot, K. J., Maas, L. R., & Piersma, T. (2010). Predator escape tactics in birds: linking ecology and aerodynamics. *Behavioral Ecology*, **21(1)**, 16-25. (https://doi.org/10.1093/beheco/arp146)

108. Ruxton, G. D., Allen, W. L., Sherratt, T. N., & Speed, M. P. (2004). *Avoiding attack: the evolutionary ecology of crypsis, aposematism, and mimicry*. Oxford university press.

109. Font, E., Carazo, P., Pérez i de Lanuza, G., & Kramer, M. (2012). Predator-elicited foot shakes in wall lizards (Podarcis muralis): Evidence for a pursuit-deterrent function. *Journal of Comparative Psychology*, **126(1),** 87. (https://doi.org/10.1037/a0025446)

110. Cooper, W. E., & Blumstein, D. T. (Eds.). (2015). *Escaping from predators: an integrative view of escape decisions*. Cambridge University Press.

Table 1

Variable	Unit	Definition	Category	Probability of Escaping	Stage	Citation
Visual attention distance	m	Head movement behaviors associated with the allocation of attention in the direction of the approaching UAS (supp table 1)	Probability of reaction	Positive association	Detection	100-102
Alert distance	m	Distinct and overt changes in behavioral states indicating associated with alert responses (supp table 1)	Probability of reaction	Positive association	Assessment	103,104
Pre-escape distance	m	Behaviors indicating the animal is preparing to initiate risk mitigation behaviors (supp table 1)	Probability of reaction	Positive association	Assessment & escape initiation	105-107
Threat display distance	m	Behaviors suggesting the animal is attempting to signal and deter the UAS from approaching (supp table 1)	Probability of reaction	Positive association/ unknown	Signal	108, 109
Flight initiation distance	m	Behaviors after pre-escape distance where the animal attempts to escape or mitigate risk (supp table 1)	Probability of reaction	Positive association	Escape initiation	13, 25, 110
Detection latency	s	Amount of time between when UAS was first visible to the animals first observed behavioral response	Probability of reaction	Negative association	Detection	37, 38
Latency to flee	s	Amount of time to initiate an escape response after becoming aware of the potential threat	Probability of Reaction	Negative association	Escape Initiation	39, 40
Escape speed	m/s	Movement speed over the distance between the start of the escape and the end of the escape response	Probability of Sufficient Time	Positive association	Escape Execution	35, 36
Take-off latency	s	Amount of time between the start of the animal initiating the escape and the animal displacing its body away from the original position	Probability of sufficient time	Positive association	Escape execution	41, 42, 77
Probability of away trajectory	%	The probability of moving eastward away from the UAS (instead of toward) during the escape response	Probability of sufficient time	Positive association	Escape execution	43, 44, 45,74,

Table 2

General Linear Model Results	***F***	***d.f***	$\omega\rho^2$	***P***
Visual attention distance (m) (n=168)				
Light treatment	7.520	2,155	0.074	**<0.001*****
Approach type treatment	0.319	1,155	-0.004	0.573
Goose weight	0.838	1,155	0.010	0.334
Speed	26.250	1,155	0.175	**<0.001*****
Irradiance	0.828	1,155	-0.002	0.364
Wind speed	0.002	1,155	-0.003	0.967
Light treatment X Approach type treatment	1.014	2,155	0.006	0.365
Light treatment X Speed	5.417	2,155	0.050	**0.005****
Approach type treatment X Speed	0.142	1,155	-0.005	0.707
Alert distance (m) (n=183)				
Light treatment	1.200	2,170	0.041	0.304
Approach type treatment	1.375	1,170	-0.001	0.243
Goose weight	0.937	1,170	0.012	0.334
Speed	38.209	1,170	0.461	**<0.001*****
Irradiance	0.156	1,170	-0.004	0.693
Wind speed	2.224	1,170	0.009	0.138
Light treatment X Approach type treatment	1.342	2,170	0.004	0.264
Light treatment X Speed	0.941	2,170	-0.001	0.392
Approach type treatment X Speed	2.602	1,170	0.009	0.109
Threat display distance (m) log transformed (n=118)				
Light treatment	0.051	2,105	0.004	0.950
Approach type treatment	1.871	1,105	0.095	0.174
Goose weight	0.003	1,105	-0.008	0.955
Speed	0.841	1,105	-0.005	0.362
Irradiance	0.410	1,105	-0.004	0.523
Wind speed	7.267	1,105	0.061	**0.008****
Light treatment X Approach type treatment	0.314	2,105	-0.012	0.731
Light treatment X Speed	0.188	2,105	-0.014	0.829
Approach type treatment X Speed	0.509	1,105	-0.004	0.477

Pre-escape distance (m) log transformed (n=148)				
Light treatment	0.592	2,135	0.008	0.555
Approach type treatment	0.286	1,135	0.001	0.594
Goose weight	0.572	1,135	-0.005	0.451
Speed	4.216	1,135	0.119	**0.042***
Irradiance	0.185	1,135	-0.003	0.668
Wind speed	9.976	1,135	0.051	**0.002****
Light treatment X Approach type treatment	1.210	2,135	0.003	0.302
Light treatment X Speed	0.268	2,135	-0.010	0.766
Approach type treatment X Speed	0.006	1,135	-0.007	0.940
Flight initiation distance (m) log transformed (n=178)				
Light treatment	3.692	2,165	0.012	**0.027***
Approach type treatment	1.806	1,165	-0.005	0.181
Goose weight	2.858	1,165	0.017	0.093
Speed	0.136	1,165	0.016	0.713
Irradiance	1.144	1,165	0.000	0.286
Wind speed	0.045	1,165	-0.005	0.832
Light treatment X Approach type treatment	3.675	2,165	0.025	**0.027***
Light treatment X Speed	0.048	2,165	-0.011	0.953
Approach type treatment X Speed	1.905	1,165	0.005	0.169
Escape speed (m/s) (n=168)				
Light treatment	1.390	2,155	0.018	0.252
Approach type treatment	0.031	1,155	0.002	0.861
Goose weight	0.011	1,155	-0.006	0.916
Speed	0.314	1,155	-0.002	0.576
Irradiance	0.431	1,155	-0.003	0.512
Wind speed	0.563	1,155	-0.002	0.454
Light treatment X Approach type treatment	0.754	2,155	-0.004	0.472
Light treatment X Speed	0.095	2,155	-0.011	0.909
Approach type treatment X Speed	0.083	1,155	-0.005	0.774
Take-off latency (ms) log transformed (n=173)				
Light treatment	3.354	2,160	-0.003	**0.037***

Approach type treatment	4.884	1,160	0.016	**0.029***
Goose weight	0.972	1,160	0.003	0.326
Speed	1.225	1,160	-0.002	0.270
Irradiance	0.456	1,160	-0.003	0.501
Wind speed	0.367	1,160	-0.005	0.545
Light treatment X Approach type treatment	1.776	2,160	0.012	0.173
Light treatment X Speed	1.629	2,160	0.007	0.199
Approach type treatment X Speed	0.126	1,160	-0.005	0.723
Detection Latency (s) (n=183)				
Light treatment	7.206	2,170	0.103	**<0.001*****
Approach type treatment	0.002	1,170	-0.003	0.960
Goose weight	0.227	1,170	0.002	0.635
Speed	34.994	1,170	0.294	**<0.001*****
Irradiance	1.226	1,170	0.001	0.270
Wind speed	0.133	1,170	-0.001	0.715
Light treatment X Approach type treatment	0.497	2,170	-0.002	0.609
Light treatment X Speed	4.119	2,170	0.032	**0.017***
Approach type treatment X Speed	0.768	1,170	-0.001	0.382
Latency to Flee (s) (n=183)				
Light treatment	3.914	2,170	0.044	**0.0218***
Approach type treatment	3.671	1,170	0.033	0.0571
Goose weight	0.429	1,170	-0.005	0.513
Speed	27.145	1,170	0.204	**<0.001*****
Irradiance	0.935	1,170	0.000	0.335
Wind speed	0.078	1,170	-0.003	0.781
Light treatment X Approach type treatment	0.957	2,170	0.003	0.386
Light treatment X Speed	3.071	2,170	0.022	**0.049***
Approach type treatment X Speed	0.013	1,170	-0.005	0.909

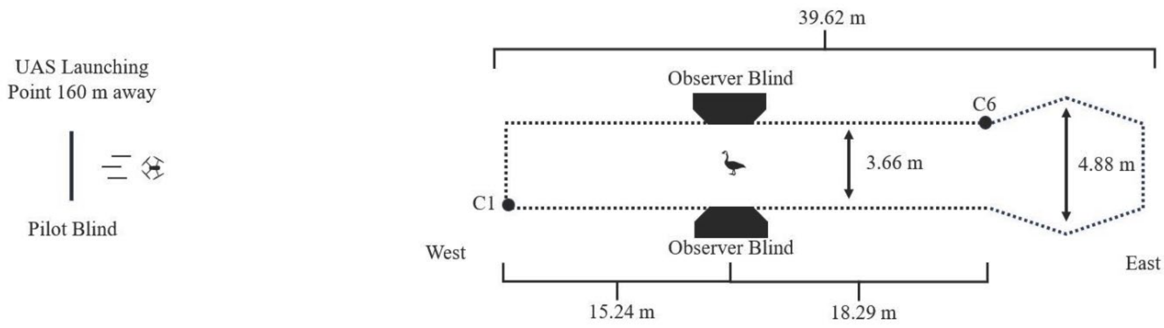
Generalized Linear Model	X^2	***d.f***	***P***
Probability of away trajectory (n=171)			
Light treatment	6.960	2	**0.031***
Approach type treatment	6.277	1	**0.012***
Goose Weight	0.652	1	0.420

Speed	1.443	1	0.230
Irradiance	0.082	1	0.774
Wind Speed	0.079	1	0.779
Light Treatment X Approach type treatment	7.950	2	**0.019***
Light Treatment: X Speed	0.646	2	0.724
Approach type treatment X Speed	1.586	1	0.208

Table 3

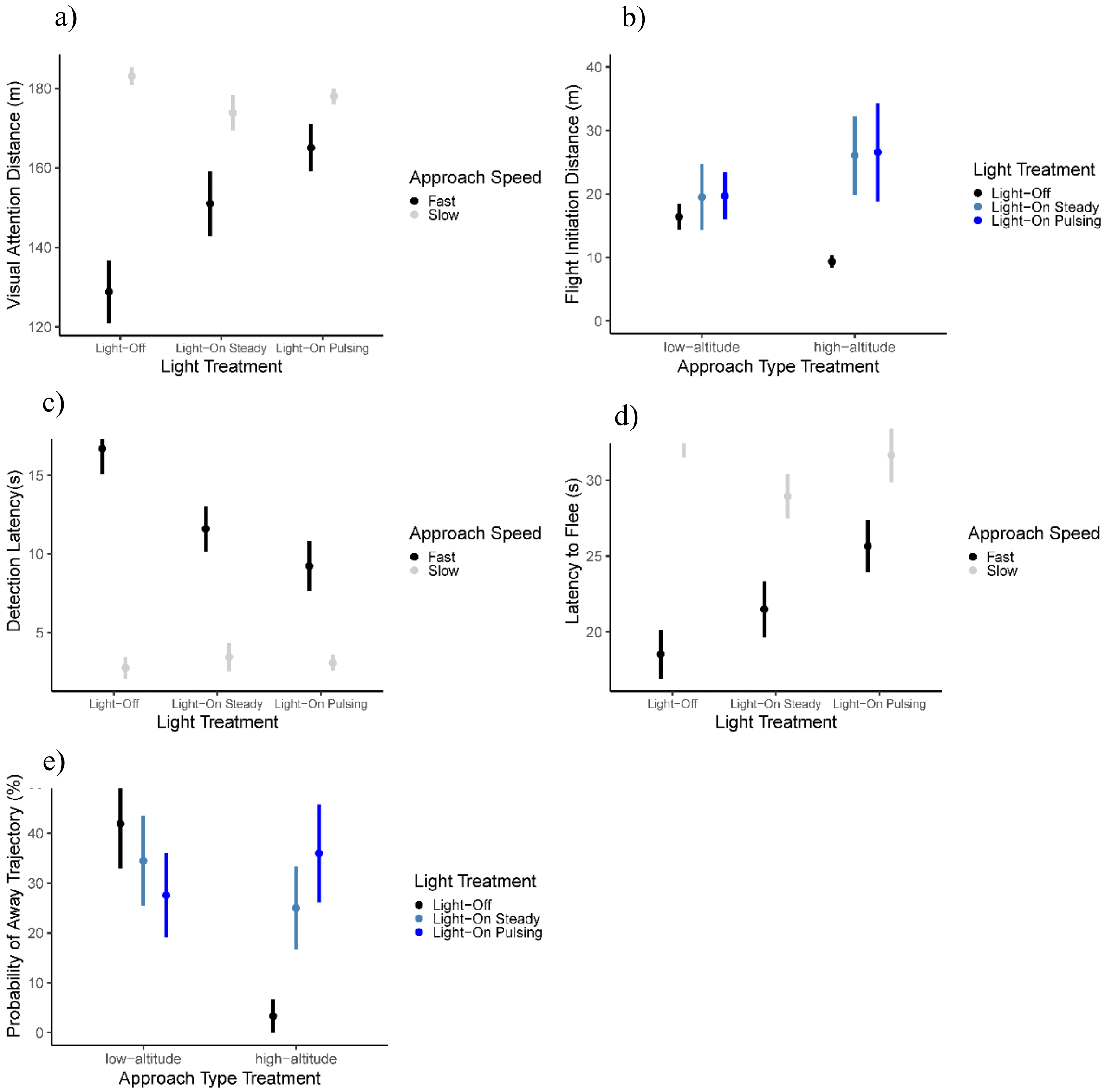
Light treatment	*Light-off (n=63)*	*Light-on steady (n=61)*		*Light-on pulsing (n=59)*	
Behavioral responses (n=183)	**n**	**n**	**Effect Size [95% CI]**	**n**	**Effect Size [95% CI]**
Visual attention distance (m) (n=168)	58	56	15.07 [2.87, 30.09]	54	22.84 [10.39,36.71]
Alert distance (m) (n=183)	63	61	17.26 [-1.72, 35.97]	59	19.44 [-1.20, 36.91]
Threat display distance (m) (n=118)	43	35	-1.078 [-5.38,10.54]	40	-1.16 [-5.1052,2.23]
Pre-escape distance (m) (n=148)	49	52	14.19 [-6.27, 36.21]	47	19.17 [-6.54, 40.10]
Flight initiation distance (m) (n=178)	61	58	9.74 [3.78, 20.44]	59	9.91 [3.82, 22.23]
Escape speed (m/s) (n=168)	58	57	-0.016 [-0.59, 0.63]	53	-0.62 [-1.12, -0.03]
Take-off latency (ms) (n=173)	60	57	119.77 [-13.81, 361.52]	56	50.93 [-71.47, 174.67]
Probability of away trajectory (%) (n=172)	61	57	6.87 [-9.63, 23.61]	54	8.53 [-7.21, 24.22]
Detection Latency (s) (n=183)	63	61	-4.69 [-7.97, -1.50]	59	-5.71 [-9.02, -2.63]
Latency to Flee (s) (n=183)	63	61	2.10 [-1.30, 5.99]	59	5.24 [1.11, 8.85]

Fig. 1



UAS Launching Point 160 m away
Pilot Blind
39.62 m
Observer Blind
C6
3.66 m
4.88 m
C1
West
Observer Blind
East
15.24 m
18.29 m

Fig. 2



a)
Visual Attention Distance (m)
120
140
160
180
Light−Off
Light−On Steady
Light−On Pulsing
Light Treatment
Approach Speed
Fast
Slow
b)
Flight Initiation Distance (m)
0
10
20
30
40
low−altitude
high−altitude
Approach Type Treatment
Light Treatment
Light−Off
Light−On Steady
Light−On Pulsing
c)
Detection Latency(s)
5
10
15
Light−Off
Light−On Steady
Light−On Pulsing
Light Treatment
Approach Speed
Fast
Slow
d)
Latency to Flee (s)
20
25
30
Light−Off
Light−On Steady
Light−On Pulsing
Light Treatment
Approach Speed
Fast
Slow
e)
Probability of Away Trajectory (%)
0
10
20
30
40
low−altitude
high−altitude
Approach Type Treatment
Light Treatment
Light−Off
Light−On Steady
Light−On Pulsing

Fig. 3

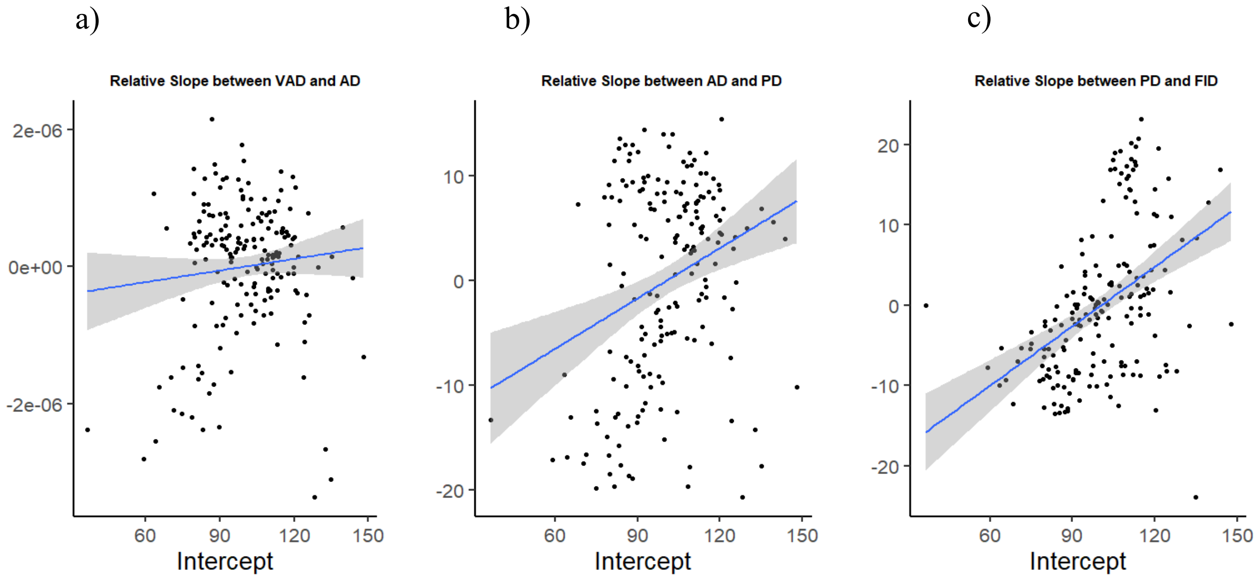

a)
Relative Slope between VAD and AD
2e-06
0e+00
-2e-06
60
90
120
150
Intercept
b)
Relative Slope between AD and PD
10
0
-10
-20
60
90
120
150
Intercept
c)
Relative Slope between PD and FID
20
10
0
-10
-20
60
90
120
150
Intercept

Fig 4.

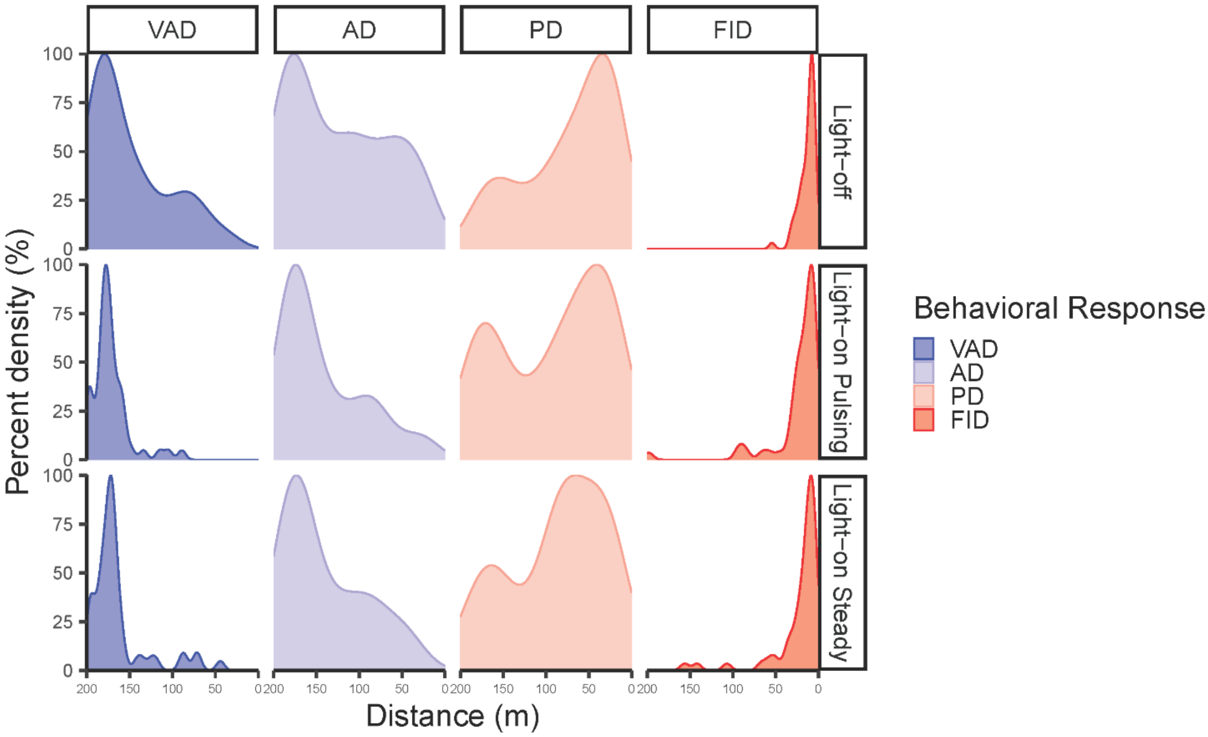

VAD
AD
PD
FID
Light–off
Light–on Pulsing
Light–on Steady
Percent density (%)
100
75
50
25
0
200
150
100
50
0
Distance (m)
Behavioral Response
VAD
AD
PD
FID

Figure and table captions

Table 1. For each dependent variable considered in our analysis we provide the definition, whether it influenced the probability of reaction or the probability of sufficient time and how a change in that dependent variable resulted in an increase in the probability of escape. We then included the general categorization of each behavior as a part of the larger escape sequence and supporting citation.

Table 2. General linear and generalized linear model results (significant values are bolded) for visual attention distance, alert distance, threat display distance, pre-escape distance, flight initiation distance, escape speed, take-off latency, detection latency, latency to flee, and the probability of away trajectory. Each model for the general linear and generalized linear models included the following independent variables: light treatment, approach type treatment, log goose weight, speed, irradiance, wind speed, and the interactions between light and approach type treatment, light and speed, and approach type and speed. $\omega\rho^2$ is a measure of effect size (partial Omega squared).

Table 3. Sample size for each dependent variable per the three different light treatments. Effect size is the difference between the means in meters of that specific light-on treatments compared to the light off treatment and the 95% confidence intervals estimated from a bootstrap of 1000 iterations.

Fig. 1. Schematic design of the experimental arena. The focal animal was released into the arena from a one-way flap from the middle of either observer blind. The UAS was launched from behind a blind 160 m away. The UAS flew directly at the arena from the west and through the entirety of the arena until the animal responded. C1 and C6 refer to cameras 1 and 2.

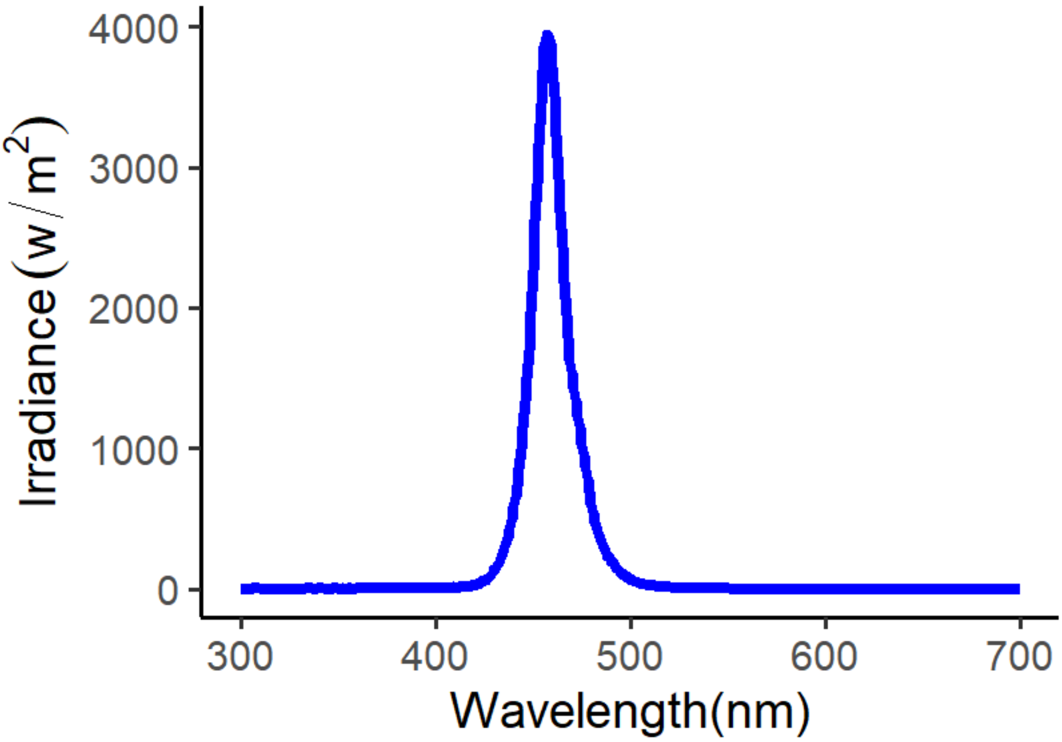
Fig. 2. Plots of the five significant interaction effects. The circles represent the mean of the dependent variable for that specific combination of categorical variables and the error bars are their 95% confidence intervals. Plots a), c), and d) show the significant interaction between light treatment and

UAS approach speed for (a) visual attention distance, (c) detection latency, and (d) latency to flee. Plots (b) and (e) show the significant interaction between approach type treatment and light treatment for (b) flight initiation distance and (e) probability of away trajectory.

Fig. 3. Plots of the relationship between the random intercepts and random slopes based on the random effect structure of the mixed model, considering the transitions between (a) visual attention (VAD_ to alert distance (AD), (b) alert distance to pre-escape distance (PD), and (c) pre-escape distance to flight initiation distance (FID).

Fig. 4. Density plots of sequential behaviors in response to different light treatments. Each plot represents the proportion of observations at different distances away from the UAS scaled to a maximum of 1. Abbreviations: VAD=visual attention distance, AD=alert distance, PD= pre-escape distance, and FID=flight initiation distance.

Supplementary Material 1. Irradiance spectra of the light stimulus.



The irradiance spectra measured in watts per meter squared binned in 1-nm intervals. Measurements were made with an Ocean Optics, Inc. (Orlando, FL, USA) Flame-S-UV-VIS spectrometer and a P400-2-SR optical fiber with CC-3 cosine corrector attached. The peak nm of the light was 457 nm, where the sum of the total spectral irradiance was 931.63 W/m^2 .

Supplementary Material 2. Definitions of behavioral category and the sub-behaviors included.

	Definition
<u>Visual Attention Behavior</u>	Behaviors associated with the appearance of the animal adjusting orientation to allocate attention in the direction of the approaching UAS
Abrupt Westward Head Rotation	The animal abruptly and drastically rotating its head on the yaw axis and stopping with its beak facing a towards a westward direction where the drone is approaching from
Horizontal Neck Extension	The animal extending its neck horizontally

Visual Exploration	The animal briefly pauses and makes a series of smaller head movements on the yaw axis in the direction of the approaching drone
Head Tilting	Subtle changes in the animal's head position along the roll and pitch axes. Movements are typically slower and changes in angle from the previous position can be defined as acute or small.
<u>Alert Behavior</u>	Behavior that occurs after visual attention is directed towards the UAS, characterized by distinct and overt changes in behavioral states and stereotyped cues goose stress responses
Fanning Tail Feathers	Tail feathers widening horizontally to expose the white plumage on the animal's torso. Typically, the feathers are pointed downward to the ground
Head Pumping and Tossing	Repeated lowering and raising of the head along the pitch axis
Vertical Neck Extension/ Upright Posture	Vertical neck and/or body extension
Vertical Neck Lowering	Vertical head lowering below the typical head position (i.e., the goose making itself look smaller)
Vocalization/Honk	Any audible noise (i.e., honking, hucka, or cackle) be it quiet or loud
Flinch	A slight and quick shake or backwards movement or change in posture in response to the approaching UAS followed by the animal returning to its previous posture
Freeze	Ceasing or noticeably and drastically reducing all body and head movements
<u>Threat Display Behavior</u>	Behavior where it appears the animal is signaling to the UAS that it is dangerous
Signaling	A combination of simultaneously adopting a wings open, feathers extended, hissing (i.e., protruding tongue), vertically elevated neck and torso posture then orienting the anterior side of the body towards the approaching UAS

<u>Pre-escape Behavior</u>	Behavior after alert behavior, where it appears, the animal is preparing to enact risk mitigation behavior
Crouch	Leg bend slowly lowering the torso closer to the ground in anticipation of escape
Walking/Low Intensity Escape	Moves only a few slow steps (i.e., slow escape speed) in any direction away from the path trajectory (i.e., to the sides of the arena) after alerting
Eastern Body Rotation	The animal rotates its torso in the yaw axis where the anterior side is facing a eastern direction, opposite of where the UAS is approaching from
<u>Flight Initiation Behavior</u>	Behavior after pre-escape behavior that is the animals final attempt to mitigate risk at the UAS approaches closer
Attack/Lunge	An attempt to lunge or fly directly at the UAS
Duck	Quickly dropping the head and torso closer to the ground to avoid the UAS as it moves over and above the animal
Feign	As the UAS approaches closer laying down on the ground and completely extending the neck to flattens itself onto the ground
Running/High Intensity Escape	A faster bi-pedal escape where the animal moves in a direction away from the approaching UAS
Take Flight	An attempt to take flight to move away from the UAS

Supplementary Material 3: Approach Speed Estimates Methodology

DJI flight recording software, accessed via Airdata.com (OSF), only considers horizontal movement speed, not vertical speed. At the start of each trial, that is once the UAS first became visible from behind the pilot's blind, the UAS would either descend or ascend in altitude depending on the approach treatment. To account for both vertical and horizontal speed of the UAS for the entirety of the trial whenever horizontal speed was record as 0 m/s because the UAS was changing altitudes we replaced those values with estimates of vertical movement speed. We estimated vertical movement speed as the difference in the UAS recorded altitude divided by 200 msec, the time interval between flight recordings. For each behavioral response we measured the average vertical movement adjusted approach speed recorded just before and just after the behavioral response was observed.

As our study shows and other have shown approach speed has a strong influence on animal escape responses (Stankowich & Blumstein 2005, DeVault et al. 2015). However, presently it is impossible to discern over what time interval prior to the observed response influenced the animal's behavior. Rather than assume about which time interval prior to the behavioral response was important we decided to summarize the UAS's approach speed for each trial by taking the average of the recorded vertical movement adjusted speed at the instance of each observed behavioral response, herein referred to as approach speed.

Supplementary Material 4: Distance Estimation Methodology

Visual attention distance, alert distance, pre-escape distance, threat display distance, and flight initiation distance were estimated using the UAS's GPS location and estimates of the animals location within the arena. All flight logs were recorded and subsequently uploaded to Airdata.com (https://airdata.com/). The data available for each flight can be found on (Open Science Framework).

DJI UAS flight records provide information on distance away from the launch point, speed, and altitude in 200 msec intervals. Flight records began recording the instances the pilot initiated a launch. There was a brief delay (approximately 2 seconds) from the launch initiation to the instance when the UAS lifted off the take-off platform. We recorded from the UAS camera the first frame where it began to elevate off the launch platform. With the first launch frame we were able to synchronize the UAS flight records with trial videos based on the first recorded increase in UAS altitude. Importantly, the UAS was initially elevated at 0.41-m due to the launch platform when it began its take-off. After synchronizing the flight data with the video recordings, we were able to measure the time difference between the first frame the UAS took-off and the first frame the animal enacted a behavior, and consequently the distance the UAS was away from the launch point. Due to the limited resolution of the flight data (i.e., data recording occurred every 200-ms) we adjusted for the UAS's position away from the launch point by taking the average of the UAS's speed (see below) at the recording prior and after a given behavioral response. Then we multiplied this average speed by the temporal difference between the previous flight data record and the exact frame the behavior was initiated to estimate how much farther the UAS travelled from the launch point from the previous flight record.

We estimated the animal's position within the arena at the video frame the behavior was initiated. To estimate the animal's location within the arena we first re-created a map of the experimental arena by overlaying a schematic with proportional dimensions of the experimental arena on an aerial image of the experimental site using adobe illustrator (OSF)(Supplementary material 4, Fig.1). Then using multiple cameras and known arena features (i.e., the t-posts) we estimated the animals' location within the arena. Then using ImageJ (https://imagej.net/ij/) we estimated the animal's position in x and y coordinates on the arena map which was scaled with the exact dimensions of the actual experimental arena. For each trial we saved images of where we marked the locations within the experimental arena for each relevant behavior (OSF) Supplementary Materials 4.

Given the issues with estimating depth from camera images at unknown and varying viewing angles (Rowcliffe et al. 2011, Caravaggi et al. 2016, Corlatti et al. 2020, Leorna et al.2022, Haucke et al. 2022) we validated our arena location estimates with an additional supplemental test by recreating trials with a human standing at a variety of different known locations within the arena. Then with the footage from a single stationary camera placed at varying distances away from the observer and heights, along with the footage of a moving UAS flying by, we had a blind observer attempt to estimate the location of the participant. On average the location estimates were off by 20 cm (Supplementary Materials 4).

Once we knew the animal's location within the arena and the UAS's distance away from the launch point we were able to indirectly measure the distance between the UAS and the animal. We did so by subtracting the linear distance of the animal from the eastern wall of the arena and the UAS's distance from the launch point by the total distance (i.e., 199.624 m) of the experimental site (Fig.1).

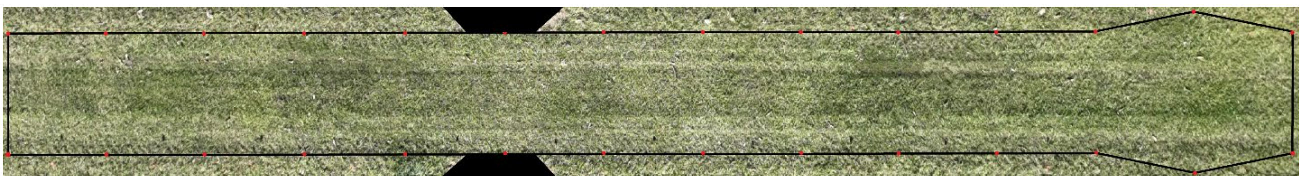


Figure 1. The raster file of a map of the experimental arena where trials took place. The map was used to estimate the goose location at the instance the animal enacted each behavioral response measured in terms of distance.

Supplementary Material 5.

Table with general linear and generalized linear model results (significant values are bolded) for visual attention distance, alert distance, threat display distance, pre-escape distance, flight initiation distance, escape speed, take-off latency, detection latency, latency to flee, and the probability of away trajectory *without the irradiance imputed values*. The different significant results are featured in red text. Each model for the general linear and generalized linear models included the following independent variables: light treatment, approach type treatment, log goose weight, speed, irradiance, wind speed, and the interactions between light and approach type treatment, light and speed, and approach type and speed. $\omega\rho^2$ is a measure of effect size (partial Omega squared).

General Linear Model Results	***F***	***d.f***	$\boldsymbol{\omega\rho^2}$	***P***
Visual attention distance (m) (n=168)				
Light treatment	8.141	2,144	0.077	**<0.001*****
Approach type treatment	0.247	1,144	-0.004	0.620
Goose weight	0.666	1,144	0.008	0.416
Speed	27.457	1,144	0.190	**<0.001*****
Irradiance	0.919	1,144	-0.001	0.339
Wind speed	0.125	1,144	-0.005	0.724
Light treatment X Approach type treatment	0.472	2,144	0.001	0.625
Light treatment X Speed	6.296	2,144	0.063	**0.002****
Approach type treatment X Speed	0.378	1,144	-0.004	0.540

Alert distance (m) (n=183)				
Light treatment	3.46	2,157	0.061	**0.0336 ***
Approach type treatment	0.606	1,157	-0.003	0.437
Goose weight	0.898	1,157	0.018	0.345
Speed	43.631	1,157	0.480	**<0.001*****
Irradiance	0.146	1,157	-0.004	0.703
Wind speed	1.640	1,157	0.009	0.202
Light treatment X Approach type treatment	2.016	2,157	0.013	0.137
Light treatment X Speed	1.534	2,157	0.006	0.219
Approach type treatment X Speed	3.073	1,157	0.012	0.082
Threat display distance (m) log transformed (n=118)				
Light treatment	0.061	2,99	-0.001	0.940
Approach type treatment	1.311	1,99	0.107	0.255
Goose weight	0.144	1,99	-0.008	0.705
Speed	0.981	1,99	-0.006	0.364
Irradiance	0.432	1,99	-0.004	0.513
Wind speed	7.048	1,99	0.062	**0.009****
Light treatment X Approach type treatment	0.163	2,99	-0.015	0.850
Light treatment X Speed	0.184	2,99	-0.014	0.832
Approach type treatment X Speed	0.984	1,99	0.000	0.324
Pre-escape distance (m) log transformed (n=148)				
Light treatment	0.324	2,122	0.001	0.724
Approach type treatment	0.033	1,122	-0.002	0.856
Goose weight	0.692	1,122	-0.005	0.407
Speed	2.723	1,122	0.118	0.101
Irradiance	0.109	1,122	-0.005	0.742
Wind speed	9.962	1,122	0.056	**0.002****
Light treatment X Approach type treatment	0.890	2,122	-0.003	0.413
Light treatment X Speed	0.166	2,122	-0.012	0.847
Approach type treatment X Speed	0.159	1,122	-0.006	0.691
Flight initiation distance (m) log transformed (n=178)				
Light treatment	3.790	2,152	0.013	**0.025***
Approach type treatment	2.260	1,152	-0.002	0.135

Goose weight	1.913	1,152	0.011	0.169
Speed	0.089	1,152	0.018	0.766
Irradiance	0.600	1,152	-0.004	0.440
Wind speed	0.031	1,152	-0.006	0.861
Light treatment X Approach type treatment	4.129	2,152	0.031	**0.018***
Light treatment X Speed	0.034	2,152	-0.012	0.967
Approach type treatment X Speed	2.588	1,152	0.010	0.110
Escape speed (m/s) (n=168)				
Light treatment	1.186	2,142	0.016	0.308
Approach type treatment	0.038	1,142	0.010	0.846
Goose weight	0.046	1,142	-0.006	0.831
Speed	0.749	1,142	-0.003	0.388
Irradiance	0.296	1,142	-0.005	0.587
Wind speed	0.093	1,142	-0.006	0.762
Light treatment X Approach type treatment	0.867	2,142	-0.003	0.422
Light treatment X Speed	0.086	2,142	-0.012	0.917
Approach type treatment X Speed	0.232	1,142	-0.005	0.631
Take-off latency (ms) log transformed (n=160)				
Light treatment	3.318	2,147	-0.003	**0.039***
Approach type treatment	2.845	1,147	0.013	0.094
(log) Goose weight	0.359	1,147	-0.002	0.550
Speed	1.142	1,147	0.001	0.287
Irradiance	0.311	1,147	-0.004	0.578
Wind speed	0.537	1,147	-0.005	0.465
Light treatment X Approach type treatment	1.712	2,147	0.011	0.184
Light treatment X Speed	1.448	2,147	0.006	0.238
Approach type treatment X Speed	0.741	1,147	-0.002	0.391
Detection Latency (s) (n=183)				
Light treatment	10.063	2,157	0.121	**<0.001*****
Approach type treatment	0.161	1,157	-0.003	0.689
(log) Goose weight	0.214	1,157	0.005	0.633
Speed	40.706	1,157	0.310	**<0.001*****
Irradiance	0.995	1,157	0.000	0.320

Wind speed	<0.001	1,157	-0.003	0.979
Light treatment X Approach type treatment	0.319	2,157	-0.005	0.727
Light treatment X Speed	5.861	2,157	0.054	**0.004****
Approach type treatment X Speed	0.593	1,157	-0.002	0.443
Latency to Flee (s) (n=183)				
Light treatment	5.924	2,157	0.044	**0.003***
Approach type treatment	1.800	1,157	0.033	0.182
(log) Goose weight	0.356	1,157	-0.005	0.552
Speed	35.485	1,157	0.204	**<0.001*****
Irradiance	0.452	1,157	0.000	0.502
Wind speed	0.001	1,157	-0.003	0.977
Light treatment X Approach type treatment	0.136	2,157	0.003	0.873
Light treatment X Speed	4.772	2,157	0.022	**0.010****
Approach type treatment X Speed	0.038	1,157	-0.005	0.846

Generalized Linear Model	X^2	***d.f***	***P***
Probability of an Away Trajectory (n=172)			
Light treatment	6.687	2	**0.035***
Approach type treatment	4.693	1	**0.030***
(log) Goose Weight	0.089	1	0.766
Speed	2.336	1	0.126
Irradiance	0.144	1	0.704
Wind Speed	0.018	1	0.895
Light Treatment X Approach type treatment	9.096	2	**0.011***
Light Treatment: X Speed	3.189	2	0.203
Approach type treatment X Speed	3.3029	1	0.069

Literature Cited

Caravaggi, A., Zaccaroni, M., Riga, F., Schai-Braun, S. C., Dick, J. T., Montgomery, W. I., & Reid, N. (2016). An invasive-native mammalian species replacement process captured by camera trap survey random encounter models. *Remote Sensing in Ecology and Conservation*, *2*(1), 45-58.

Corlatti, L., Sivieri, S., Sudolska, B., Giacomelli, S., & Pedrotti, L. (2020). A field test of unconventional camera trap distance sampling to estimate abundance of marmot populations. *Wildlife Biology*, *2020*(4), 1-11.

Haucke, T., Kühl, H. S., Hoyer, J., & Steinhage, V. (2022). Overcoming the distance estimation bottleneck in estimating animal abundance with camera traps. *Ecological Informatics*, *68*, 101536.

Leorna, S., Brinkman, T., & Fullman, T. (2022). Estimating animal size or distance in camera trap images: Photogrammetry using the pinhole camera model. *Methods in Ecology and Evolution*, *13*(8), 1707-1718.

Rowcliffe, J., Carbone, C., Jansen, P. A., Kays, R., & Kranstauber, B. (2011). Quantifying the sensitivity of camera traps: an adapted distance sampling approach. *Methods in Ecology and Evolution*, *2*(5), 464-476.

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature methods*, *9*(7), 671-675.