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Not So Bold After All? A Study of Personality and Anti-Predator Responses in Graylag Geese

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1 Abstract

Background: Animals face a critical trade-off between vigilance (scanning for predators) and foraging (obtaining food). This balance is crucial for survival, as vigilance enhances threat detection while foraging provides essential energy. Individual boldness, a personality trait reflecting an animal's response to perceived threats, can influence this trade-off. Bolder individuals may prioritize foraging over vigilance, potentially increasing their vulnerability to predators.

Aims: This study investigated the relationship between boldness, vigilance, and foraging behavior in Graylag geese (*Anser anser*) using a predator-mimicking drone (Robot Falcon).

Methods: Focal observations were conducted on 61 individually marked geese from a semi-tamed non-migratory flock. The geese were exposed to a Robot Falcon performing swooping maneuvers while foraging at a feeding site. Their behavior was recorded and coded using BORIS software to quantify vigilance and foraging-related behaviors. Flight Initiation Distance (FID), obtained and validated as a personality trait from previous research, was used as a proxy for boldness. Generalized Linear Mixed Models (GLMMs) were used to analyze the effects of the Robot Falcon and boldness on vigilance and feeding durations.

Results: The presence of the Robot Falcon increased vigilance and decreased feeding durations. However, boldness did not significantly influence the extent of these durations. Vigilance durations were consistently shorter before the Robot Falcon was launched compared to during exposure (Estimate = -0.49 ± 0.14 , $p = 0.001$). While a reduction in vigilance was observed between the exposure and the post-threat phase (after landing of the Robot Falcon), there was no statistically significant difference. Feeding durations reduced during the Robot Falcon exposure as they were significantly longer before the exposure phase (Estimate = 0.39 ± 0.15 , $p = 0.010$) as well as after landing (Estimate = 0.82 ± 0.12 , $p < 0.001$), compared to exposure.

Conclusions: While the Robot Falcon elicited anti-predator responses, boldness did not significantly affect vigilance or foraging behavior, suggesting that factors other than boldness may play a more prominent role in this context. Potential habituation to the drone and the presence of researchers may have influenced the results. These findings highlight the complex interplay between personality, vigilance, and foraging behavior in social species, and the need to consider multiple factors when assessing anti-predator responses.

Applications: This research contributes to our understanding of how animals respond to novel threats, such as drones, and has implications for wildlife monitoring and conservation efforts. The findings emphasize the importance of considering individual differences and potential habituation effects when using drones for wildlife research.

2 Introduction

Survival in the face of predation is a fundamental challenge for all animals. Anti-predator behaviors, such as vigilance, are crucial for mitigating this risk. Vigilance, the act of scanning the environment for potential threats, allows prey to detect predators early and initiate appropriate escape responses, directly enhancing survival¹. This early detection gives prey a critical time advantage, increasing their chances of successful escape and reducing the likelihood of being captured². However, vigilance comes at a cost. Time spent scanning for predators is time not spent foraging, leading to a vigilance-feeding trade-off³. This trade-off can have sub-lethal effects, as reduced foraging opportunities can lead to decreased energy intake, potentially impacting growth, reproduction, and overall fitness⁴. Reducing energy intake can lead to slower growth rates in young animals, delayed sexual maturity, and decreased reproductive output in adults and in the long term, these sub-lethal effects can influence population dynamics and even the evolution of life history strategies^{5,6}.

Individual behavior variation on the other hand, often referred to as personality or temperament, can significantly influence how animals respond to predation risk where personality encompasses consistent behavioral differences between individuals across time and contexts⁷. Five main personality axes have been established: exploration, activity, sociality, aggressiveness, and boldness⁸. This study focuses on boldness, which is characterized by an individual's reaction to perceived threats, such as predators or humans, with individuals ranging from bold to shy^{8,9}. Boldness can be measured through various behavioral tests, including predator presentations or simulated threats. These tests assess an animal's response to potential danger using metrics such as Flight Initiation Distance (FID)¹⁰, Response to Threat Stimuli¹¹, Trappability¹², and Resistance to Handlers¹³. Each method provides insights into different facets of boldness and anti-predator behavior. Aggressiveness can be assessed using the standardized mirror test^{14,15}. In this test, a mirror is placed in front of the individual, and their aggressive behaviors (e.g., pecking, wing flapping, vocalizations) directed towards their reflection are recorded and quantified. Higher scores indicate greater aggressiveness. Exploratory behavior was evaluated using the novel object test^{16,17}. In this test, a novel object (e.g., a brightly colored object or an unfamiliar structure) is introduced into the individual's environment, and their exploratory behaviors (e.g., approaching, pecking, manipulating the object) are recorded and quantified. Higher scores indicate greater exploratory tendencies. Boldness has been linked to various fitness consequences, including survival rates¹⁸. Bolder individuals may exhibit reduced vigilance, allocating more time to foraging, but potentially increasing their vulnerability to predation^{19,20}. Conversely, shy individuals may prioritize vigilance, sacrificing foraging opportunities to minimize predation risk^{21,22}. This intricate relationship between boldness, vigilance, and feeding behavior highlights the complex interplay between personality and survival.

In birds, boldness has been positively associated with learning²³ and social dominance rank in social species²⁴. For example, bolder individuals may be more likely to explore novel environments and learn about new food sources or potential threats²⁵. Within flocking birds, boldness can influence individual responses to threats and the overall dynamics of the group. Bolder individuals may be less reliant on social information cues when deciding between foraging and vigilance, as shown in barnacle geese (*Branta leucopsis*)²⁶. This is because bolder individuals may be more inclined to take risks and rely on their own assessment of danger rather than following the cues of others²⁷. This variation in boldness within a flock can lead to differential anti-predator behaviors and vigilance levels, potentially affecting the group's overall ability to detect and respond to threats as for

instance, a flock with a higher proportion of bold individuals may exhibit a lower overall vigilance level, making them more susceptible to surprise attacks ²⁸.

Graylag geese (*Anser anser*) are highly social waterfowl that typically live in large flocks ²⁹. These play a crucial role in their local ecosystem as bioindicators for the condition of aquatic systems and as dispersal mechanisms for aquatic organisms ^{30,31}. Understanding their behavior, particularly in response to predation risk, is therefore important for both ecological and conservation purposes. Previous research has demonstrated a link between personality in intraspecies interactions ³², including boldness and aggressiveness, and anti-predator behavior in various bird species, such as tits (Paridae) ^{33,34} and barnacle geese ²⁶. The studies indicate that bolder individuals tend to exhibit lower levels of vigilance and react less strongly to perceived threats. In the Graylag goose flock under investigation, a correlation between aggressiveness and boldness has been observed ³⁵, with personality influencing flock-level behavior ³⁶. This suggests that individual differences in personality can have a significant impact on the collective behavior and dynamics of the flock. While the influence of personality on the response to predation risk has not been investigated so far.

In efforts to close this research gap, multiple other studies are undertaken during this setup. Two of them investigate the influence of aggressiveness and exploratory tendencies in the same individuals using the vigilance and foraging data generated by the experiment and utilizing pre-existing personality score data. The personality scores were derived from previous research projects conducted on the same individuals used as focals in this study, in which aggressiveness, boldness, and exploration were measured ^{36,37}. FID, in particular, measures the distance at which an animal initiates escape behavior when approached by a potential threat where shorter FIDs indicate bolder individuals, as they tolerate closer proximity to the threat before reacting ³⁸. This metric has been widely used in studies to quantify boldness and investigate its relationship with other behavioral and physiological traits ^{39,40}. This study utilizes FID, derived from previous research on a flock of Graylag geese collected by Common et al. in 2023 ⁴¹, to assess individual boldness and its influence on vigilance and foraging behavior in response to a predator-mimicking drone. This study aims to investigate the relationship between boldness, foraging and vigilance behavior in Graylag geese using a predator-mimicking drone and hypothesizes that:

1. The presence of the Robot Falcon will reduce time spent feeding in Graylag geese, but this reduction will be less pronounced in bolder individuals.
2. The presence of the Robot Falcon will increase the duration of vigilance behaviors in Graylag geese.
3. Bolder Graylag geese will spend less time on vigilance compared to their less bold peers.

Based on these hypotheses, this study predicts the following:

- **Prediction 1:** Feeding durations in the Graylag geese will decrease during exposure to the Robot Falcon compared to before, but the difference will be bigger for the lowest boldness (1/FID) quartile, compared to the highest (1/FID) quartile.
- **Prediction 2:** During exposure to the Robot Falcon the duration of vigilance behaviors in the Graylag geese will increase.
- **Prediction 3:** The increase in vigilance durations will be stronger in lowest boldness (1/FID) quartile, compared to the highest (1/FID) quartile.

3 Methods

The KLF, part of the University of Vienna ⁴², stands at the forefront of efforts to understand the delicate interaction between birds, especially waterbirds, and their local environment in the Austrian Alps ⁴³. Its namesake, Konrad Lorenz, personally established a flock of Graylag geese (*Anser anser*) in the Almtal valley in 1973, leading to **extensive** research on the behavior of geese and other local wildlife ⁴⁴⁻⁴⁶. Graylag geese and other waterbirds play a crucial role in their local ecosystem as bio-indicators for the condition of aquatic systems and as dispersal mechanisms for aquatic organisms ^{30,31}. To this day research on the non-migratory, semi-tamed descendants of the original flock continues to be made ^{37,47-49}. One of these ongoing research projects involves drone exposure experiments to test the application of unmanned aerial vehicles (UAVs) in monitoring the flock and the influence their presence has on the flock's behavior (data not yet published). Therefore, in the newest phase of the KLF's ongoing research effort on the Graylag geese, a study into their vigilance behavior in the presence of two different UAVs was undertaken: one quadcopter UAV as the silent monitor constantly flying overhead of the flock and the other in the shape of a Peregrine falcon (*Falco peregrinus*), a known predator to waterfowl ⁵⁰, acting in the role of the Robot Falcon. The geese of the KLF flock already have been shown to react differently to certain cues in strength and time based on individual differences ⁵¹.

3.1 UAVs in Waterbird Research

Since the dawn of off-the-shelf consumer product drones in the last 20 years, UAV usage to monitor waterbirds and other species has undergone extensive testing, with successful trials on tracking flocks of geese ⁵². The topic of tracking birds through UAVs gained the attention of the scientific community during the late 2000s and momentum during the 2010s, with the first systematic evaluation of UAVs for wildlife tracking by Iv et al. 2006 ⁵³ and Chabot 2009 ⁵⁴, with Koh & Wich 2012 announcing the age of drone ecology ⁵⁵. Since 2012, numerous studies with UAVs as data collectors have been undertaken, first in combination with tracking devices attached to animals ^{56,57}. In their 2015 review, Linchant et al. concluded that UAVs possess the necessary capabilities for effective wildlife tracking in general ⁵⁸. Towards the mid to late 2010s, researchers started to rely solely on either remotely piloted UAVs or even autonomous UAVs for research that incorporates wildlife tracking ⁵⁹⁻⁶³. In a 2014 follow-up evaluation by Chabot, UAVs were confirmed to be effective tools for tracking waterbirds in particular and conducting wildlife research in general, particularly when discreet, fine-scale, and timely data collection is needed ⁶⁴. A publication by Dulava et al. 2015 evaluated different UAV types for the surveillance of waterbirds and found electric propelled ones to have the lowest effect on the surveilled animals ⁶⁵. Further evaluations of electric UAVs in waterbird surveillance by Han et al. 2017 concluded that their appliance offers high-quality monitoring of waterbirds in vast, difficult-to-access habitats ⁶⁶, similar to that of the Almtal, where rivers and lakes cut through manmade roads and forest ways. A Spanish research team led by Afán et al. 2018 successfully monitored the nesting behavior of Ibis in the Spanish Doñana National Park ⁶⁷. This is especially important because the Almtal, besides being a similar habitat, is also home to an Ibis species that has been established through the research efforts of the KLF personnel ⁶⁸ providing direct evidence for the feasibility of surveillance efforts of waterbirds in such habitats. While there are studies on general waterbird surveillance using UAVs, such as roosting birds ⁶⁹ or counting non-endangered ⁷⁰ or endangered waterbirds ⁷¹, a considerable amount focuses on nesting surveillance ⁷²⁻⁸⁰ or the effect of UAVs on the behavior of nesting waterbirds ⁸¹⁻⁸⁴. While there are still some studies on the effect of UAVs on waterbird behavior in their natural habitats outside of breeding colonies

or nests⁸⁵⁻⁸⁸, the imbalance between these topics points towards a possible research gap for the effect of general flock size surveillance on waterbirds. Jarrett et al. 2020 reported behavioral responses to differ between habitats, as waterbirds from coastal sites responded stronger to UAV exposure than their inland wetland peers⁸⁶. Howell et al. 2023, on the other hand, reported no response at all for most of the surveillance time during 50 quad-rotor UAV flights over different species of waterfowl in Australian wetlands⁸⁸. While McEvoy et al. 2016 reported different reactions depending on the species to different types of UAVs, with the strongest results using fixed-winged platforms compared to rotatory propelled ones⁸⁵. Ryckman et al. 2022 found the UAVs' launch distance to be the strongest predictor for the behavioral response of ducks and teal in their wetland habitats⁸⁷.

In addition to research and tracking of wildlife and waterbirds, commercial UAVs are also often applied to disperse bird flocks from farmlands using birds of prey shaped drones or so-called "Robot Falcons"⁸⁹. The effectiveness of UAVs varies between studies. Positive effects on pest bird dispersal from Australian vineyards were reported by Wang et al. 2019 with specialized automated UAV systems that incorporate distress calls and predator shapes akin to "Robot Falcons"^{90,91}. While Egan et al. 2023 reported no significant difference between predator-shaped and off-the-shelf UAV types⁹². Some simulated data has been produced to further research that purpose⁹³⁻⁹⁵. Thus, there remains a lack of data on bird dispersal in response to UAVs, and it is likely that the effects vary depending on the interaction between UAV shape and bird species. This raises the question of whether UAV applications could inadvertently subject monitored flocks, such as the KLF Graylag geese, to the potential risk of habituation to aerial predator presence due to frequent UAV exposure. Conversely, the absence of habituation could mean that species experience constant stress from ongoing surveillance, highlighting the need to carefully consider the stress responses of specific species under UAV monitoring.

3.2 Study Site and Subjects

Over a two-week period between September and August 2024, drone exposure experiments were conducted daily under dry conditions, including recordings on the 29th, 30th, and 31st of September and 6th, 7th, as well as 8th of August accounting for the 6 days included in the statistics. Plus 2 additional days on the 9th and 10th of August, dedicated to parallel held experiments but excluding focal recordings, involving the additional exposure to the Robot Falcon. Totaling 8 exposure days.

Each morning at 8:00 am Central European Time (GMT+2), the geese were fed at their usual feeding location (47°48'49.9"N, 13°56'50.6"E) in feeding trays and food spread evenly between, situated in the Grünau-im-Almtal valley adjacent to a decommissioned research building of the Konrad Lorenz Research Center (KLF). This location is consistently used by the research personnel who care for the geese throughout the year.

While not explicitly stated in this thesis, the geese had been previously habituated to a quad copter UAV during a 2020 habituation study and through repeated UAV-based filming and photography. This habituation was reinforced prior to the Robot Falcon experiment by flying the UAV daily for two weeks above the flock, mirroring the standardized flight patterns used during the actual exposure experiment where the was launched from an adjacent field, followed a straight path to the feeding area, hovered over the area at 30 meters height and then followed the same path back.

Once feeding commenced, research personnel assumed positions around the feeding area. Each researcher was assigned a focal goose to record with a smartphone camera throughout the experiment. If the focal goose had a bonded partner, the researcher was also informed of the partner's identity and instructed to film both, if possible. Both focal geese and their partners were identifiable by leg bands applied by KLF personnel. Of the 122 flock members, 62 individuals (focals & their partners) were recorded and later analyzed in BORIS.

3.3 Experimental Procedure

At all days as soon as all researchers had located their focal geese and had started recording, the monitoring UAV drone was launched and hovered above the flock at an altitude of 30 meters in a fixed position. Once the position was reached this initiated the 5 minute long baseline observation period began. Right after the Robot Falcon was launched at a height of up to 20 meters, from a field adjacent to the feeding grounds which was obscured by a tree line. During the first 3 experiment days the Robot Falcon was airborne for approximately 10 minutes and performed swooping maneuvers over the flock that incorporated 3 stoops in random order into its flight path (see Supplementary Figure 1). Right after the Robot Falcon had landed, an additional 5-minute post-baseline period was observed before recording ceased, marking the end of the day's experiment.

The duration between the beginning of the first and end of the last stoop of the swooping maneuvers was taken as exposure duration (exact height reduction during stoops was not measured). An additional 4th day (1st of Aug 24) following the above protocol but without focal recordings was held, followed by a 3 day pause (2nd till 4th of Aug 24).

Afterwards a second 3 day long experiment phase including Robot Falcon exposure and focal recordings were held but with adjusted swooping protocol. The 5 minute baseline and 5 minutes post-baseline phases remained unchanged. Only during the 10 minute airborne phase of the Robot Falcon the swooping maneuvers were de-randomized. Instead, a designated exposure area at the western end of the feeding ground was marked (approx. 10 m long and 3 m wide) in which the Robot Falcon would do 6 subsequent stoops to up to half a meter above ground level. The second phase was also followed by an additional day without recording but following the same protocol as the 3 days before nonetheless, as part of parallel ongoing research efforts.

Researchers followed and recorded their designated focals at all times as well as their partners (if close enough).

3.4 Behavioral Coding

The video recordings were analyzed to quantify movement and vigilance/feeding time budgets at the individual behavioral level. An ethogram, adapted from Konrad Lorenz⁹⁶ (see Supplementary Figure 2) and further modified by KLF research personnel based on Barnas et al.⁹⁷ (see Supplementary Figures 3 and 4), was used for behavioral coding. This ethogram, originally designed for nesting lesser snow geese (*Anser caerulescens caerulescens*), comprised the following behaviors:

(i) feeding (non-vigilant, foraging), (ii) non-feeding (non-vigilant, non-foraging), (iii) short neck vigilance (low vigilance), (iv) long neck vigilance (moderate vigilance), (v) one-eye up (highest vigilance), (vi) standing, (vii) walking, (viii) running, (ix) swimming, (x) flying, and (xi) lying (see Supplementary Figure 4). Periods where the focal goose was out of view were also recorded and deducted from the total observation time in both cases. Behavioral coding was performed using the video

coding software BORIS v.8.27.7⁹⁸, with the assistance of two additional raters. Vigilance and foraging-related behaviors (i-v) are mutually exclusive from movement-related behaviors (vi-xi) as each video recording was coded twice in sequence using different coding masks for either. Ensuring that the dataset for each goose represents both scorings simultaneously for each time frame. While each 20 minutes long recording was fully coded twice, in each case the timeframes between before launch and exposure as well as exposure and after landing were excluded in subsequent analyses.

Whenever during vigilance/foraging coding a behavior, falling into either category was displayed by the focal, a start time for the dedicated behavior was registered in the coding mask. Once another behavior was displayed the stop time for the previous and a start time (same timepoint) for the new behavior was registered. If a behavior could not be assigned as feeding (i), or one of the 3 vigilance behaviors (iii) – (v), the start and stop points were registered under non-feeding (ii). If the focal was not in display the start and stop timepoints were registered as out of view. The second movement related coding mask followed the same underlying structure (for behaviors (vi) – (xi)).

To account for potential observer bias, an inter-observer reliability test using the interclass correlation coefficient (ICC) for continuous measurements⁹⁹ was applied using the R package “irr” v. 0.84.1¹⁰⁰, for both vigilance (ICC = 0.948, $p = 0.001$) and feeding (ICC = 0.892, $p = 0.005$) behavior durations. Individual data on age, sex, and pairing status were obtained from life-history records maintained by KLF research personnel. These were used as co-variables as an influence of age on vigilance has been directly observed in *Anser albifrons* a close relative of the Graylag geese¹⁰¹. Age and sex were also shown to influence aggressiveness and sociability in Graylag geese^{102,103}. Sex as well as pairing status has also been shown to influence foraging behavior in Graylag geese, with paired males observed to be more vigilant to allow their female partners to spend more time feeding¹⁰⁴. Personality scores, derived from prior research projects conducted by KLF personnel on the same individuals^{36,41}, were also included. These scores, quantifying aggressiveness, boldness, and exploration behavior, were based on standardized tests: FID test for boldness, mirror test for aggressiveness, and novel object test for exploration. The raw FID results, collected by Common et al. in 2023, were utilized as the personality axis for boldness, by $1 / \text{FID}$ as higher FIDs equal to less bold birds, while lower FIDs equal to bolder birds (see Supplementary Figure 5).

3.5 Model Construction and DHARMA Diagnostics

All p-values are derived from a Generalized Linear Mixed Model (GLMM)¹⁰⁵ using the glmmTMB¹⁰⁶ land model fit was assessed using the DHARMA¹⁰⁷ libraries in R¹⁰⁸. Additional Post hoc analysis and analysis of deviance were conducted using the Car library¹⁰⁹.

Coding data was summarized for the duration of individuals behaviors from START to STOP points within each phase of the Robot Falcon flight path. The timeframes before launch (pre-exposure/baseline), exposure (stooping) to the Robot Falcon, as well as after landing (post-exposure/baseline) were compared. Since the durations of each timeframe differed in length to each other and between experiment days, a subsets from the baseline and post-baseline periods were selected, denoted as before launch and after landing durations respectively, to match the exact length of the exposure duration of the respective day: 98 seconds for Day 1, 138 seconds for Day 2, 99 seconds for Day 3, 100 seconds for Day 4, 138 seconds for Day 5, and 119 seconds for Day 6.

The GLMM accounted for sex, age, pairing status, exposure day, each focals starting quadrant and boldness represented by the $1/\text{FID}$ quartile ranks as fixed effects as well as rater identifier and bird

identifier as random effects with the behavior durations as response variable. Additionally, an observation level random effect (OLRE) was included in the model applied for the feeding durations to reduce overdispersion¹¹⁰. The starting quadrants (aviary, quadrant A, quadrant B, quadrant C, and river) are derived from markings on the feeding area and surrounding terrain (see Supplementary Figure 6).

To analyze how behavior durations changed during Robot Falcon exposure, a model was fit using the feeding data before launch and exposure data subset. This subset of the full dataset was chosen because feeding behavior is mutually exclusive to vigilance and thus represents the minimal requirement for a suitable model. Prior to fitting the models, the feeding data underwent preprocessing. Outliers were identified using z-scores, with data points exceeding a z-score of 3 being classified as outliers. The Anderson-Darling test was used to assess normality for both the raw duration data ($A = 614.04$, $p < 0.001$) and the log-transformed duration data ($A = 586.32$, $p < 0.001$). Both tests indicated non-normal distributions. Levene's test revealed significant heterogeneity of variance in feeding duration across time points ($F = 29.031$, $p < 0.001$). Multicollinearity among predictors was checked using the Variance Inflation Factor (VIF) in a preliminary linear model, with VIF values ranging from 1.00 to 1.28, indicating no significant multicollinearity. The density histogram of the duration data suggested a possible gamma distribution with a strong right skew, which was further emphasized by taking the square root of the duration (see Supplementary Figure 7).

Initially, a null model was fitted to assess the baseline effects of drone exposure on feeding duration. A reduced model was then fitted to evaluate the interaction between exposure phase and boldness. Finally, a full model was constructed, incorporating (besides timeframes and boldness quartiles) age, sex and pairing status, as fixed effects, with bird identifier, starting quadrant and exposure day as random effects, along with an observation-level random effect (OLRE), which represented the index of each behavioral instance.

The final model selected was a generalized linear mixed model (GLMM) with a gamma distribution and a log link function, utilizing the square roots of the numerical values (duration & age). This choice was based on the non-normality of the data and the positive skew often observed in duration data. To assess the adequacy of the fitted models, diagnostic analysis of the residuals was performed using the DHARMA package in R. This package provides a standardized and comprehensive approach to evaluate model fit by simulating residuals based on the fitted model and comparing them to the observed residuals. This approach is particularly useful for mixed models and models with non-normal distributions, where traditional residual diagnostics may be unreliable.

Likelihood ratio tests (LRTs) were again conducted to assess model fit. For feeding, the full model remained the best fit for feeding duration ($\chi^2 = 23.00$, $df = 13$, $p = 0.005$), showing a significant improvement over the null model. The reduced model did not significantly improve upon the null model ($\chi^2 = 2.68$, $df = 6$, $p = 0.848$).

To assess the adequacy of the fitted models, residual diagnostics were performed using the DHARMA package in R. This package simulates residuals based on the fitted model and compares them to the observed residuals, providing a standardized approach to evaluate model fit, particularly useful for mixed models and those with non-normal distributions. DHARMA implements several diagnostic tests. First the feeding behavior was examined, using the Kolmogorov-Smirnov test for uniformity for all three models (null, reduced, and full). This test assesses whether the simulated residuals follow a uniform distribution, as expected for a well-fit model. The null model showed no significant deviations from uniformity ($D = 0.04$, $p = 0.485$), indicating that the residuals

follow the expected distribution. Similarly, the reduced model also showed no significant deviations from uniformity ($D = 0.03$, $p = 0.911$). The full model also demonstrated good uniformity ($D = 0.03$, $p = 0.8673$).

Next, the quantile test was applied. This test compares the distribution of simulated residuals to observed residuals across quantiles, identifying if the model performs better in certain data ranges. The quantile test was not applicable for the null and reduced models (errors occurred due to convergence issues). However, for the full model, the quantile test showed no significant deviations ($p = 0.754$), suggesting that the model performs consistently across the data range. Then a dispersion test which checks for over- or underdispersion in the model was applied. The null model showed no significant deviations from the expected dispersion (dispersion = 1.06, $p = 0.528$). Similarly, the reduced model also showed no significant dispersion deviations (dispersion = 1.05, $p = 0.64$). As well as for the full model (dispersion = 1.02, $p = 0.696$). Finally, an outlier test that identifies potential outliers that may be unduly influencing the model fit was performed. The outlier test for the null model was not significant ($p = 0.776$), indicating no concerning outliers. Similarly, the outlier test for the reduced model was also not significant ($p = 0.387$). The outlier test for the full model was also not significant ($p = 0.777$). Therefore, the full model was picked as the best fit, with no significant concerns regarding uniformity, quantiles, dispersion, or outliers (see Supplementary Figure 8).

While models incorporating both exposure and after-landing timeframes did not yield adequate fits for other behaviors, a suitable model for the feeding durations that compared after landing and exposure was found (see Supplementary Figure 8). This model followed the reduced configuration including timeframes and boldness quartiles as fixed effects and bird identifier as a random effect. LRTs indicated that neither the reduced model nor the full model significantly improved upon the null model (reduced model: $\chi^2 = 1.36$, $df = 6$, $p = 0.968$; full model: $\chi^2 = 13.19$, $df = 13$, $p = 0.433$). DHARMA residual diagnostics revealed no significant issues with outliers in any of the models (null model: $p = 0.338$; reduced model: $p = 0.749$; full model: $p = 0.338$), nor were there any significant dispersion issues (null: dispersion = 1.07, $p = 0.568$; reduced: dispersion = 1.07, $p = 0.536$; full: dispersion = 1.04, $p = 0.728$). The Kolmogorov-Smirnov test for uniformity also showed no significant deviations from uniformity for any of the models (null: $D = 0.03$, $p = 0.832$; reduced: $D = 0.04$, $p = 0.760$; full: $D = 0.04$, $p = 0.724$). However, the full model showed potential misspecification, indicated by a significant quantile test ($p = 0.005$). Therefore, based on these results and the requirement for the inclusion of boldness quartiles, the reduced model was chosen. To directly infer the difference in overall vigilance between boldness quartiles, the durations of the vigilance-related behaviors (short-neck, long-neck, and one-eye-up) were pooled. In contrast to the individual behaviors, the pooled vigilance did yield a fitting model that incorporated all three timeframes. Therefore, before launch and after landing timeframes were compared with the exposure. LRTs indicated that the full model ($\chi^2 = 48.39$, $df = 14$, $p < 0.001$) provided a significantly better fit to the data than the null model, while the reduced model ($\chi^2 = 11.12$, $df = 9$, $p = 0.268$) did not. This suggests that the inclusion of additional predictors and interactions in the full model significantly improves its explanatory power compared to the null model.

DHARMA residual diagnostics were conducted to assess model fit. The null model exhibited significant deviations from uniformity ($D = 0.08$, $p = 0.011$) and overdispersion (dispersion = 1.24, $p = 0.016$), suggesting potential issues with its assumptions. The reduced model showed significant overdispersion (dispersion = 1.24, $p < 0.001$) but no significant deviations from uniformity ($D = 0.06$, $p = 0.115$). The full model demonstrated a good fit with no significant deviations from uniformity (D

= 0.03, $p = 0.876$) or expected dispersion (dispersion = 1.14, $p = 0.16$). Outlier tests were non-significant for the full model ($p = 0.181$) and marginally non-significant for the null model ($p = 0.1$), with the reduced model showing the same tendency ($p = 0.1$). Quantile tests for the reduced and full models were non-significant ($p = 0.178$ and $p = 0.3$, respectively).

Nonetheless, the full model, despite not significantly improving upon the null model in terms of LRTs, provided the best fit for the pooled vigilance data when considering the DHARMA diagnostics (see Supplementary Figure 8). The final model incorporated all 3 timeframes in an interaction with the boldness quartiles, as well as age (square root taken, as numerical), sex, and pairing status as fixed effects, with bird identifier, rater identifier and starting quadrant as random effects as well as the OLRE. All values and estimates are stated with the standard deviation (\pm SD).

4 Results

Over a two-week period in July and August 2024, a series of experiments (focal recordings) were conducted to observe the behavior of Graylag geese in response to a Robot Falcon. Due to unfavorable weather conditions, such as rain or strong winds, which prevented UAV flights, the focal observations took place on six days, and the experiments with the Robot Falcon were limited to six days within this period. The first set of experiments occurred on consecutive days from the 29th to the 31st of July, while the second set took place from the 6th to the 8th of August.

4.1. Data Inclusion and FID

Initially, 61 individual geese (both paired and unpaired) were recorded. Of these, 55 had sufficient life history and personality data for inclusion in the study. Females made up 38% of the flock ($n=21$), with 15 paired and 4 unpaired. Males constituted 62% ($n=34$), with 26 paired and 8 unpaired. The geese ranged in age from 2 to 21 years old, with a median age of 7 years. The average FID for the flock was 2.02 meters, with a range of 0.4 to 3.97 meters (see Supplementary Figure 5). Females had a slightly lower average FID (1.91 meters) than males (2.24 meters). Paired individuals had a lower average FID (1.88 m) than unpaired individuals (2.33 m). Analysis of FID across age quartiles, where geese were grouped into four equally sized groups based on their age, revealed the following: youngest (2.12 ± 0.005 m), younger (2.30 ± 0.011 m), older (2.32 ± 0.007 m), and oldest (1.75 ± 0.006 m).

4.2 Behavior Observations

An analysis of the recorded behaviors revealed that walking accounted for the majority of the time spent on movement-related behaviors. In contrast, lying, flying, swimming, and running were observed minimally, with very few or no seconds recorded (see Supplementary Figures 9 and 10). Of the total time recorded, geese spent 71.94% of their total time standing, with a mean bout duration of 20.16 ± 0.82 seconds while walking accounted for 17.31% of their total time, with a mean bout duration of 5.78 ± 0.21 seconds.

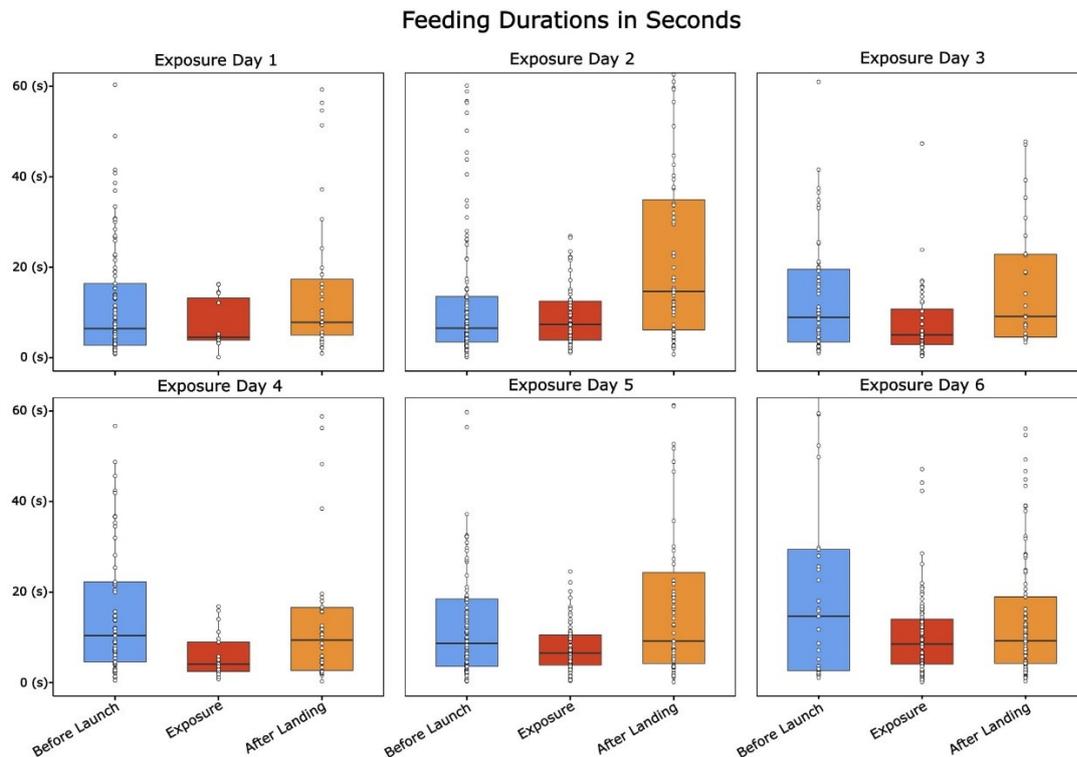


Figure 1 Boxplot of Feeding Durations in Seconds

Feeding durations of a flock ($n = 55$) of Graylag geese (*Anser anser*) in seconds before (Before Launch), during (Exposure), and after (After Landing) a simulated aerial predator (Robot Falcon) was launched, compared between each timeframe; Zoomed into the range of 0 to 60 seconds (s); **Before Launch** represents the timeframe before the Robot Falcon was launched; **Exposure** represents the timeframe during which the flock was exposed to the Robot Falcon; **After Landing** represents the timeframe after the Robot Falcon has been landed; timeframe durations varied between and within experiment days, subsets (Before Launch and After Landing) were adjusted to match the exposure duration for each experiment day: 98s (Exposure Day 1), 138s (Exposure Days 2 & 5), 99s (Exposure Day 3), 100s (Exposure Day 4), and 119s (Exposure Day 6); white dots represent individual values

Foraging-related behaviors were categorized as "feeding" (Fig. 1) and "non-feeding" (Fig. 2, see Supplementary Figure 11). Feeding durations were recorded when the focal goose had its beak on the ground, while non-feeding was recorded when the beak was directed towards the ground without feeding or when other non-vigilant behaviors, such as self-cleaning or sleeping, were displayed. Vigilance-related behaviors (Fig.3) encompassed short-neck vigilance (see Supplementary Figure 12), long-neck vigilance (see Supplementary Figure 13), and one-eye-up vigilance (see Supplementary Figure 14 & Supplementary Tables 1). Short-neck vigilance, where a goose holds its head and beak straight to observe its surroundings, was commonly displayed during interactions in the flock, even without predator presence. Long-neck vigilance, with a straightened neck and beak positioned away from the ground, often served as an intermediate behavior between short-neck and one-eye-up vigilance. One-eye-up vigilance, characterized by a direct gaze towards the sky through a head tilt, was more strongly associated with the presence of aerial predators (see Supplementary Figure 4).

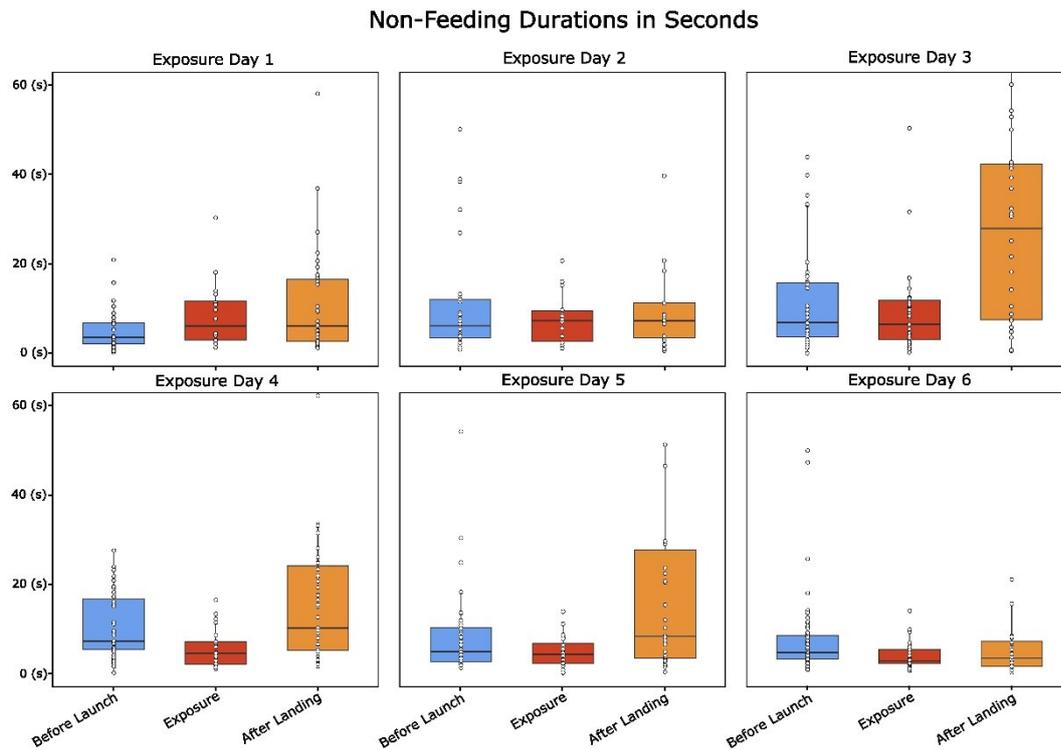


Figure 2 Boxplot of Non-Feeding Durations in Seconds

Non-Feeding (miscellaneous category for all non-vigilant, non-foraging behaviors) durations of a flock ($n = 55$) of Graylag geese (*Anser anser*) in seconds before (Before Launch), during (Exposure), and after (After Landing) a simulated aerial predator (Robot Falcon) was launched, compared between each timeframe; Zoomed into the range of 0 to 60 seconds (s); **Before Launch** represents the timeframe before the Robot Falcon was launched; **Exposure** represents the timeframe during which the flock was exposed to the Robot Falcon; **After Landing** represents the timeframe after the Robot Falcon has been landed; timeframe durations varied between and within experiment days, subsets (Before Launch and After Landing) were adjusted to match the exposure duration for each experiment day: 98s (Exposure Day 1), 138s (Exposure Days 2 & 5), 99s (Exposure Day 3), 100s (Exposure Day 4), and 119s (Exposure Day 6); white dots represent individual values

Of all the foraging or vigilance-related behaviors short-neck and non-feeding were the second most common behaviors, each at 21.83% of the total time. The mean duration of short-neck bouts was 5.91 ± 0.24 seconds, and the mean duration of non-feeding bouts was 13.20 ± 0.91 seconds. One-eye-up vigilance was displayed 11% of the total time, with a mean bout duration of 8.15 ± 0.54 seconds, while long-neck vigilance accounted for 5.50% of the total time, with a mean bout duration of 6.43 ± 0.49 seconds. Feeding behavior was the most common overall, accounting for 40.77% of the total time recorded, with a mean bout duration of 14.25 ± 0.57 seconds.

Looking at the age groups, youngest geese had a mean feeding bout duration of 17.41 ± 2.76 seconds (2.80% of their total time) and a mean non-feeding bout duration of 15.32 ± 4.53 seconds (1.74% of their total time). Their most prominent vigilance behavior was short-neck, with a mean duration of 7.62 ± 0.94 seconds (2.04% of their total time). Younger geese had a mean feeding bout duration of 12.06 ± 1.44 seconds (3.62% of their total time) and a mean non-feeding bout duration of 7.39 ± 2.05 seconds (0.96% of their total time). Short-neck was also their most prominent vigilance behavior with a mean duration of 4.18 ± 0.42 seconds (1.37% of their total time). Older geese had a mean feeding bout duration of 12.54 ± 1.64 seconds (3.09% of their total time) and a mean non-feeding bout duration of 14.06 ± 2.05 seconds (3.55% of their total time), with short-neck being

their most prominent vigilance behavior with a mean duration of 7.43 ± 0.81 seconds (3.07% of their total time). The oldest geese had a mean feeding bout duration of 13.41 ± 1.70 seconds (2.88% of their total time) and a mean non-feeding bout duration of 7.79 ± 1.68 seconds (0.37% of their total time), and their most prominent vigilance behavior was short-neck, with a mean duration of 4.76 ± 0.77 seconds (1.26% of their total time). The mean duration of vigilance bouts (short-neck, long-neck, and one-eye-up combined) varied across age groups youngest 2.15 ± 0.02 seconds, younger 2.34 ± 0.05 seconds, older 2.35 ± 0.04 seconds, and oldest 1.67 ± 0.03 seconds.

Females had a mean feeding bout duration of 16.52 ± 1.16 seconds (16.16% of their total time), and their most prominent vigilance behavior was short-neck, with a mean duration of 6.59 ± 0.44 seconds (8.42% of their total time). The mean duration of all vigilance bouts for females was 1.93 ± 0.03 seconds. Males had a mean feeding bout duration of 13.06 ± 0.62 seconds (24.61% of their total time), and their most prominent vigilance behavior was short-neck, with a mean duration of 5.56 ± 0.28 seconds (13.41% of their total time). The mean duration of all vigilance bouts for males was 2.23 ± 0.02 seconds. Paired individuals had a mean feeding bout duration of 14.21 ± 0.61 seconds (35.33% of their total time) and their most prominent vigilance behavior was short-neck, with a mean duration of 6.00 ± 0.27 seconds (18.21% of their total time). The mean duration of all vigilance bouts for paired individuals was 2.17 ± 0.02 seconds, while for unpaired individuals it was 1.91 ± 0.04 seconds.).

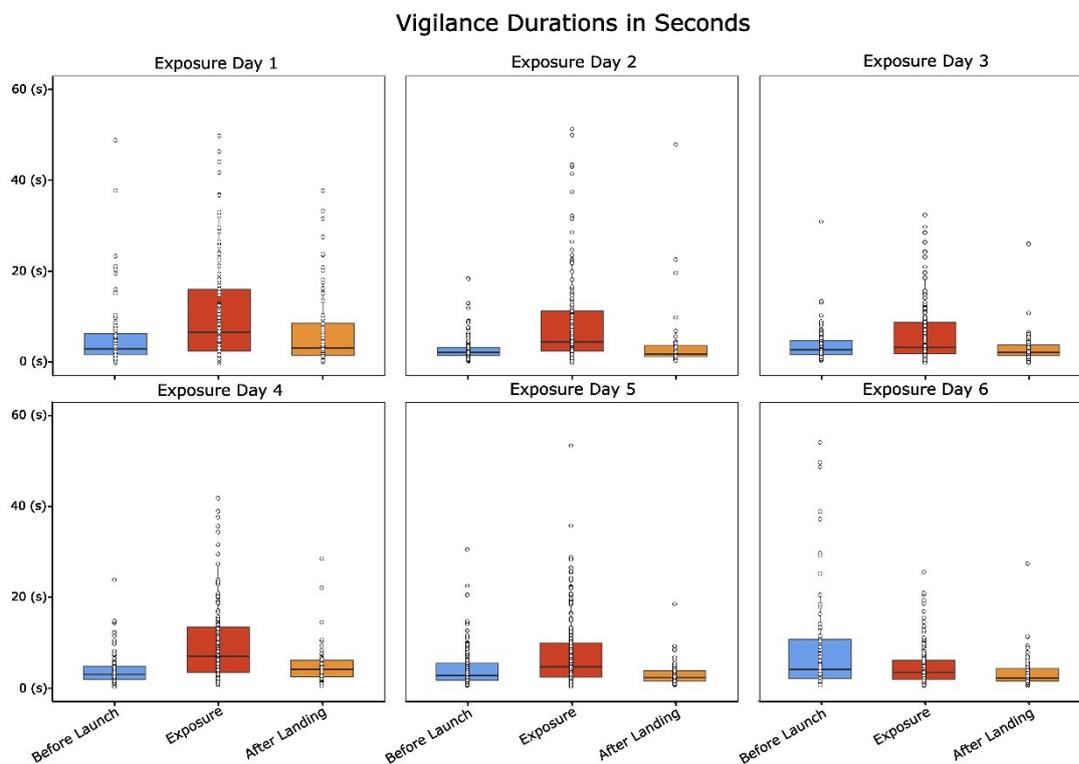


Figure 3 Vigilance Durations in Seconds

Pooled

Vigilance durations of a flock ($n = 55$) of Graylag geese (*Anser anser*) in seconds before (Before Launch), during (Exposure), and after (After Landing) an artificial predator (Robot Falcon) was launched, compared between each timeframe; Zoomed into the range of 0 to 60 seconds (s); encompassing the behaviours short-neck, long-neck, and one-eye-up; **Before Launch** represents the timeframe before the Robot Falcon was launched; **Exposure** represents the timeframe during which the flock was exposed to the Robot Falcon; **After Landing** represents the timeframe after the Robot Falcon has

been landed; timeframe durations varied between and within experiment days, subsets (Before Launch and After Landing) were adjusted to match the exposure duration for each experiment day: 98s (Exposure Day 1), 138s (Exposure Days 2 & 5), 99s (Exposure Day 3), 100s (Exposure Day 4), and 119s (Exposure Day 6); white dots represent individual values

4.3 Statistical Results Feeding

During exposure, the mean duration of feeding bouts was 8.79 ± 0.51 seconds (7.27% of the exposure phase time). Before launch, feeding bouts lasted 14.92 ± 0.90 seconds on average (17.51% of the time in this phase). After landing, the mean duration of feeding bouts was 18.56 ± 1.29 seconds (15.99% of the time in this phase).

The comparison between before launch and exposure timeframes for the feeding behavior showed a statistically significant effect (Estimate = 0.39 ± 0.15 , $p = 0.010$), indicating that feeding durations were longer before the launch of the Robot Falcon compared to during exposure (Fig. 5, Tab. 1).

However, further analysis looking at the interaction between boldness and the effect of the Robot Falcon revealed no significant differences in feeding duration between the lowest boldness quartile (Quartile 1) and the others in either timeframe (before launch: Quartile 2: Estimate = -0.22 ± 0.22 , $p = 0.311$; Quartile 3: Estimate = -0.17 ± 0.27 , $p = 0.529$; Quartile 4: Estimate = -0.35 ± 0.22 , $p = 0.119$; during exposure: Quartile 2: Estimate = -0.01 ± 0.28 , $p = 0.974$; Quartile 3: Estimate = 0.39 ± 0.30 , $p = 0.189$; Quartile 4: Estimate = 0.28 ± 0.28 , $p = 0.313$). This suggests that boldness did not significantly influence how feeding duration changed in response to the Robot Falcon (Fig. 4).

Additionally, a significant main effect for sex (Estimate = -0.29 ± 0.11 , $p = 0.013$) was found, while pairing status (Estimate = 0.16 ± 0.15 , $p = 0.269$). However, there was a significant effect of age (Estimate = 0.20 ± 0.06 , $p < 0.001$), indicating that across all phases older birds had longer feeding durations compared to younger birds.

A significant difference in overall feeding duration between exposure days was found (Estimate = 0.12 ± 0.03 , $p < 0.001$), while no significant effects were found between starting quadrants (aviary: Estimate = -0.16 ± 0.26 , $p = 0.539$; quadrant A: Estimate = -0.17 ± 0.18 , $p = 0.341$; quadrant B: Estimate = -0.14 ± 0.19 , $p = 0.443$; quadrant C: Estimate = 0.01 ± 0.17 , $p = 0.946$; quadrant D: Estimate = -0.54 ± 0.18 , $p = 0.003$; river: Estimate = 0.20 ± 0.06 , $p = 0.002$), or age (Estimate = 0.12 ± 0.03 , $p < 0.001$).

Similarly, the analysis of feeding durations in comparison of after landing and exposure timeframes revealed a significant effect (Estimate = 0.82 ± 0.12 , $p < 0.001$), too. Thus, indicating that more time was spent feeding, after the Robot Falcon had landed again, compared to the exposure. However, the interaction between boldness quartiles (Quartile 1) and the after landing timeframe compared to the exposure (baseline) was also non-significant (Quartile 2: Estimate = 0.16 ± 0.22 , $p = 0.471$; Quartile 3: Estimate = -0.28 ± 0.21 , $p = 0.177$; Quartile 4: Estimate = -0.03 ± 0.24 , $p = 0.901$), suggesting that the feeding durations did not significantly differ between timeframes across levels of boldness.

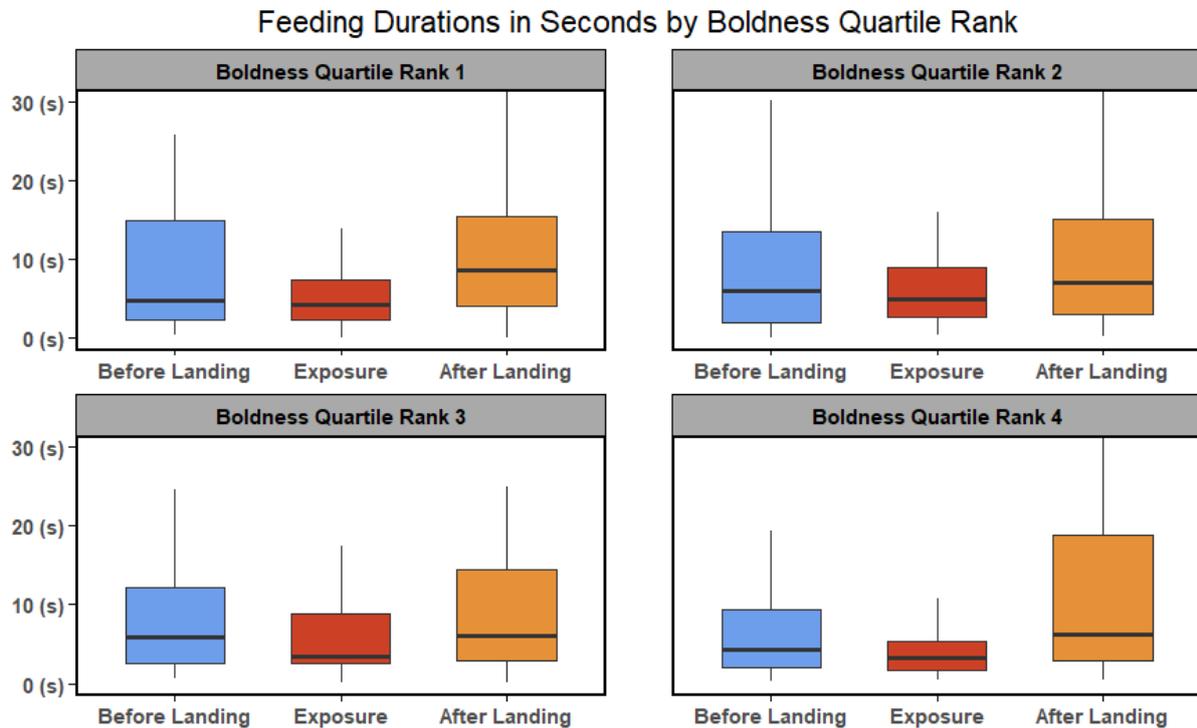


Figure 4 Boxplots of Feeding Durations by Timeframe for each Boldness Quartile Rank

Feeding durations of a flock ($n = 55$) of Graylag geese (*Anser anser*) in seconds before (Before Launch), during (Exposure), and after (After Landing) a simulated aerial predator (Robot Falcon) was launched, compared between each timeframe and Boldness Quartile Rank derived from the flight initiation distance (FID) of each individual; Zoomed into the range of 0 to 30 seconds (s); **Before Launch** represents the timeframe before the Robot Falcon was launched; **Exposure** represents the timeframe during which the flock was exposed to the Robot Falcon; **After Landing** represents the timeframe after the Robot Falcon has been landed; timeframe durations varied between and within experiment days, subsets (Before Launch and After Landing) were adjusted to match the exposure duration for each experiment day: 98s (Exposure Day 1), 138s (Exposure Days 2 & 5), 99s (Exposure Day 3), 100s (Exposure Day 4), and 119s (Exposure Day 6); white dots represent individual values; no significant differences between boldness quartile ranks were observed (see Table 1; Supplementary Table 2)

Post hoc analyses were conducted to further explore the pairwise comparisons between timeframes within each boldness quartile (see Supplementary Table 2). Specifically, during exposure to the Robot Falcon, no significant differences were found between Quartile 1 and Quartile 2 (Estimate = 0.22 ± 0.22 , $p = 0.973$), Quartile 1 and Quartile 3 (Estimate = 0.17 ± 0.27 , $p = 0.999$), Quartile 1 and Quartile 4 (Estimate = 0.35 ± 0.22 , $p = 0.775$), Quartile 2 and Quartile 3 (Estimate = -0.05 ± 0.31 , $p = 1.00$), Quartile 2 and Quartile 4 (Estimate = 0.12 ± 0.27 , $p = 0.999$), or Quartile 3 and Quartile 4 (Estimate = 0.18 ± 0.26 , $p = 0.998$).

Before the Robot Falcon launch, there were also no significant differences in feeding duration between Quartile 1 and Quartile 2 (Estimate = -0.16 ± 0.22 , $p = 0.996$), Quartile 1 and Quartile 3 (Estimate = -0.61 ± 0.25 , $p = 0.219$), Quartile 1 and Quartile 4 (Estimate = -0.32 ± 0.20 , $p = 0.731$), Quartile 2 and Quartile 3 (Estimate = -0.83 ± 0.29 , $p = 0.071$), Quartile 2 and Quartile 4 (Estimate = -0.54 ± 0.25 , $p = 0.367$), or Quartile 3 and Quartile 4 (Estimate = -0.49 ± 0.29 , $p = 0.702$).

After the Robot Falcon had landed, no significant differences in feeding duration were found between any of the boldness quartiles either, including comparisons between Quartile 1 and Quartile 2 (Estimate = 0.05 ± 0.21 , $p = 1.00$), Quartile 1 and Quartile 3 (Estimate = 0.13 ± 0.22 , $p = 1.00$), Quartile 1 and Quartile 4 (Estimate = 0.09 ± 0.24 , $p = 1.00$), Quartile 2 and Quartile 3 (Estimate =

0.07 ± 0.25, p = 1.00), Quartile 2 and Quartile 4 (Estimate = 0.04 ± 0.26, p = 1.00), and Quartile 3 and Quartile 4 (Estimate = -0.03 ± 0.27, p = 1.00).

An analysis of deviance was made to summarize which predictor had the strongest influence on feeding durations, indicating that for both models the timeframes were the most significant predictor (Before: $\chi^2 = 8.18$, df = 1, p = 0.004; After: $\chi^2 = 44.01$, df = 1, p < 0.001). Before the launch, additional significant effects were observed for sex ($\chi^2 = 5.68$, df = 1, p = 0.017) and age ($\chi^2 = 8.89$, df = 1, p = 0.003). However, neither boldness quartile (Before: $\chi^2 = 2.22$, df = 3, p = 0.53; After: $\chi^2 = 2.04$, df = 3, p = 0.56) nor the interaction between phase and quartile (Before: $\chi^2 = 1.35$, df = 3, p = 0.72; After: $\chi^2 = 3.34$, df = 3, p = 0.34) had a significant effect on feeding durations in either model. Suggesting that feeding durations were not influenced by boldness.

Table 1 GLMM Results for Feeding Durations

This table presents the results of two generalized linear mixed models (GLMMs) analyzing the feeding behavior of a flock (n = 55) of Greylag geese (*Anser anser*) across three timeframes: 'Before Launch,' the timeframe before the Robot Falcon was launched; 'Exposure,' the timeframe during which the flock was exposed to the Robot Falcon; and 'After Landing,' the timeframe after the Robot Falcon has been landed. The square root of feeding duration (in seconds) was fitted as the response variable in a GLMM with timeframes, boldness quartiles (interaction), sex, pairing status, and the square root of age as fixed effects, as well as bird identifier (variance = $3.56 \cdot 10^{-9} \pm 5.97 \cdot 10^{-5}$), rater identifier (variance = 0.20 ± 0.45), starting quadrant (variance = 0.10 ± 0.11), day of the experiment (variance = 0.06 ± 0.24), and an OLRE (variance = 0.02 ± 0.13) as random effects. Only exposure vs. before launch timeframes were fitted in the 'Before Launch' model, and only exposure vs. after landing timeframes were fitted in the 'After Landing' model; **Model:** Indicates which model the values are derived from; **Predictor:** Variable used as a fixed effect in the model; **Estimate:** Effect size coefficient; **SE:** Standard error of the estimate; **Chisq:** Chi-square statistic; **df:** Degrees of freedom; **p-value:** Statistical significance; **Signif.:** Significance indicator (*** p < 0.001, ** p < 0.01, * p < 0.05).

Note: All estimates represent contrasts between categorical variables or the square root of the relationship to the baseline level, as all numerical variables have been square root transformed to fit the model ¹

Taken from an ANOVA analysis of deviance (only available for the impact of the overall category, not intracategorical) ³

² Category for which Chisq and df are available (4 following variables are part of the same category)

Used as baseline in model

Model	Predictor	Estimate	SE	Chisq. ¹	df ¹	p value	Signif.
Before Launch	Intercept	1.77	0.27	21.71	1	< 0.001	***
	Timeframes (exposure ³ vs. before)	0.39	0.15	8.18	1	0.001	**
	Boldness Quartiles ²			2.21	3		
	Quartile 1 ³						
	Quartile 2	-0.22	0.22			0.311	
	Quartile 3	-0.17	0.27			0.529	
	Quartile 4	-0.35	0.22			0.119	
	Sex (M ³ vs. F)	-0.29	0.11	5.68	1	0.013	*
	Pairing (unpaired ³ vs. paired)	0.16	0.15	1.86	1	0.269	
	Age	0.2	0.06	8.88	1	0.002	**

	Timeframe (TF) & Boldness Quartiles² Contrast (:)			1.35	3		
	TF:Quartile1³						
	TF:Quartile2	-0.01	0.28			0.974	
	TF:Quartile3	0.39	0.3			0.189	
	TF:Quartile4	0.28	0.28			0.313	
After Landing	Intercept	2.12	0.13	268.88	1	< 0.001	***
	Timeframes (exposure³ vs. after)	0.82	0.12	44.01	1	< 0.001	***
	Boldness Quartiles²			2.04	3		
	Quartile1³						
	Quartile2	-0.21	0.23			0.347	
	Quartile3	0.15	0.22			0.488	
	Quartile4	-0.06	0.25			0.805	
	Timeframe (TF) & Boldness Quartiles² Contrast (:)			3.34	3		
	TF:Quartile1³						
	TF:Quartile2	0.16	0.22			0.471	
	TF:Quartile3	-0.28	0.21			0.177	
	TF:Quartile4	-0.03	0.24			0.901	

4.4 Statistical Results Vigilance

The duration of vigilance behaviors varied across the three observational phases. During exposure, the mean duration of standing bouts was 30.05 ± 2.05 seconds. Standing was the most common behavior, accounting for 27.12% of the total time spent in all behaviors during this phase. The mean duration of short-neck vigilance bouts was 7.52 ± 0.47 seconds (10.75% of the exposure phase time), and one-eye-up vigilance bouts lasted 9.43 ± 0.65 seconds on average (10.09% of the exposure phase time). The mean duration of all vigilance bouts during exposure was 2.11 ± 0.03 seconds. Before launch, the mean duration of feeding bouts was 14.92 ± 0.90 seconds (17.51% of the time in this phase). The mean duration of all vigilance bouts before launch was 2.14 ± 0.04 seconds.

For the pooled vigilance behaviors, the contrast between the before launch and exposure timeframes showed a statistically significant effect (Estimate = -0.49 ± 0.14 , $p = 0.001$), indicating

that vigilance durations were shorter before the launch of the Robot Falcon compared to during exposure (Fig. 5, Tab. 2). However, there was no significant difference in vigilance durations between the after landing and exposure timeframes (Estimate = -0.08 ± 0.18 , $p = 0.652$).

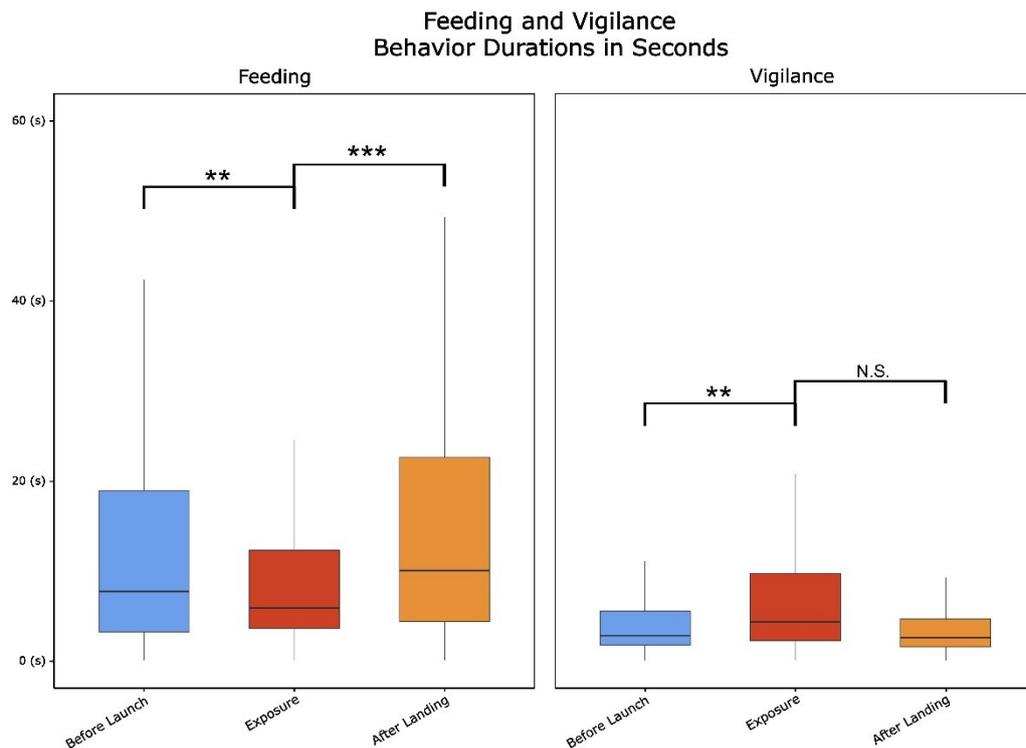


Figure 5 Feeding and Vigilance Behavior Durations in Seconds

Feeding (left) and **Vigilance** (right) durations of a flock ($n = 55$) of Graylag geese (*Anser anser*) in seconds (s) before (Before Launch), during (Exposure), and after (After Landing) an artificial predator (Robot Falcon) was launched, compared between each timeframe; Zoomed into the range of 0 to 60 seconds; Shown are the sums of the feeding (Feeding) and short-neck, long-neck, and one-eye-up (Vigilance Behavior) durations during each timeframe; **Before Launch** represents the timeframe before the Robot Falcon was launched; **Exposure** represents the timeframe during which the flock was exposed to the Robot Falcon; **After Landing** represents the timeframe after the Robot Falcon has been landed; white dots represent individual values; Significance level indicated by ** ($p < 0.01$) and *** ($p < 0.001$); **N.S.** represents non-significance ($p > 0.05$) derived from a generalized linear mixed model comparing the Before Launch and After Landing durations each against the Exposure; feeding durations were significantly longer before launch compared to during exposure (Estimate = 0.44 ± 0.15 , $p = 0.004$) and significantly longer after landing compared to during exposure (Estimate = 0.82 ± 0.12 , $p < 0.001$); vigilance durations were significantly shorter before launch compared to during exposure (Estimate = -0.49 ± 0.14 , $p = 0.001$), but there was no significant difference between after landing and exposure (Estimate = -0.08 ± 0.18 , $p = 0.652$)

Examining the interaction between boldness quartiles and timeframes, no significant difference in how vigilance durations changed between before launch and exposure across the quartiles was found (Quartile 2: Estimate = 0.21 ± 0.16 , $p = 0.170$; Quartile 3: Estimate = 0.27 ± 0.17 , $p = 0.122$; Quartile 4: Estimate = 0.26 ± 0.22 , $p = 0.232$). Similarly, there was no significant interaction effect between boldness quartiles and the comparison of the after landing and exposure timeframes, with exposure and Quartile 1 as baselines (Quartile 2: Estimate = -0.30 ± 0.19 , $p = 0.129$; Quartile 3: Estimate = -0.30 ± 0.21 , $p = 0.145$; Quartile 4: Estimate = -0.02 ± 0.24 , $p = 0.927$).

Considering the main effects of boldness quartiles alone, there was no significant difference in vigilance duration between the lowest quartile and the others (Quartile 2: Estimate = 0.10 ± 0.07 , $p = 0.184$; Quartile 3: Estimate = 0.08 ± 0.08 , $p = 0.334$; Quartile 4: Estimate = 0.05 ± 0.09 , $p = 0.623$). Additionally, no significant effects were found for age (Estimate = 0.02 ± 0.02 , $p = 0.297$), sex (Estimate = -0.01 ± 0.04 , $p = 0.818$), or pairing status (Estimate = 0.02 ± 0.05 , $p = 0.744$).

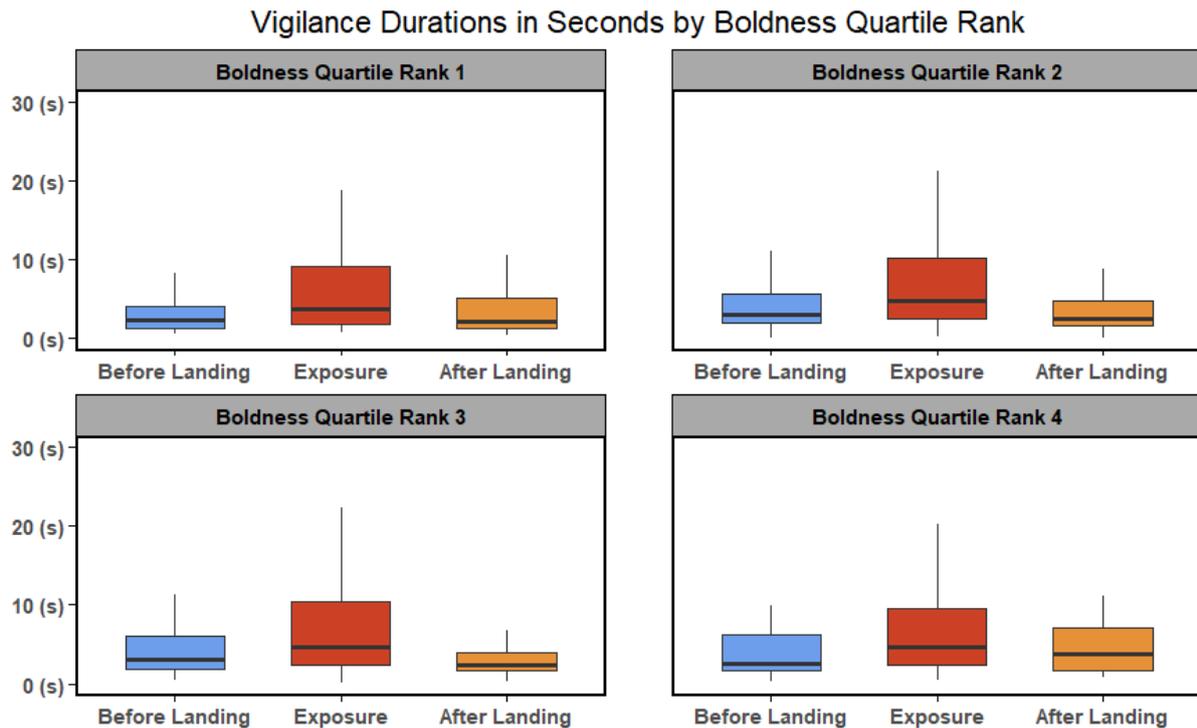


Figure 6 Vigilance Durations by Timeframe for each Boldness Quartile Rank Vigilance durations of a flock ($n = 55$) of Graylag geese (*Anser anser*) in seconds before (Before Launch), during (Exposure), and after (After Landing) a simulated aerial predator (Robot Falcon) was launched, compared between each timeframe and Boldness Quartile Rank derived from the flight initiation distance (FID) of each individual; Zoomed into the range of 0 to 60 seconds (s); **Before Launch** represents the timeframe before the Robot Falcon was launched; **Exposure** represents the timeframe during which the flock was exposed to the Robot Falcon; **After Landing** represents the timeframe after the Robot Falcon has been landed; timeframe durations varied between and within experiment days, subsets (Before Launch and After Landing) were adjusted to match the exposure duration for each experiment day: 98s (Exposure Day 1), 138s (Exposure Days 2 & 5), 99s (Exposure Day 3), 100s (Exposure Day 4), and 119s (Exposure Day 6); white dots represent individual values; no significant differences between boldness quartiles were observed (see Table 2; Supplementary Table 3)

Similarly, post hoc tests examining pairwise comparisons of vigilance durations across boldness quartiles also revealed no significant differences in vigilance between boldness quartiles during any of the timeframes (see Supplementary Table 3). Specifically, during exposure to the Robot Falcon, no significant differences were found between Quartile 1 and Quartile 2 (Estimate = -0.10 ± 0.07 , $p = 0.976$), Quartile 1 and Quartile 3 (Estimate = -0.08 ± 0.08 , $p = 0.998$), Quartile 1 and Quartile 4 (Estimate = -0.05 ± 0.09 , $p = 1.00$), Quartile 2 and Quartile 3 (Estimate = 0.02 ± 0.05 , $p = 1.00$), Quartile 2 and Quartile 4 (Estimate = 0.05 ± 0.07 , $p = 1.00$), or Quartile 3 and Quartile 4 (Estimate = 0.03 ± 0.08 , $p = 1.00$).

Likewise, before the Robot Falcon launch, no significant differences in vigilance were observed between Quartile 1 and Quartile 2 (Estimate = -0.31 ± 0.14 , $p = 0.482$), Quartile 1 and Quartile 3 (Estimate = -0.35 ± 0.16 , $p = 0.537$), Quartile 1 and Quartile 4 (Estimate = -0.31 ± 0.20 , $p = 0.926$), Quartile 2 and Quartile 3 (Estimate = -0.03 ± 0.11 , $p = 1.00$), Quartile 2 and Quartile 4 (Estimate = 0.00 ± 0.17 , $p = 1.00$), or Quartile 3 and Quartile 4 (Estimate = 0.04 ± 0.18 , $p = 1.00$).

Finally, vigilance durations remained consistent across boldness quartiles after the Robot Falcon landing, with no significant differences identified between Quartile 1 and Quartile 2 (Estimate = 0.20 ± 0.18 , $p = 0.995$), Quartile 1 and Quartile 3 (Estimate = 0.22 ± 0.19 , $p = 0.992$), Quartile 1 and Quartile 4 (Estimate = -0.02 ± 0.22 , $p = 1.00$), Quartile 2 and Quartile 3 (Estimate = 0.03 ± 0.12 , $p = 1.00$), Quartile 2 and Quartile 4 (Estimate = -0.22 ± 0.16 , $p = 0.963$), or Quartile 3 and Quartile 4 (Estimate = -0.25 ± 0.17 , $p = 0.952$).

The analysis of deviance for predictor influence revealed that the timeframes (before launch, exposure, after landing) had a significant effect on vigilance duration ($\chi^2 = 11.09$, $df = 2$, $p = 0.004$). However, neither boldness quartile ($\chi^2 = 1.48$, $df = 3$, $p = 0.69$), age ($\chi^2 = 0.08$, $df = 1$, $p = 0.77$), sex ($\chi^2 = 0.001$, $df = 1$, $p = 0.98$), pairing status ($\chi^2 = 0.10$, $df = 1$, $p = 0.75$), nor the interaction between phase and quartile ($\chi^2 = 3.68$, $df = 6$, $p = 0.72$) significantly influenced vigilance durations. This suggests that while the Robot Falcon's presence influenced vigilance behavior in geese, individual boldness and other measured factors did not have a significant impact.

Table 2 Vigilance Behaviors Comparison Model Results

This table presents the results of a generalized linear mixed model (GLMM) analyzing the **vigilance behavior** of a flock ($n = 55$) of Greylag geese (*Anser anser*) across three timeframes: "exposure," "before" (the timeframe before the Robot Falcon was launched), and "after" (the timeframe after the Robot Falcon has been landed). The square root of **vigilance duration** (in seconds), encompassing "short-neck," "long-neck," and "one-eye-up" behaviors, was fitted as the response variable in a GLMM with timeframes, boldness quartiles (interaction), sex, pairing status, and the square root of age as fixed effects, as well as bird identifier (variance = $2.34 \cdot 10^{-12} \pm 1.53 \cdot 10^{-6}$), rater identifier (variance = $1.92 \cdot 10^{-9} \pm 4.39 \cdot 10^{-5}$), starting quadrant (variance = $3.95 \cdot 10^{-13} \pm 6.29 \cdot 10^{-7}$) and an OLRE (variance = 0.12 ± 0.34) as random effects; **Model:** Indicates which model the values are derived from; **Predictor:** Variable used as a fixed effect in the model; **Estimate:** Effect size coefficient; **SE:** Standard error of the estimate; **Chisq:** Chi-square statistic; **df:** Degrees of freedom; **p-value:** Statistical significance; **Signif.:** Significance indicator (** $p < 0.001$, * $p < 0.01$, * $p < 0.05$). **Note:** All estimates represent contrasts between categorical variables or the square root of the relationship to the baseline level, as all numerical variables have been square root transformed to fit the model

Taken from an ANOVA analysis of deviance (only available for the impact of the overall category, not intracategorical) Category for which Chisq and df are available (4 following variables are part of the same category)

³ Used as baseline in model

Predictor	Estimate	SE	Chisq ¹	df ¹	p value	Signif.
Intercept	0.76	0.1	50.55	1	< 0.001	***
Timeframes ²			11.09	2		
exposure ³ vs. before	-0.49	0.14			0.004	**
exposure ³ vs. after	-0.08	0.18			0.652	
Boldness Quartiles ²			1.48	3	0.688	
Quartile1 ³						
Quartile2	0.1	0.07			0.184	
Quartile3	0.08	0.08			0.334	
Quartile4	0.05	0.09			0.623	

Sex (M² vs. F)	-0.01	0.04	0	1	0.98
Pairing (unpaired² vs. paired)	0.02	0.05	0.1	1	0.751
Age	0.02	0.02	0.08	1	0.771
Timeframes & Boldness Quartiles²					
Contrast (:)			3.68	6	
Before:Quartile1³					
Before:Quartile2	0.21	0.16			0.17
Before:Quartile3	0.27	0.17			0.122
Before:Quartile4	0.26	0.22			0.232
After:Quartile1³					
After:Quartile2	-0.3	0.19			0.129
After:Quartile3	-0.3	0.21			0.145
After:Quartile4	-0.02	0.24			0.927

5 Discussion

This study investigated the influence of a predator-mimicking drone (Robot Falcon) on the vigilance and feeding behavior of Graylag geese, focusing on the role of individual boldness. As expected, the Robot Falcon triggered anti-predator behaviors, displayed through increased vigilance coinciding with decreased feeding behavior. However, contrary to expectations, bolder individuals did not exhibit either reduced vigilance or higher feeding compared to less bold geese. These findings challenge a common assumption that bolder animals, in general, exhibit reduced vigilance in the face of predation risk¹¹¹⁻¹¹⁴.

5.1 Broader Context

The increase in vigilance behaviors observed in response to the Robot Falcon aligns with the well-established understanding of anti-predator responses in prey species. Prey animals must constantly balance the need to acquire resources with the need to avoid becoming prey themselves. Vigilance is a crucial component of this balance, allowing individuals to detect predators early and take evasive action¹¹⁵.

The lack of a significant relationship between boldness and vigilance, however, is somewhat surprising. Previous research in various bird species has suggested that bolder individuals tend to be less vigilant and react less strongly to perceived threats. For example, research on great tits (*Parus major*) has shown a clear link between boldness and risk-taking behavior in the presence of predators¹¹⁶. Similarly, studies on blackbirds (*Turdus merula*) have demonstrated that bolder individuals are less likely to exhibit anti-predator behaviors like alarm calling¹¹⁷. This discrepancy could be attributed to several factors, including species-specific differences in anti-predator strategies or the specific context of the threat

However, these findings are consistent with other research that suggests the relationship between boldness and anti-predator behavior can be context-dependent and vary across species. A study on yellow-bellied marmots (*Marmota flaviventris*) indicated that boldness did influence survival and therefore indirectly may indicate vigilance towards predators¹¹⁸. This variability highlights the need for further investigation into the factors that moderate the relationship between boldness and anti-predator responses, such as social structure, predator type, and environmental conditions. This

nuanced relationship is further supported by research on barnacle geese (*Branta leucopsis*), where bolder individuals were more likely to take risks when foraging in exposed areas ¹¹⁹, but this risk-taking did not necessarily translate to reduced vigilance. Similarly, a study on captive zebra finches (*Taeniopygia guttata*) showed that bolder individuals, while more likely to approach novel objects, did not differ in overall vigilance levels compared to less bold individuals ¹²⁰.

Flocking birds might exhibit different vigilance patterns in relation to their spatial position within the flock when a predator is detected. In a study on scaled doves (*Columbina squammata*), vigilance decreased and foraging increased with larger flock sizes, and peripheral birds were more vigilant than central ones¹²¹. While a study on European starlings (*Sturnus vulgaris*) found that individuals on the edge of the flock were more vigilant and less engaged in foraging than center ones, regardless of flock size, further emphasizing the role of spatial position in vigilance behavior ¹²². Furthermore, a study on redshanks (*Tringa totanus*), which live in flocks outside of their breeding season, found that boldness had a small influence on natural risk management, with vigilance levels being highly flexible and adjusted to the perceived risk of the situation ¹²³. In a study on great tits, which (while not directly counting as flock birds) form flocks during winter seasons, bolder individuals were most often found on the periphery of the flock ¹²⁴. Thus, the relationship between boldness and vigilance might have been masked by the interaction between increased vigilance and peripheral spatial flock positions, which in turn may be more often inhabited by bolder individuals.

This suggests that the relationship between boldness and anti-predator behavior is not a simple linear one, and that other factors, such as social context, individual experience, and the specific type of predator threat, may play a significant role. In the case of the Graylag geese studied here, previous research on this same flock by Common et al. ⁴¹ provides a compelling example of how the influence of boldness in one situation (breeding) does not necessarily translate to other contexts (responding to a Robot Falcon). While similar boldness levels in breeding pairs improved hatching success, this trait did not influence mate choice or other key breeding outcomes like clutch size and fledgling success.

It is also possible that the perceived threat level of the Robot Falcon was not high enough to elicit differential responses based on boldness. While the drone was designed to mimic a natural predator, the geese may have recognized it as an inanimate object and adjusted their behavior accordingly. Alternatively, the social nature of Graylag geese could play a role. In group-living species, individuals may rely on social cues and collective vigilance, potentially diminishing the influence of individual boldness on anti-predator behavior. It's also important to consider how the type of predator (aerial vs. ground) might influence the relationship between boldness and vigilance.

5.2 Limitations

This habituation effect could be due to the geese employing transitive inference. This cognitive ability allows animals to deduce relationships between items that haven't been directly compared ^{125,126}. Previous research has demonstrated transitive inference in Graylag geese ¹²⁷. In this case, the geese may have observed the UAV (a potential predator) and noticed it did not attack when humans were present. Thus, the geese may have used transitive inference, where they A) observe a predator, and B) notice it doesn't attack when humans are present, to C) deduce that humans deter predators or at least reduce the likelihood of predation. Which might have masked the differences between boldness ranks.

Furthermore, previous research has shown that habituation towards the quadcopter drone, as a silent observer, occurs (data not yet published). This habituation may be relevant to the current study's Robot Falcon as well, because the same quadcopter was used during this study in parallel experiments, hovering 30 meters above the flock at all times. This constant presence could have influenced the geese's behavior in several ways. It's possible that the quadcopter, through its repeated co-occurrence with the Robot Falcon, became a conditioned stimulus. A key principle of classical conditioning¹²⁸, where a previously neutral stimulus (the quadcopter) becomes associated with another stimulus that evokes a response (the Robot Falcon triggering vigilance). Over time, the conditioned stimulus alone can elicit the same response, even without the original trigger. This learning process has been widely observed in various animal species, including birds¹²⁹.

However, the nature of this conditioning and its effects on the geese could be more nuanced. First, the quadcopter, despite its association with the Robot Falcon's threatening presence, might have become a conditioned stimulus for a stress response, particularly for the bolder individuals. Its continuous, unnatural presence in their environment might have induced a general state of heightened stress in the bolder geese, who are naturally less cautious. This increased baseline stress level could have led them to be more vigilant overall, potentially masking the expected lower vigilance associated with their boldness. Second, the Robot Falcon itself might have become the conditioned stimulus, but for a reduced vigilance response. This could occur if the geese, through repeated exposure, learned to associate the Robot Falcon with the non-threatening presence of the quadcopter. Essentially, the quadcopter's "safety signal" might have transferred to the Robot Falcon, leading to a weaker vigilance response over time, particularly in the less bold individuals who are typically more cautious. This could have diminished the expected differences in vigilance between bold and less bold geese.

These two contrasting scenarios find support in existing research on animal behavior and cognition, though the evidence remains inconclusive. Extensive research demonstrates classical conditioning in birds across various contexts, including anti-predator responses¹³⁰. On the one hand, studies have shown that non-threatening UAVs on their own can induce physiological and behavioral stress responses, even when not presented as predators, in animals¹³¹ and birds¹³², and that individuals differ in their sensitivity to UAVs¹³³. This supports the possibility of the quadcopter increasing stress levels in bolder individuals, despite its association with the non-threatening Robot Falcon. On the other hand, a recent study by Li et al.¹³⁴ on coots (*Fulica atra*) for habituation to UAVs, with repeated exposure to non-threatening drones, led to significant decreases in both flight initiation and alert distances. However, it remains unclear whether this habituation would transfer to the Robot Falcon, or whether the geese might instead learn to associate the Robot Falcon with the 'safety signal' of the quadcopter, leading to a more complex pattern of vigilance responses. You could expand on the discussion of classical conditioning by mentioning the concept of "stimulus generalization," where the geese might generalize their learned association of the quadcopter with safety to other similar drones or even to humans in general.

The after landing timeframe, encompassing the first 2 minutes after the Robot Falcon landed, presented particular challenges. Although a visual reduction in vigilance was observed (see Supplementary 11), the variance in behavior types increased during this timeframe. This increased variability might be attributed to several factors, including individual differences in personality traits (other than boldness) or lingering internal stress responses influencing behavior. This may explain why a simplified model provided the best fit for the feeding durations when incorporating the timeframe. While no optimal fit was achieved for the non-feeding durations, it's important to

acknowledge that this category encompasses a broad range of activities, such as self-cleaning, resting, and ground observation without feeding. This inherent heterogeneity within the non-feeding category, coupled with the unique characteristics of the after landing timeframe, likely contributed to the difficulties in achieving a suitable model fit. Splitting non-feeding into more specific subcategories might improve model performance in future analyses. You could add a sentence about the potential influence of individual differences in other personality traits (besides boldness) on the geese's behavior during this timeframe.

Interestingly, the models did not converge when rater identifiers, experiment days and starting quadrants were all used at once (as random effects). An explanation would be that the limited number of raters as well as experiment days provided insufficient data sizes to accurately estimate the variance associated with a rater ID random effect ¹³⁵. This could have led to overfitting and convergence issues, particularly when combined with the challenges of modeling the after-landing timeframe, where a model simplification was also necessary for the feeding duration analysis.

Additionally, a potential habituation effect to the UAV predator simulation may have occurred, when looking at the ratios between vigilance and non-vigilant behavior over the course of experiment day 1 to 3 and 4 to 6 (see Supplementary Figure 15). This may be linked to the presence of researchers during the experiments. Due to cost constraints, multiple experiments were conducted simultaneously, involving up to 15 researchers. The geese were familiar with at least half of these researchers, and focal individuals sometimes stood in close proximity to those recording them. Graylag geese can discriminate between individuals from a young age ¹³⁶, raising the possibility that the presence of familiar humans influenced their vigilance behavior. This familiarity may have emboldened less bold individuals, leading to reduced vigilance and diminishing the differences between bold and less bold geese.

5.3 Conclusion

In conclusion, this study provides valuable insights into the anti-predator behavior of Graylag geese and the role of individual boldness. While the Robot Falcon did elicit anti-predator responses in form of vigilance behaviors, there was no clear evidence to suggest that bolder individuals were less vigilant than shyer individuals. This finding highlights the complexity of anti-predator strategies and the need to consider species-specific factors, social dynamics, and the potential for habituation to novel stimuli.

The study also underscores the importance of careful model selection and interpretation in analyzing behavioral data. While the GLMM framework proved effective for comparing behavior durations at different timeframes, challenges arose when incorporating the after landing timeframe and analyzing the heterogeneous non-feeding category.

However, the potential for habituation to both the predator-mimicking drone and the observer drone, coupled with the possible influence of transitive inference and classical conditioning, adds further layers of complexity to the interpretation of the findings. Future research should aim to address these confounding factors and explore the long-term effects of repeated exposure to UAVs on the behavior of geese and other bird species.

Ultimately, this study contributes to our understanding of the intricate interplay between personality, vigilance, and survival in a social species. The findings suggest that while boldness may have

influenced overall activity levels and responses to certain types of threats in other studies, its impact on predator-specific vigilance in Graylag geese may be less pronounced than anticipated, potentially reflecting an adaptive balance between minimizing risk and maximizing foraging efficiency. By continuing to unravel these complex relationships, we can gain a deeper appreciation for the challenges faced by animals in their natural environment and inform conservation efforts aimed at protecting vulnerable species.

5.4 Future research

Further research is necessary to understand the specific effects of drones on geese behavior (like the silent observer quadcopter) and how this dynamic interacts with individual boldness, as well as other personality traits such as activity, sociability, exploration, and aggressiveness. Although the quartile-based analysis did not demonstrate a strong influence of boldness on predator-specific vigilance, it is crucial to consider that boldness may manifest differently across various behavioral contexts. Further investigation incorporating diverse behavioral metrics, environmental factors and spatial positioning of individuals within the flock is necessary to fully elucidate the intricate interplay between personality and anti-predator strategies.

Future research should include a prolonged experiment with minimal human presence, including more exposure days and compare periods with consecutive and non-consecutive exposure days. Also to further investigate habituation to UAVs in combination with other UAVs and humans. Comparing a human-free setup with a human-present setup would help isolate the impact of human presence on Graylag geese anti-predator behavior. Investigating the influence of human presence on habituation will also help clarify the interplay between boldness and anti-predator behavior, as the presence of familiar humans may have masked subtle differences in vigilance between boldness ranks.

Furthermore, to gain a more comprehensive understanding of the complex interactions between UAVs, individual differences, and anti-predator behavior, future studies should incorporate more detailed investigations into the potential of conditioning individuals to perceive one UAV as stress or safety signals when its use coincides with another. This could involve manipulating the presence of the quadcopter and the Robot Falcon independently to assess their individual and combined effects on vigilance, measuring physiological responses, such as heart rate or corticosterone levels, which are known indicators for stress levels in Graylag geese¹³⁷, to assess potential anxiety induction.

Future research should also focus on individual differences in boldness by testing geese with known boldness scores in various UAV exposure conditions to assess how their vigilance behaviors vary. This could be complemented by eye-tracking studies to assess visual attention and risk assessment, and by standardized behavioral assays to quantify alert distance, flight initiation distance, and group cohesion. Additionally, comparative studies with other goose species or populations could help assess the generality of findings and identify species-specific factors influencing anti-predator responses to drones. It would also be valuable to investigate how individual learning and prior experience, including age and previous exposure to predators, might influence habituation to drones and the potential for generalization of this habituation to other types of drones or even to real falcons (or similar aerial predators to Graylag geese).

Lastly, future research should also be done on fully wild migratory flocks of Graylag geese to assess how the semi-tamed non-migratory state of the KLF flock influences experiment outcomes.

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7 Appendix

7.1 Supplementaries

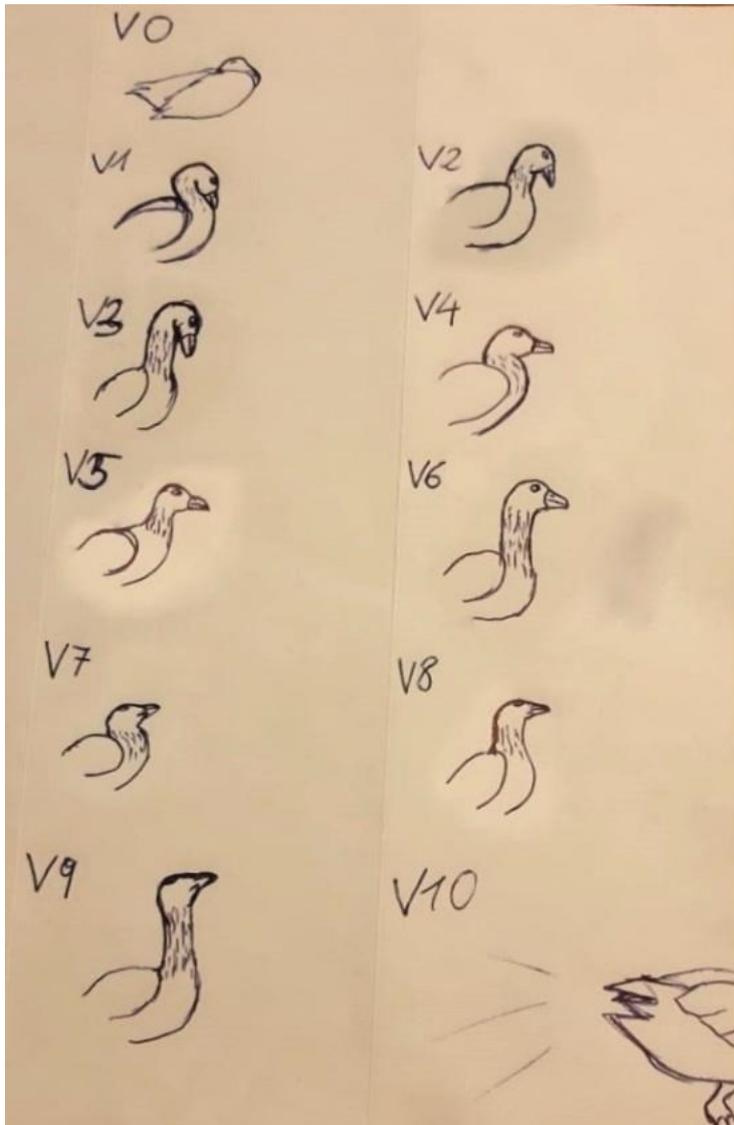


Supplementary Figure 1 Exposure Experiment Procedure

Ro-

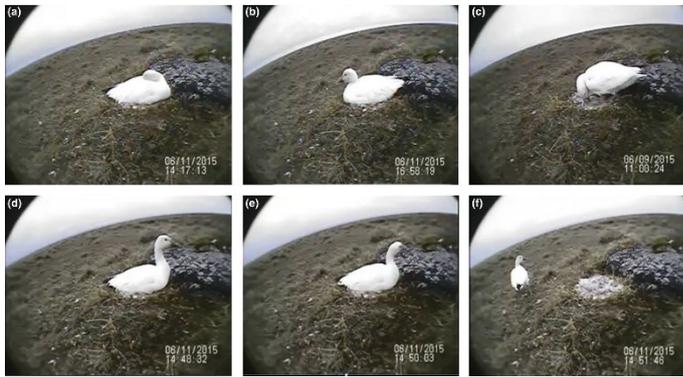
bot Falcon (UAV) flight path, with falcon pictogram used as a stand-in; **(1)** Launch and later landing position; **(2)** Position from which the stooping maneuvers started; **(3)** Position from which the UAV was withdrawn back to the landing zone.

Lightning symbol indicates area of stooping maneuvers (up to 6); **Arrows** indicate flight path outside stooping maneuvers; **Circle** indicate feeding grounds and geese location; Image generated as a screenshot from publicly available satellite imagery using the Maps service from Google LLC setting 47.814014, 13.948065 as coordinates; The depicted area is located in Grünau im Almtal, 4645, Upper Austria, Austria

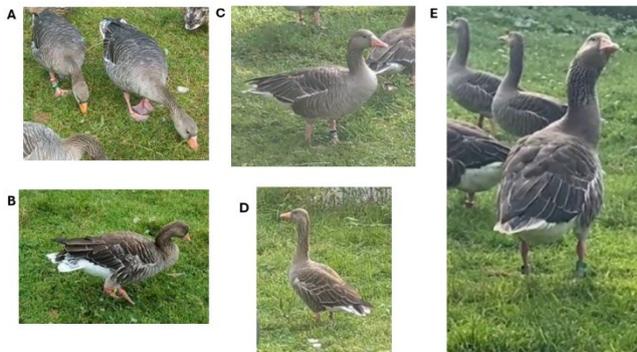


Supplementary Figure 2 Vigilance Ethogram derived from Konrad Lorenz ⁹⁶

V0 head tucked, V1 Short neck, beak-down, V2 Mid neck, beak down,
 V3 Long neck, beak-down, V4 Short neck, beak-straight, V5 Mid neck,
 beak-straight, V6 Long neck, beak straight, V7 short neck, one eye-up,
 Mid neck, one eye-up, V9 Long neck, one eye-up, V10 Flight.

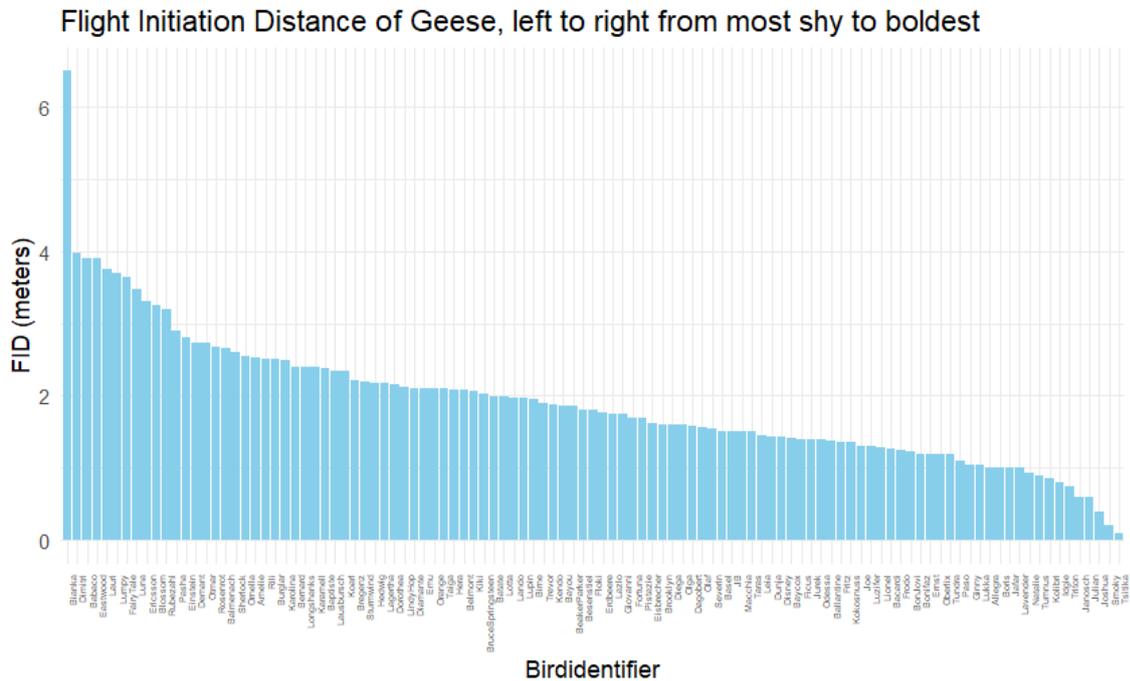


Supplementary Figure 3 **Vigilance Ethogram observed by Barnas et. al** ⁹⁷
(a) Resting, (b) Low Scan, (c) Nest Maintenance, (d) High Scan, (e) Head Cock, (f) Off Nest



Supplementary Figure 4 **Vigilance Ethogram used in this Thesis**

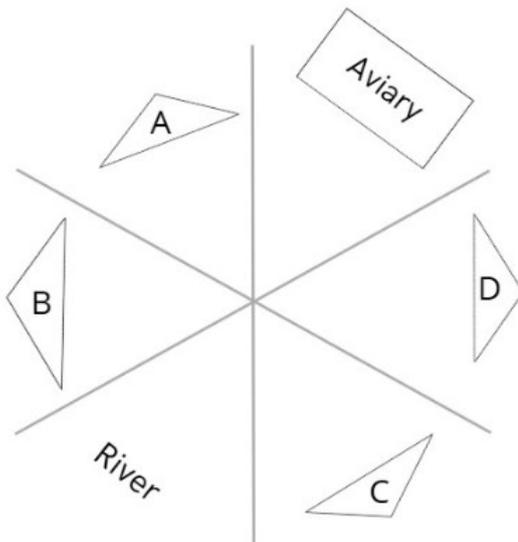
- A:** Feeding – goose's beak on the ground (non-vigilant)
- B:** Non-Feeding – beak directed at the ground without feeding or during non-vigilant behaviors (e.g. scanning the ground)
- C:** Short-Neck Vigilance – head and beak held straight to monitor surroundings (lowest form of vigilance)
- D:** Long-Neck Vigilance – straightened neck with the beak to sky (higher form of vigilance)
- E:** One-Eye-Up Vigilance – tilted head and direct gaze at the sky (highest form of vigilance)



Supplementary Figure 5 Flight Initiation Distance

Original

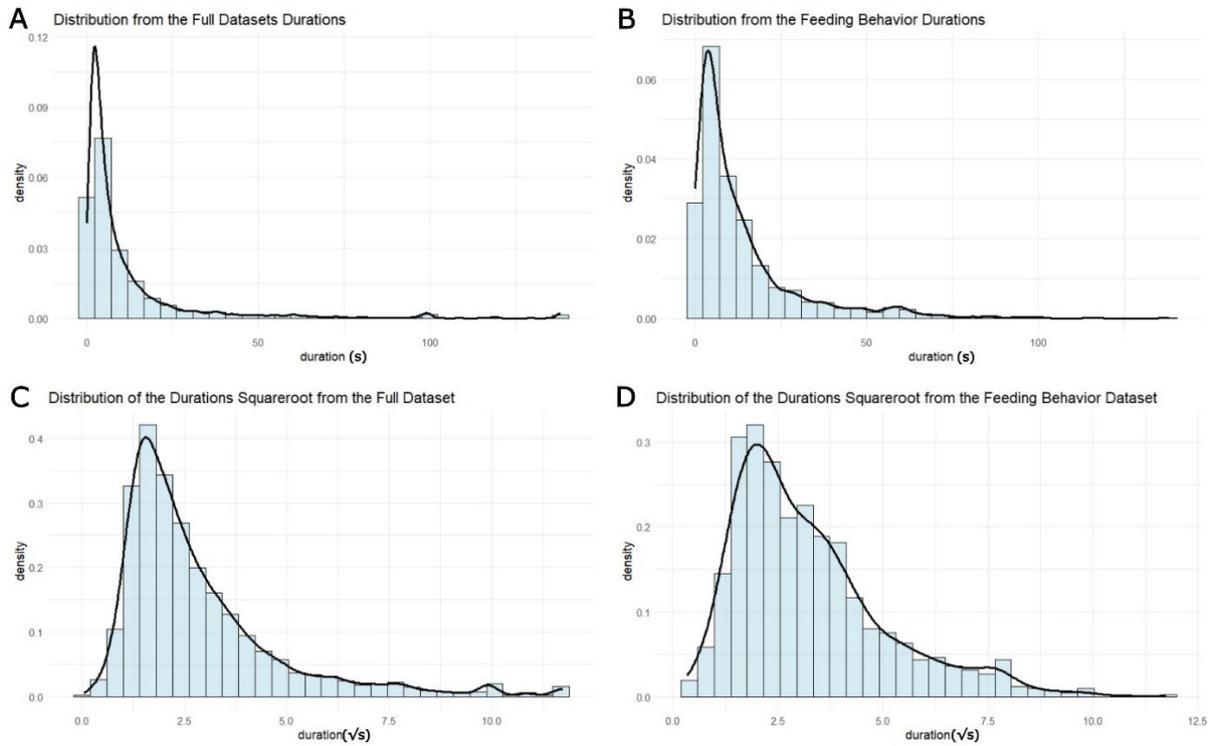
dataset of a flock (n = 120) of semitamed non-migratory Graylag geese (*Anser anser*) from Common et al. 2024; shows flight initiation distance (FID) in meters for each Goose sampled; Y-Achse shows **FID**; X-Achse shows **Birdidentifier**; Boldest geese are to the right and least bold to the left



Supplementary Figure 6 Quadrants of the Feeding Area

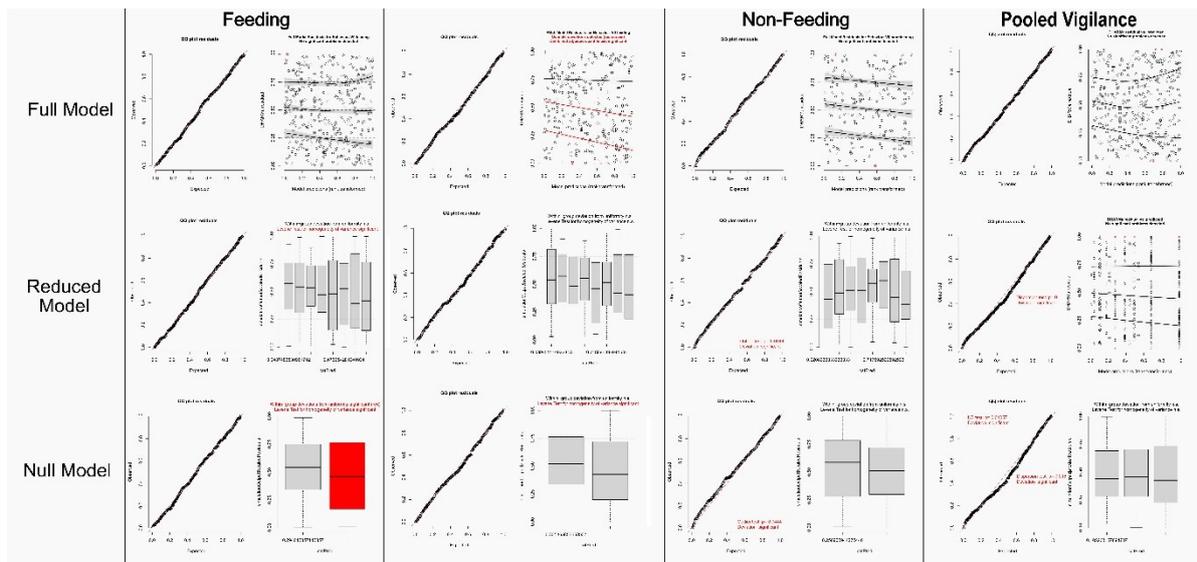
Diagram

shows the order of quadrant of the feeding area at which the simulated predator (Robot Falcon) experiments were held; A, B, D and C represent feeding trough, while Aviary represents an adjacent aviary used for banding birds, and River represents the river adjacent to the feeding area, at which the flock (n = 120) of non-migratory semi-tamed Graylag geese (*Anser anser*) tend to gather before flight



Supplementary Figure 7 Density Distribution Histogram

Shown are the Behavior Durations either in raw seconds or rooted for better visibility of the Gamma distribution; **A** the Durations of the Full Dataset in seconds (s); **B** the Durations of the Feeding Behavior Dataset in seconds (s); **C** the Squareroot of the Durations of the Full Dataset (\sqrt{s}); **D** the Squareroot of the Durations of the Feeding Behavior Dataset (\sqrt{s})

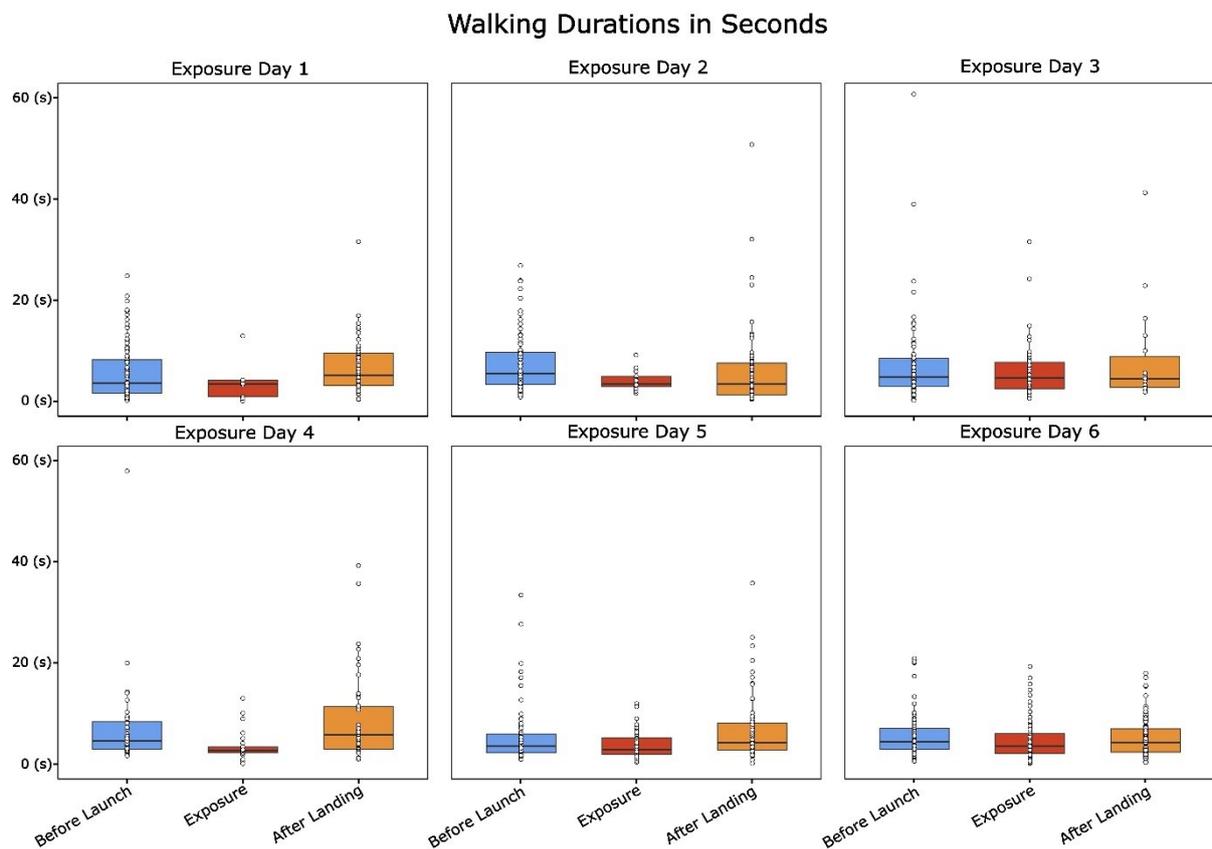


Supplementary Figure 8 DHARMA Plots for each Individual Model Fit

Shown

are the DHARMA plots generated from simulated residuals for **Feeding**, **Non-Feeding**, and **Pooled Vigilance (Short-Neck, Long-Neck, and One-Eye-Up)** behaviors; for **Feeding** the model incorporating before launch and exposure timeframes (left) and the model incorporating exposure and after landing timeframes (right) were done separately, while **Non-Feeding** and **Pooled Vigilance** incorporated all 3 timeframes (before launch, exposure, and after landing) at once; **Full Model** contains Timeframes, Boldness, Age, Sex, Pairing, and Startingquadrant as fixed and Bird Identifier as well

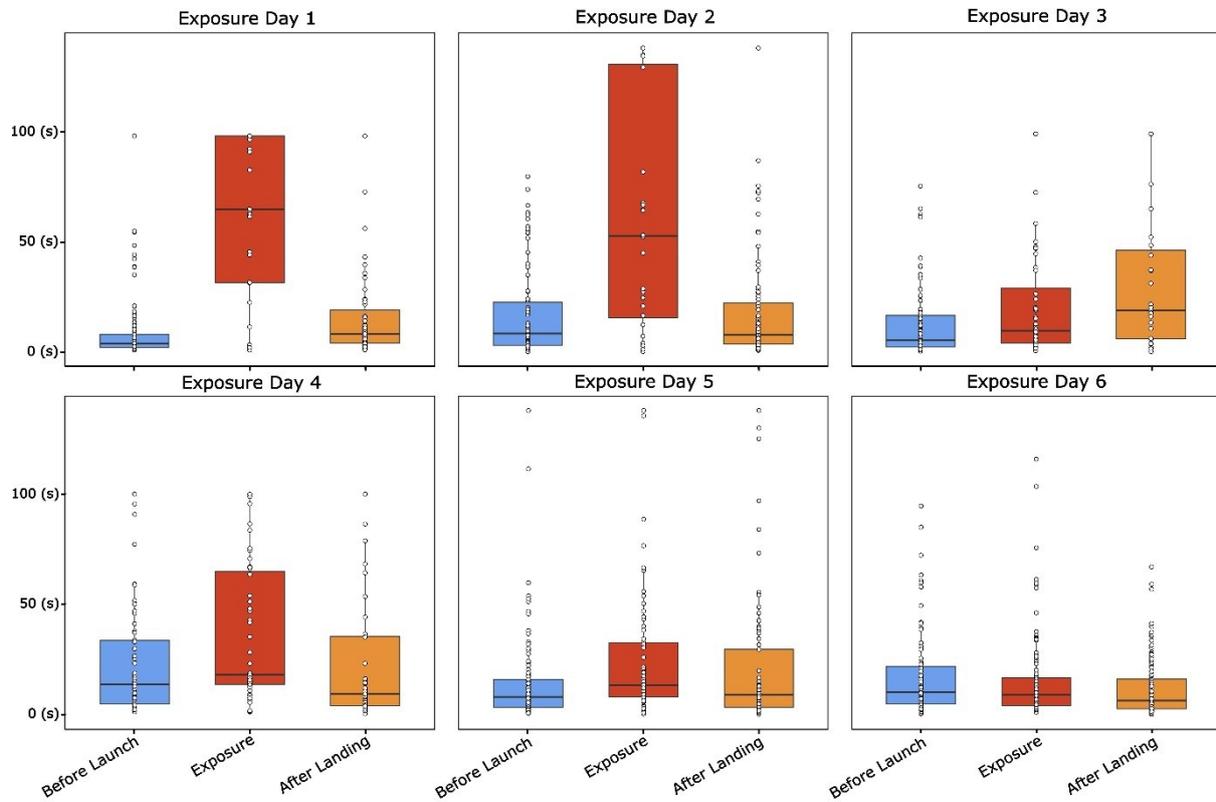
Rater Identifier and only for **Feeding** an OLR as random effects; **Reduced Model** contains only Timeframes and Boldness as fixed and Bird Identifier as Random effects; **Null Model** contains only Timeframes as fixed effect and Bird Identifier as random effect; left QQ plots assess residual uniformity, with the Y-axis representing the observed residuals (transformed to a uniform distribution by DHARMA) and the X-axis representing the expected quantiles under the null hypothesis of uniformity and the closer the points align with the 45-degree line, the better the model fit; right plots assess residual independence and variance homogeneity, with the Y-axis showing DHARMA residuals and the X-axis representing either rank-transformed model predictions (for the Full and Reduced Models) or categorical predictor levels (catPred) for the Null Model; Note catPred represents different categories of a predictor variable used to check if residual variance changes across groups, with significant results indicating heteroscedasticity across groups; all black graphs represent successful model fits, while red values indicate deviations (exclusion criteria)



Supplementary Figure 9 Boxplot of Walking Durations in Seconds

Walking durations of a flock ($n = 55$) of Graylag geese (*Anser anser*) in seconds before (Before Launch), during (Exposure), and after (After Landing) a simulated aerial predator (Robot Falcon) was launched, compared between each timeframe; Zoomed into the range of 0 to 60 seconds (s); **Before Launch** represents the timeframe before the Robot Falcon was launched; **Exposure** represents the timeframe during which the flock was exposed to the Robot Falcon; **After Landing** represents the timeframe after the Robot Falcon has been landed; timeframe durations varied between and within experiment days, subsets (Before Launch and After Landing) were adjusted to match the exposure duration for each day: 98s (Day 1), 138s (Days 2 & 5), 99s (Day 3), 100s (Day 4), and 119s (Day 6); white dots represent individual values

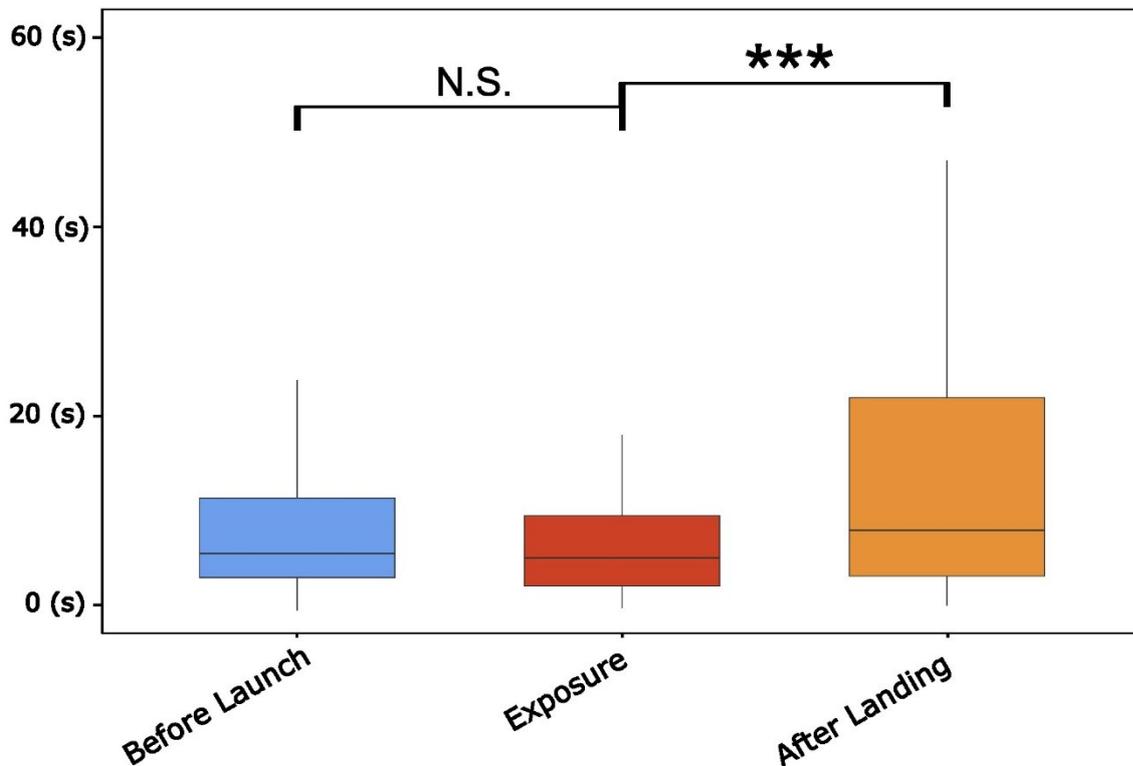
Standing Durations in Seconds



Supplementary Figure 10 Boxplot of Standing Durations in Seconds

Standing durations of a flock ($n = 55$) of Graylag geese (*Anser anser*) in seconds before (Before Launch), during (Exposure), and after (After Landing) an artificial predator (Robot Falcon) was launched, compared between each timeframe; Zoomed into the range of 0 to 60 seconds (s); **Before Launch** represents the timeframe before the Robot Falcon was launched; **Exposure** represents the timeframe during which the flock was exposed to the Robot Falcon; **After Landing** represents the timeframe after the Robot Falcon has been landed; timeframe durations varied between and within experiment days, subsets (Before Launch and After Landing) were adjusted to match the exposure duration for each day: 98s (Day 1), 138s (Days 2 & 5), 99s (Day 3), 100s (Day 4), and 119s (Day 6); white dots represent individual values

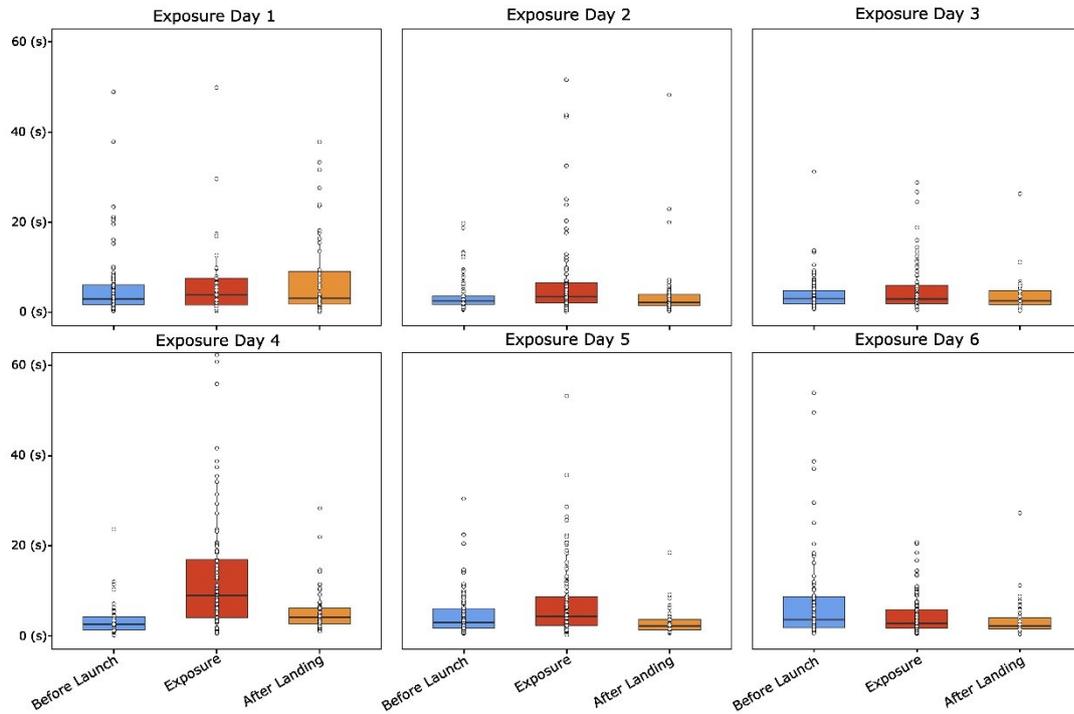
Non-Feeding Behavior Durations in Seconds



Supplementary Figure 11 Boxplot of Non-Feeding Durations in Seconds

Non-feeding durations of a flock ($n = 55$) of Graylag geese (*Anser anser*) in seconds, before (**Before Launch**), during (**Exposure**), and after (**After Landing**) a simulated aerial predator (Robot Falcon) was launched. This figure compares the time spent not feeding in each timeframe. The Robot Falcon was a remote-controlled aircraft used to simulate a predator. Before Launch represents the timeframe before the Robot Falcon was launched. The Exposure represents the timeframe during which the flock was exposed to the Robot Falcon flying overhead. After Landing represents the timeframe after the Robot Falcon had landed. The timeframe durations varied between and within experiment days. The durations of the Before Launch and After Landing periods were adjusted to match the Exposure duration for each day: 98s (Day 1), 138s (Days 2 & 5), 99s (Day 3), 100s (Day 4), and 119s (Day 6). An analysis utilizing a generalized linear mixed model revealed a significant increase in non-feeding duration after the Robot Falcon landed compared to during exposure (Estimate = 0.47 ± 0.10 , $p < 0.001$). No significant difference was found between the non-feeding duration before launch and during exposure (Estimate = 0.12 ± 0.10 , $p = 0.235$) nor between boldness quartiles (see Supplementary Table 1); zoomed into the range of 0 to 60 seconds to better visualize the differences between timeframes. The model included all 3 timeframes in an interaction with the boldness quartiles as well as age, sex and pairing status as fixed effects, with bird identifier, rater identifier, and starting quadrant as random effects. The figure is zoomed into the range of 0 to 60 seconds to better visualize the differences between timeframes and boldness quartiles.

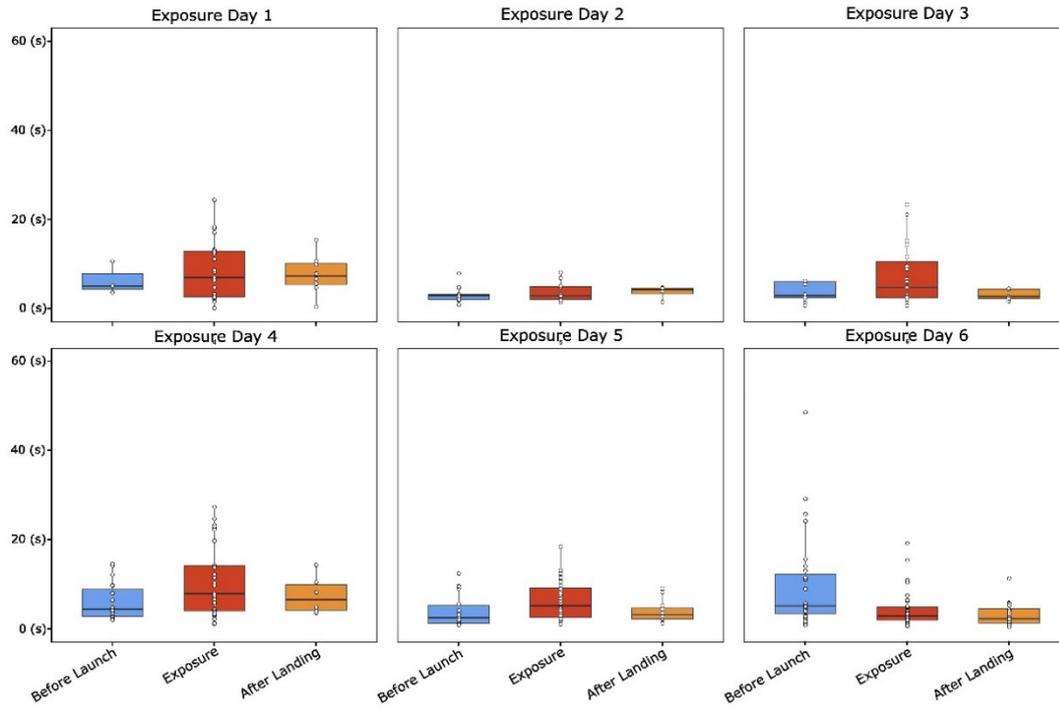
Short-Neck Vigilance Durations in Seconds



Supplementary Figure 12 Boxplot of Short-Neck Vigilance Durations in Seconds

Short-Neck (displayed behavior) durations of a flock ($n = 55$) of Graylag geese (*Anser anser*) in seconds before (Before Launch), during (Exposure), and after (After Landing) a simulated aerial predator (Robot Falcon) was launched, compared between each timeframe; Zoomed into the range of 0 to 60 seconds (s); **Before Launch** represents the timeframe before the Robot Falcon was launched; **Exposure** represents the timeframe during which the flock was exposed to the Robot Falcon; **After Landing** represents the timeframe after the Robot Falcon has been landed; timeframe durations varied between and within experiment days, subsets (Before Launch and After Landing) were adjusted to match the exposure duration for each day: 98s (Day 1), 138s (Days 2 & 5), 99s (Day 3), 100s (Day 4), and 119s (Day 6); white dots represent individual values; a generalized linear mixed model revealed a significant increase in short-neck vigilance during exposure compared to before launch (Estimate = -0.18 ± 0.09 , $p = 0.047$), but not for the timeframes exposure compared to after landing (Estimate = -0.17 ± 0.10 , $p = 0.085$); no significant differences between boldness quartiles (see Supplementary Table 1)

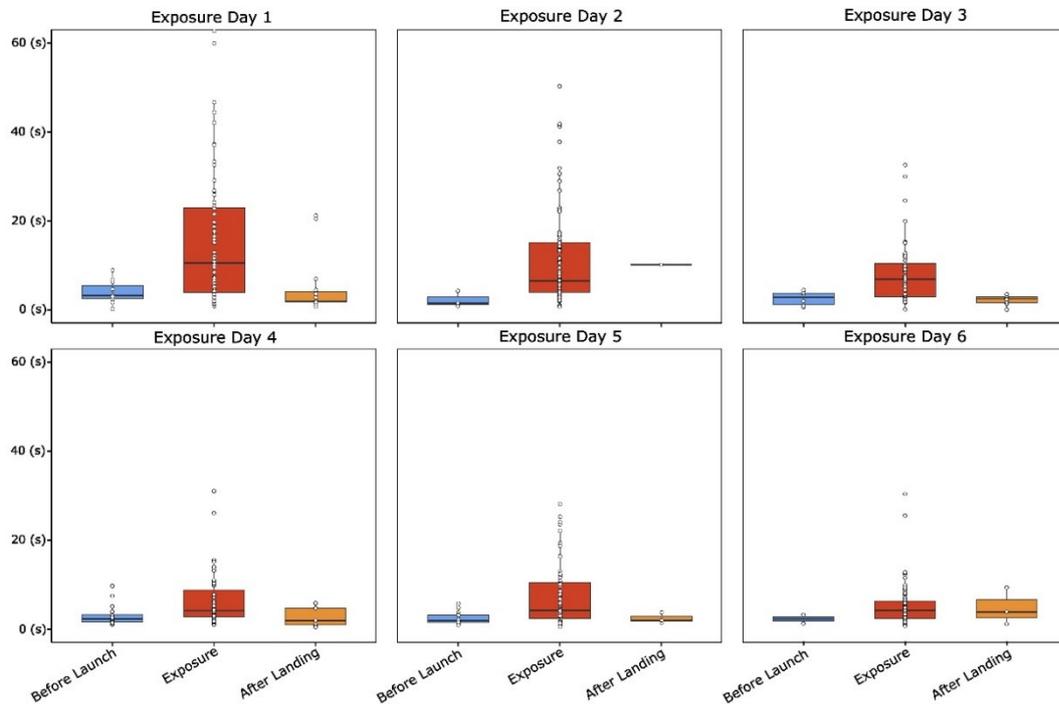
Long-Neck Vigilance Durations in Seconds



Supplementary Figure 13 Boxplot of Long-Neck Vigilance Durations in Seconds

Long-Neck (displayed behavior) durations of a flock ($n = 55$) of Graylag geese (*Anser anser*) in seconds before (Before Launch), during (Exposure), and after (After Landing) a simulated aerial predator (Robot Falcon) was launched, compared between each timeframe; Zoomed into the range of 0 to 60 seconds (s); **Before Launch** represents the timeframe before the Robot Falcon was launched; **Exposure** represents the timeframe during which the flock was exposed to the Robot Falcon; **After Landing** represents the timeframe after the Robot Falcon has been landed; timeframe durations varied between and within experiment days, subsets (Before Launch and After Landing) were adjusted to match the exposure duration for each day: 98s (Day 1), 138s (Days 2 & 5), 99s (Day 3), 100s (Day 4), and 119s (Day 6); white dots represent individual values; a generalized linear mixed model revealed no significant difference during exposure compared to before launch (Estimate = -0.79 ± 0.48 , $p = 0.109$), nor for the timeframes exposure compared to after landing (Estimate = -0.26 ± 0.31 , $p = 0.402$); no significant differences between boldness quartiles (see Supplementary Table 1)

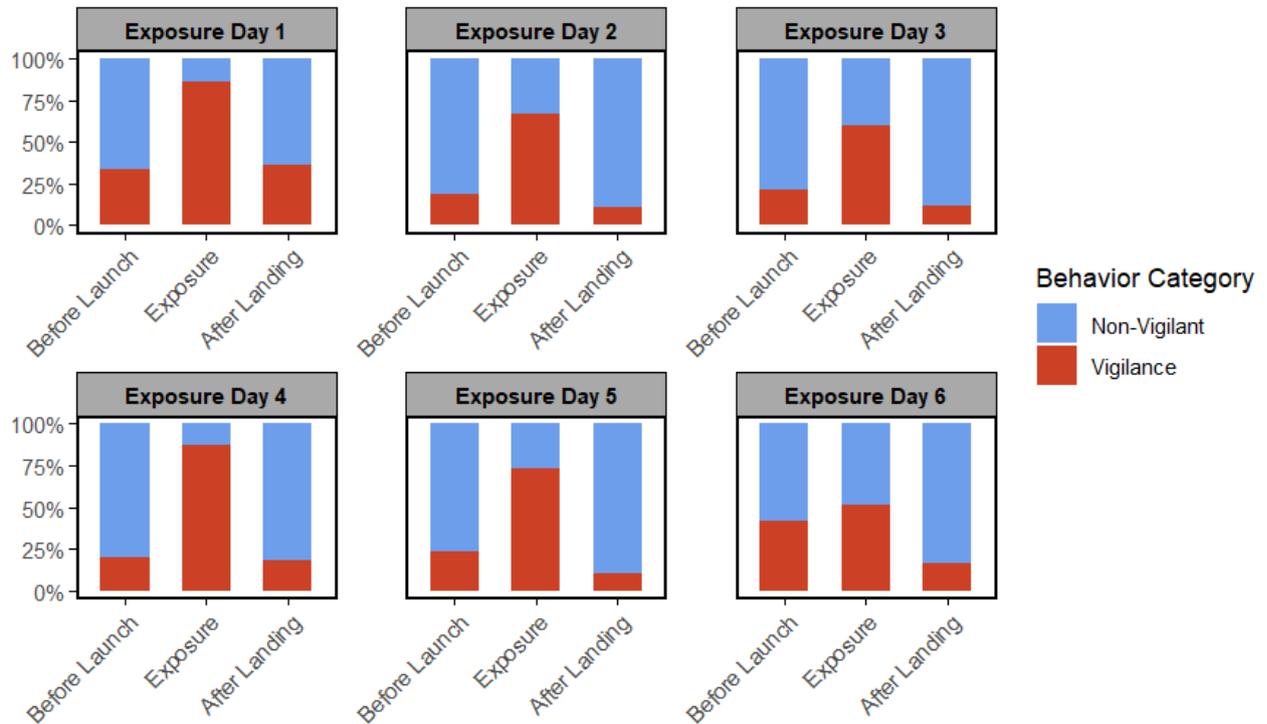
One-Eye-Up Vigilance Durations in Seconds



Supplementary Figure 14 Boxplot of One-Eye-Up Vigilance Durations in Seconds

One-Eye-Up (displayed behavior) durations of a flock ($n = 55$) of Graylag geese (*Anser anser*) in seconds before (Before Launch), during (Exposure), and after (After Landing) a simulated aerial predator (Robot Falcon) was launched, compared between each timeframe; Zoomed into the range of 0 to 60 seconds (s); **Before Launch** represents the timeframe before the Robot Falcon was launched; **Exposure** represents the timeframe during which the flock was exposed to the Robot Falcon; **After Landing** represents the timeframe after the Robot Falcon has been landed; timeframe durations varied between and within experiment days, subsets (Before Launch and After Landing) were adjusted to match the exposure duration for each day: 98s (Day 1), 138s (Days 2 & 5), 99s (Day 3), 100s (Day 4), and 119s (Day 6); white dots represent individual values; a generalized linear mixed model revealed a significant increase in short-neck vigilance during exposure compared to before launch (Estimate = -0.54 ± 0.16 , $p = 0.033$), but not for the timeframes exposure compared to after landing (Estimate = -0.26 ± 0.30 , $p = 0.383$); no significant differences between boldness quartiles (see Supplementary Table 1)

Vigilance and Non-Vigilant Behavior Durations by Timeframe



Supplementary Figure 15 Vigilance and Non-Vigilant Behavior Durations by Timeframes

The contrast in durations is shown across each individual's exposure day; **blue** percentage (%) proportion of **non-vigilant** behavior durations consisting of the feeding and non-feeding behaviors; **red** represents the percentage (%) proportion of **vigilance** durations consisting of the short-neck, long-neck, and one-eye-up behaviors; Note each proportion was calculated by division of the individual behavior duration through the sum of both behavior durations within each timeframe; Exposure represents the timeframe during which the flock was exposed to a simulated aerial predator (Robot Falcon), while Before Launch represents the timeframe before the Robot Falcon was launched and After Landing represents the timeframe after which the Robot Falcon was landed; timeframe durations varied between and within experiment days, subsets (Before Launch and After Landing) were adjusted to match the exposure duration for each day: 98s (Day 1), 138s (Days 2 & 5), 99s (Day 3), 100s (Day 4), and 119s (Day 6); a two-way repeated measures ANOVA with post-hoc t-tests revealed a significant decrease in vigilance duration over time: Vigilant individuals showed a significant decrease from day 1 to 3 ($p < 0.00158$, estimate = 0.6608) and from day 4 to 6 ($p < 0.00148$, estimate = 1.022). Interestingly, non-vigilant individuals showed no significant change between days 1 and 3, but a significant increase in vigilance from day 4 to 6 ($p = 0.0427$, estimate = -0.431). This pattern was mirrored in the foraging vs. vigilance subset analysis, with vigilant individuals showing a significant decrease in vigilance duration from day 1 to 3 ($p < 0.00158$, estimate = 0.6608) and from day 4 to 6 ($p < 0.00148$, estimate = 0.459), and no significant difference for foraging individuals.

Supplementary Table 1 GLMM Results for Non-Feeding, Short-neck, Long-neck, and One-eye-up Durations

This table presents the results of four generalized linear mixed models (GLMMs), one for each of the following behaviors exhibited by a flock ($n = 55$) of Greylag geese (*Anser anser*): non-feeding, short-neck vigilance, long-neck vigilance, and one-eye-up vigilance. These behaviors were observed across three timeframes: "exposure," "before" (the timeframe before the Robot Falcon was launched), and "after" (the timeframe after the Robot Falcon has been landed). The square root of the duration (in seconds) for each behavior was fitted as the response variable in separate GLMMs. Each model included timeframes, boldness quartiles (and their interaction), sex, pairing status, and the square root of age as fixed effects. Random effects were different between models and included bird identifier (Variances \pm SE: Non-feeding = 0.06 ± 0.25 , short-neck = 0.02 ± 0.13 , Long-neck = $< 0.01 \pm 0.00$, One-eye-up = 0.01 ± 0.07), rater identifier: (Variances \pm SE: Non-feeding = $< 0.01 \pm 0.00$, short-neck = 0.00 ± 0.03 , Long-neck = $< 0.01 \pm 0.00$, One-eye-up = $< 0.01 \pm 0.00$), starting quadrant: (Variances \pm SE: Non-feeding = $< 0.01 \pm 0.00$, Short-neck = $< 0.01 \pm 0.00$, Long-neck = $< 0.01 \pm 0.00$, One-eye-up = $< 0.01 \pm 0.00$), day of the experiment: (Variance \pm SE: Long-neck = 0.01 ± 0.11), observation-level random effect (OLRE): (Variances \pm SE: Short-neck = 0.19 ± 0.43). **Behavior**: indicator to which behavioral analysis values belong; **Predictor**:

Variable used as a fixed effect in the model; **Estimate:** Effect size coefficient; **SE:** Standard error of the estimate; **Chisq:** Chi-square statistic; **df:** Degrees of freedom; **p-value:** Statistical significance; **Signif.:** Significance indicator (***) p < 0.001, ** p < 0.01, * p < 0.05)

Note

all estimates represent contrasts between categorical variables or the square root of the relationship to the baseline level, as all numerical variables have been square root transformed to fit the model

¹ Taken from an ANOVA (only available for the impact of the overall category, not intracategorical)

Category for which Chisq and df are available (following variables are part of the same category)

Used as baseline in model

²

³

Behavior	Predictor	Estimate	SE	Chisq ¹	df ¹	p value	Signif.
Non-feeding	Intercept	0.36	0.2	2.01	1	0.156	
	Timeframes ²			15.89	2		
	exposure ³ vs. before	0.12	0.1			0.235	
	exposure ³ vs. after	0.47	0.1			< 0.001	***
	Boldness Quartiles ²			0.71	3	0.871	
	Quartile1 ³						
	Quartile2	0.02	0.18			0.922	
	Quartile3	0.09	0.16			0.562	
	Quartile4	0.13	0.18			0.451	
	Sex (M ² vs. F)	0.13	0.11	2.34	1	0.126	
	Pairing (unpaired ² vs. paired)	0.32	0.17	3.08	1	0.079	
	Age	0.08	0.06	0.59	1	0.444	
	Timeframes & Boldness Quartiles ² Contrast (:)			4.56	6	0.602	
	Before:Quartile1 ³						
	Before:Quartile2	0.17	0.17			0.312	
	Before:Quartile3	0.05	0.15			0.749	
	Before:Quartile4	-0.06	0.17			0.714	
	After:Quartile1 ³						
	After:Quartile2	0.19	0.18			0.292	
	After:Quartile3	0.03	0.15			0.829	
After:Quartile4	-0.2	0.18			0.261		
Short-neck	Intercept	0.68	0.14	25.93	1	< 0.001	***
	Timeframes ²			6.31	2		
	exposure ³ vs. before	-0.18	0.09			0.047	*
	exposure ³ vs. after	-0.17	0.1			0.085	
	Boldness Quartiles ²			1.83	3	0.608	
Quartile ³							

	Quartile2	0.01	0.1			0.9	
	Quartile3	-0.03	0.1			0.747	
	Quartile4	-0.14	0.15			0.35	
	Sex (M² vs. F)	0.01	0.06	0	1	0.962	
	Pairing (unpaired² vs. paired)	0.01	0.07	0.02	1	0.896	
	Age	0.02	0.03	0.15	1	0.694	
	Timeframes & Boldness Quartiles² Contrast (:)			1.99	6	0.921	
	Before:Quartile1³						
	Before:Quartile2	0.09	0.11			0.43	
	Before:Quartile3	0.08	0.11			0.472	
	Before:Quartile4	0.13	0.16			0.408	
	After:Quartile1³						
	After:Quartile2	0.02	0.12			0.888	
	After:Quartile3	-0.04	0.12			0.731	
	After:Quartile4	-0.02	0.19			0.903	
Long-neck	Intercept	0.83	0.22	14.69	1	< 0.001	***
	Timeframes²			2.93	2		
	exposure³ vs. before	-0.79	0.48			0.103	
	exposure³ vs. after	-0.26	0.31			0.402	
	Boldness Quartiles²			1.49	3	0.685	
	Quartile1³						
	Quartile2	0.12	0.19			0.506	
	Quartile3	0.1	0.2			0.613	
	Quartile4	-0.02	0.22			0.933	
	Sex (M² vs. F)	-0.05	0.09	0.32	1	0.574	
	Pairing (unpaired² vs. paired)	-0.18	0.1	3.19	1	0.074	
	Age	0.02	0.05	0.09	1	0.761	
	Timeframes & Boldness Quartiles² Contrast (:)			4.63	6	0.592	
	Before:Quartile1³						
	Before:Quartile2	0.75	0.5			0.132	
	Before:Quartile3	0.7	0.5			0.167	

	Before:Quartile4	0.61	0.56			0.283	
	After:Quartile1³						
	After:Quartile2	-0.04	0.33			0.896	
	After:Quartile3	-0.03	0.34			0.92	
	After:Quartile4	0.44	0.47			0.348	
One-eye-up	Intercept	0.75	0.16	23.32	1	< 0.001	***
	Timeframes²			5.73	2		
	exposure³ vs. before	-0.54	0.25			0.033	*
	exposure³ vs. after	0.26	0.3			0.383	
	Boldness Quartiles²			1.24	3	0.743	
	Quartile 1³						
	Quartile 2	0.06	0.1			0.566	
	Quartile 3	0.1	0.12			0.382	
	Quartile 4	0.15	0.16			0.336	
	Sex (M² vs. F)	0.06	0.07	0.72	1	0.397	
	Pairing (unpaired² vs. paired)	0.12	0.08	2.18	1	0.14	
	Age	0.01	0.04	0.02	1	0.894	
	Timeframes & Boldness Quartiles² Contrast (:)			8.7	6	0.191	
	Before:Quartile1³						
	Before:Quartile2	0.18	0.28			0.525	
	Before:Quartile3	-0.03	0.34			0.94	
	Before:Quartile4	0.39	0.39			0.319	
	After:Quartile1³						
	After:Quartile2	-0.87	0.35			0.612	
	After:Quartile3	-0.58	0.37			0.114	
	After:Quartile4	-0.51	0.47			0.276	

Supplementary Table 2 Post Hoc results for Feeding Durations Model

This

table presents the results of post-hoc pairwise comparisons for feeding durations in Greylag geese (*Anser anser*) across different boldness quartiles (Quartile 1 to 4) and timeframes ("exposure," "before," and "after"). The data were analyzed using two generalized linear mixed models (GLMMs): one comparing "before" and "exposure" timeframes, and another comparing "after" and "exposure" timeframes. **Contrast:** Specifies the pairwise comparison being made, indicating the timeframe and boldness quartile for each group (e.g., "exposure:Quartile1- before:Quartile2"); **Estimate:** The estimated difference in feeding duration (on the log scale) between the two groups being compared; **SE:** The standard error of the estimate; **z ratio:** The z-statistic for the comparison; **p value:** The p-value, indicating the statistical significance of the difference between the two groups; **Model:** Specifies whether the contrast belongs to the "before vs. exposure" model or the

"after vs. exposure" model; **Note** the "before vs. exposure" model includes contrasts where "before" is one of the timeframes being compared; "after vs. exposure" model includes contrasts where "after" is one of the timeframes being compared; results are presented on the log scale (not the response scale); p-values were adjusted using the Tukey method for comparing a family of 12 estimates; significant p-values are bold

Contrast	Estimate	SE	z.ratio	p.value
exposure:Quartile1 - before:Quartile1	-0.39	0.15	-2.59	0.159
exposure:Quartile1 - exposure:Quartile2	0.22	0.22	1.01	0.973
exposure:Quartile1 - before:Quartile2	-0.16	0.22	-0.73	0.996
exposure:Quartile1 - exposure:Quartile3	0.17	0.27	0.63	0.999
exposure:Quartile1 - before:Quartile3	-0.61	0.25	-2.45	0.219
exposure:Quartile1 - exposure:Quartile4	0.35	0.22	1.56	0.775
exposure:Quartile1 - before:Quartile4	-0.32	0.2	-1.63	0.731
before:Quartile1 - exposure:Quartile2	0.61	0.22	2.82	0.091
before:Quartile1 - before:Quartile2	0.23	0.2	1.15	0.946
before:Quartile1 - exposure:Quartile3	0.56	0.26	2.14	0.392
before:Quartile1 - before:Quartile3	-0.22	0.23	-0.95	0.982
before:Quartile1 - exposure:Quartile4	0.74	0.22	3.4	0.016
before:Quartile1 - before:Quartile4	0.07	0.18	0.39	1
exposure:Quartile2 - before:Quartile2	-0.38	0.24	-1.58	0.764
exposure:Quartile2 - exposure:Quartile3	-0.05	0.31	-0.17	1
exposure:Quartile2 - before:Quartile3	-0.83	0.29	-2.91	0.071
exposure:Quartile2 - exposure:Quartile4	0.12	0.27	0.45	1
exposure:Quartile2 - before:Quartile4	-0.54	0.25	-2.18	0.367
before:Quartile2 - exposure:Quartile3	0.33	0.31	1.05	0.967
before:Quartile2 - before:Quartile3	-0.45	0.27	-1.64	0.723
before:Quartile2 - exposure:Quartile4	0.5	0.28	1.83	0.601

before:Quartile2 - before:Quartile4	-0.16	0.24	-0.7	0.997
exposure:Quartile3 - before:Quartile3	-0.78	0.26	-2.97	0.06
exposure:Quartile3 - exposure:Quartile4	0.18	0.26	0.68	0.998
exposure:Quartile3 - before:Quartile4	-0.49	0.29	-1.68	0.702
before:Quartile3 - exposure:Quartile4	0.95	0.27	3.57	0.009
before:Quartile3 - before:Quartile4	0.29	0.26	1.09	0.96
exposure:Quartile4 - before:Quartile4	-0.67	0.24	-2.79	0.097
exposure:Quartile1 - after:Quartile1	-0.82	0.12	-6.63	<0.001
exposure:Quartile1 - exposure:Quartile2	0.21	0.23	0.94	0.982
exposure:Quartile1 - after:Quartile2	-0.76	0.21	-3.62	0.007
exposure:Quartile1 - exposure:Quartile3	-0.15	0.22	-0.69	0.997
exposure:Quartile1 - after:Quartile3	-0.69	0.22	-3.11	0.04
exposure:Quartile1 - exposure:Quartile4	0.06	0.25	0.25	1
exposure:Quartile1 - after:Quartile4	-0.72	0.24	-2.99	0.056
after:Quartile1 - exposure:Quartile2	1.03	0.22	4.58	<0.001
after:Quartile1 - after:Quartile2	0.05	0.21	0.26	1
after:Quartile1 - exposure:Quartile3	0.66	0.22	3	0.055
after:Quartile1 - after:Quartile3	0.13	0.22	0.58	1
after:Quartile1 - exposure:Quartile4	0.88	0.25	3.55	0.009
after:Quartile1 - after:Quartile4	0.09	0.24	0.38	1
exposure:Quartile2 - after:Quartile2	-0.98	0.18	-5.3	<0.001
exposure:Quartile2 - exposure:Quartile3	-0.37	0.26	-1.41	0.854
exposure:Quartile2 - after:Quartile3	-0.9	0.26	-3.47	0.012
exposure:Quartile2 - exposure:Quartile4	-0.15	0.28	-0.54	1

exposure:Quartile2 - after:Quartile4	-0.94	0.27	-3.41	0.015
after:Quartile2 - exposure:Quartile3	0.61	0.25	2.47	0.209
after:Quartile2 - after:Quartile3	0.07	0.25	0.3	1
after:Quartile2 - exposure:Quartile4	0.82	0.27	3.05	0.048
after:Quartile2 - after:Quartile4	0.04	0.26	0.15	1
exposure:Quartile3 - after:Quartile3	-0.53	0.17	-3.19	0.031
exposure:Quartile3 - exposure:Quartile4	0.22	0.28	0.77	0.995
exposure:Quartile3 - after:Quartile4	-0.57	0.27	-2.08	0.427
after:Quartile3 - exposure:Quartile4	0.75	0.28	2.69	0.126
after:Quartile3 - after:Quartile4	-0.03	0.27	-0.13	1
exposure:Quartile4 - after:Quartile4	-0.79	0.21	-3.79	0.004
exposure:Quartile1 - before:Quartile1	-0.39	0.15	-2.59	0.159
exposure:Quartile1 - exposure:Quartile2	0.22	0.22	1.01	0.973
exposure:Quartile1 - before:Quartile2	-0.16	0.22	-0.73	0.996
exposure:Quartile1 - exposure:Quartile3	0.17	0.27	0.63	0.999
exposure:Quartile1 - before:Quartile3	-0.61	0.25	-2.45	0.219
exposure:Quartile1 - exposure:Quartile4	0.35	0.22	1.56	0.775
exposure:Quartile1 - before:Quartile4	-0.32	0.2	-1.63	0.731
before:Quartile1 - exposure:Quartile2	0.61	0.22	2.82	0.091
before:Quartile1 - before:Quartile2	0.23	0.2	1.15	0.946

Supplementary Table 3 Post Hoc Results for Vigilance Durations Model

This table presents the results of post-hoc pairwise comparisons for pooled vigilance durations in Greylag geese (*Anser anser*) across different boldness quartiles (Quartile 1 to 4) and timeframes ("exposure," "before," and "after"). The data were analyzed using a generalized linear mixed model (GLMM). **Contrast:** Specifies the pairwise comparison being made,

indicating the timeframe and boldness quartile for each group (e.g., "exposure:Quartile1- before:Quartile2"); **Estimate:** The estimated difference in feeding duration (on the log scale) between the two groups being compared; **SE:** The standard error of the estimate; **z ratio:** The z-statistic for the comparison; **p value:** The p-value, indicating the statistical significance of the difference between the two groups; **Model:** Specifies whether the contrast belongs to the "before vs. exposure" model or the "after vs. exposure" model; **Note** the "before vs. exposure" model includes contrasts where "before" is one of the timeframes being compared; "after vs. exposure" model includes contrasts where "after" is one of the timeframes being compared; results are presented on the log scale (not the response scale); p-values were adjusted using the Tukey method for comparing a family of 12 estimates; significant p-values are bold

Contrast	Estimate	SE	z-ratio	p-value
exposure:Quartile1 - before:Quartile1	0.49	0.14	3.43	0.030
exposure:Quartile1 - after:Quartile1	0.08	0.18	0.45	1.00
exposure:Quartile1 - exposure:Quartile2	-0.10	0.07	-1.33	0.976
exposure:Quartile1 - before:Quartile2	0.18	0.09	2.04	0.668
exposure:Quartile1 - after:Quartile2	0.28	0.10	2.86	0.155
exposure:Quartile1 - exposure:Quartile3	-0.08	0.08	-0.97	0.998
exposure:Quartile1 - before:Quartile3	0.14	0.11	1.27	0.983
exposure:Quartile1 - after:Quartile3	0.31	0.12	2.60	0.281
exposure:Quartile1 - exposure:Quartile4	-0.05	0.09	-0.49	1.00
exposure:Quartile1 - before:Quartile4	0.18	0.17	1.06	0.996
exposure:Quartile1 - after:Quartile4	0.06	0.16	0.36	1.00
before:Quartile1 - after:Quartile1	-0.41	0.21	-1.94	0.733
before:Quartile1 - exposure:Quartile2	-0.59	0.13	-4.56	< 0.001
before:Quartile1 - before:Quartile2	-0.31	0.14	-2.29	0.482
before:Quartile1 - after:Quartile2	-0.21	0.14	-1.48	0.946
before:Quartile1 - exposure:Quartile3	-0.57	0.13	-4.29	0.001
before:Quartile1 - before:Quartile3	-0.35	0.16	-2.22	0.537
before:Quartile1 - after:Quartile3	-0.18	0.16	-1.17	0.991
before:Quartile1 - exposure:Quartile4	-0.54	0.14	-3.81	0.008
before:Quartile1 - before:Quartile4	-0.31	0.20	-1.55	0.926

before:Quartile1 - after:Quartile4	-0.43	0.19	-2.30	0.480
after:Quartile1 - exposure:Quartile2	-0.18	0.17	-1.05	0.996
after:Quartile1 - before:Quartile2	0.10	0.18	0.54	1.00
after:Quartile1 - after:Quartile2	0.20	0.18	1.08	0.995
after:Quartile1 - exposure:Quartile3	-0.16	0.17	-0.92	0.999
after:Quartile1 - before:Quartile3	0.06	0.19	0.33	1.00
after:Quartile1 - after:Quartile3	0.22	0.19	1.16	0.992
after:Quartile1 - exposure:Quartile4	-0.13	0.18	-0.70	1.00
after:Quartile1 - before:Quartile4	0.10	0.23	0.43	1.00
after:Quartile1 - after:Quartile4	-0.02	0.22	-0.11	1.00
exposure:Quartile2 - before:Quartile2	0.28	0.06	4.39	0.001
exposure:Quartile2 - after:Quartile2	0.38	0.08	4.97	< 0.001
exposure:Quartile2 - exposure:Quartile3	0.02	0.05	0.43	1.00
exposure:Quartile2 - before:Quartile3	0.24	0.10	2.52	0.330
exposure:Quartile2 - after:Quartile3	0.40	0.10	3.99	0.004
exposure:Quartile2 - exposure:Quartile4	0.05	0.07	0.75	1.00
exposure:Quartile2 - before:Quartile4	0.28	0.16	1.76	0.841
exposure:Quartile2 - after:Quartile4	0.16	0.15	1.07	0.996
before:Quartile2 - after:Quartile2	0.10	0.09	1.15	0.992
before:Quartile2 - exposure:Quartile3	-0.25	0.07	-3.69	0.012
before:Quartile2 - before:Quartile3	-0.03	0.11	-0.30	1.00
before:Quartile2 - after:Quartile3	0.13	0.11	1.16	0.992
before:Quartile2 - exposure:Quartile4	-0.22	0.08	-2.67	0.244
before:Quartile2 - before:Quartile4	0.00	0.17	0.02	1.00

before:Quartile2 - after:Quartile4	-0.12	0.15	-0.79	1.00
after:Quartile2 - exposure:Quartile3	-0.35	0.08	-4.39	0.001
after:Quartile2 - before:Quartile3	-0.13	0.12	-1.16	0.992
after:Quartile2 - after:Quartile3	0.03	0.12	0.23	1.00
after:Quartile2 - exposure:Quartile4	-0.32	0.09	-3.46	0.027
after:Quartile2 - before:Quartile4	-0.10	0.17	-0.57	1.00
after:Quartile2 - after:Quartile4	-0.22	0.16	-1.41	0.963
exposure:Quartile3 - before:Quartile3	0.22	0.10	2.26	0.507
exposure:Quartile3 - after:Quartile3	0.38	0.10	3.72	0.011
exposure:Quartile3 - exposure:Quartile4	0.03	0.08	0.41	1.00
exposure:Quartile3 - before:Quartile4	0.26	0.16	1.59	0.912
exposure:Quartile3 - after:Quartile4	0.13	0.15	0.91	0.999
before:Quartile3 - after:Quartile3	0.16	0.13	1.23	0.987
before:Quartile3 - exposure:Quartile4	-0.19	0.11	-1.71	0.865
before:Quartile3 - before:Quartile4	0.04	0.18	0.20	1.00
before:Quartile3 - after:Quartile4	-0.09	0.17	-0.52	1.00
after:Quartile3 - exposure:Quartile4	-0.35	0.12	-3.04	0.097
after:Quartile3 - before:Quartile4	-0.12	0.18	-0.68	1.00
after:Quartile3 - after:Quartile4	-0.25	0.17	-1.46	0.952
exposure:Quartile4 - before:Quartile4	0.23	0.17	1.35	0.973
exposure:Quartile4 - after:Quartile4	0.10	0.16	0.66	1.00
before:Quartile4 - after:Quartile4	-0.12	0.21	-0.59	1.00

7.2 Zusammenfassung

Hintergrund: Tiere stehen vor einem Dilemma zwischen Wachsamkeit (Suche nach Raubtieren) und Nahrungssuche. Dieses Gleichgewicht ist überlebenswichtig, da Wachsamkeit die Erkennung von Bedrohungen verbessert, während die Nahrungssuche wichtige Energie liefert. Individuelle Kühnheit (Boldness), ein Persönlichkeitsmerkmal, das die Reaktion eines Tieres auf wahrgenommene Bedrohungen widerspiegelt, kann diesen Kompromiss beeinflussen. Mutigere Individuen können der Nahrungssuche Vorrang vor Wachsamkeit einräumen, was möglicherweise ihre Anfälligkeit für Raubtiere erhöht, aber gleichzeitig auch ihren Nahrungserfolg.

Ziele: In dieser Studie wurde der Zusammenhang zwischen Boldness, Wachsamkeit und Nahrungssuche bei Graugänsen (*Anser anser*) mit Hilfe einer räuberähnlichen Drohne (Robot Falcon) untersucht.

Methoden: Fokale Beobachtungen wurden an 61 einzeln markierten Gänsen aus einem halbgezähmten nicht migrierenden Schwarm durchgeführt. Die Gänse wurden dem Robot Falcon ausgesetzt, der während der Nahrungssuche an einem Futterplatz Sturzflugmanöver über ihnen durchführte. Ihr Verhalten wurde aufgezeichnet und mit der Software BORIS kodiert, um die Wachsamkeit und das Verhalten bei der Nahrungssuche zu quantifizieren. Die Flugeinleitungsdistanz (FID), die aus früheren Forschungen bereit für den Schwarm bekannt war, wurde als Proxy für Boldness verwendet. Generalisierte lineare gemischte Modelle (GLMMs) wurden verwendet, um die Auswirkungen des Robot Falcon und der Boldness auf die Wachsamkeit und die Nahrungssuche zu analysieren.

Ergebnisse: Die Anwesenheit des Robot Falcon erhöhte die Wachsamkeit und verringerte die Dauer der Nahrungsaufnahme. Die Kühnheit hatte jedoch keinen signifikanten Einfluss auf das Ausmaß dieser Veränderungen. Die Dauer der Wachsamkeit war vor dem Start des Robot Falcon durchgehend kürzer als während der Exposition (Schätzwert = $-0,49 \pm 0,14$, $p = 0,001$). Während zwischen der Expositions- und der Nach-Bedrohungsphase (nach der Landung des Robot Falcon) eine Verringerung der Wachsamkeit beobachtet wurde, gab es keinen statistisch signifikanten Unterschied. Die Dauer der Nahrungsaufnahme während der Exposition durch den Robot Falcon war geringer, da sie sowohl vor der Expositionsphase (Schätzwert = $0,39 \pm 0,15$, $p = 0,010$) als auch nach der Landung (Schätzwert = $0,82 \pm 0,12$, $p < 0,001$) im Vergleich zur Exposition signifikant länger war. **Schlussfolgerungen:** Während der Robot Falcon Anti-Raubtier-Reaktionen in Form von Wachsamkeit hervorrief, beeinflusste Boldness weder die Wachsamkeit noch die Nahrungssuche in einem signifikanten Ausmaß, was darauf hindeutet, dass andere Faktoren als Boldness in diesem Zusammenhang eine wichtigere Rolle spielen könnten. Eine mögliche Gewöhnung an die Drohne und die Anwesenheit von Forschern könnten die Ergebnisse beeinflusst haben. Diese Ergebnisse unterstreichen das komplexe Zusammenspiel zwischen Persönlichkeit, Wachsamkeit und Nahrungssuche bei sozialen Arten und die Notwendigkeit, mehrere Faktoren bei der Bewertung der Reaktionen auf Raubtiere zu berücksichtigen.

Relevanz: Die Forschung bietet Anregungen für den Bereich Überwachung und Schutz von Wildtieren und trägt zum Verständnis über die Reaktionen von Wildtieren auf Bedrohungen bei. Die Ergebnisse unterstreichen, wie wichtig es ist, individuelle Unterschiede und mögliche Gewöhnungseffekte beim Einsatz von Drohnen für die Wildtierforschung zu berücksichtigen.