Old habits die hard: pigeons maintain route fidelity but reduce flight altitude when exposed to a raptor-like robot

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Abstract

Prey organisms employ a range of adaptive strategies to mitigate predation risk, including camouflage, active predator deterrence by collective anti-predator behaviours, specialized predator evasion tactics, and spatial or temporal avoidance of predators. The latter may involve memorizing locations of non-lethal predator encounters and altering movement routines to subsequently avoid areas where such encounters are more likely, in line with the so-called ‘landscape of fear’ concept. We investigated whether and how experienced homing pigeons (*Columba livia*) altered their homing behaviour upon repeated exposures to simulated attacks by a robot mimicking a peregrine falcon (RobotFalcon), a common aerial predator of pigeons, along their consolidated homing route. Pigeons showed evidence of immediate responses to predator detection, considerably reducing their flight altitude (by ~ 50%) when they approach the RobotFalcon, starting when ~ 200 m from it, and maintained such lower altitude also when leaving the RobotFalcon area. Yet, pigeons showed no evidence of altering their path to avoid the area where they were more likely to encounter the RobotFalcon, even in subsequent flights when the RobotFalcon was absent, indicating that the tendency to retrace consolidated routes was not affected by predation risk. Our experiment showed that pigeons adaptively responded to immediate predation risk by flying closer to the ground, which may reduce the success of aerial predator attacks. These findings challenge the landscape of fear paradigm, suggesting that maximising energetic efficiency and flying over well-known landscapes, which may make immediate predator responses more effective, are prioritized over minimizing predation risk by flying across novel and unknown environments.

Keywords

Anti-predator response, predator attack, RobotFalcon, landscape of fear, altitude, speed, route sinuosity.

Introduction

Predation and predator-prey interactions are among the most striking and extensively studied ecological phenomena (Caro 2005). Nevertheless, our understanding remains incomplete due to the various aspects that play a role in determining how preys respond to predators, such as prey morphology (Covich 2010) or behaviour (Gunnarson & Wiklander, 2015; Belgrand & Griffen, 2016).

Whether or not an individual is adequately equipped to face a predator determines its survival probability. Therefore, predators shape prey populations via both direct predation and indirect non-consumptive effects (Cresswell, 2008; Gehr et al., 2018). This pressure has resulted in the evolution of a wide array of defensive strategies in preys, such as aposematic signals of distastefulness/danger and/or morphological and behavioural adaptations, aimed at minimizing the predation risks (Caro 2005). Although some bird species display forms of aposematism or mimicry (Hedley & Caro, 2022), their main defence lies in their ability to fly and perform rapid and deimatic escapes with unpredictable escape trajectories (Hedenstrom & Rosen 2001). Nevertheless, escaping from a predator comes at a cost and therefore in most cases the sole appearance of a predator does not necessary induce in the prey an immediate escape response (Broom & Ruxton 2005). It is therefore crucial for prey to first assess the risk level (e.g, how close the predator is, does the predator seem to be looking for prey) to adopt the most suitable evasion tactic (Broom & Ruxton 2005). Other factors can also influence anti-predator responses, such as the age of the individual or the type of predator and attack performed (for e.g. see Probst et al. 2011; Cresswell 1993).

Another strategy preys can adopt to reduce their predation risk is to avoid areas where predator encounters are more likely. Since predation risk is often spatially variable due to e.g. predator habitat preferences, prey should move in this “risk landscape” balancing the need to gain sufficient resources for survival and reproduction and the need to avoid predation (‘landscape of fear hypothesis’ - LoF, Laundrè 2001). Even if the LoF has been mostly associated with a spatial variation of predation risk (Gaynor et al. 2019), studies have shown that risk can also vary over time in predictable ways (Palmer et al. 2022). Similarly to how predators use information on past prey presence to adjust their foraging decisions (Barraquand et al. 2009; Gurarie et al. 2022), theoretical works suggested that, if predator movement is non-random, preys should gain an advantage from the ability of forming spatial memory of predator encounters (Avgar et al. 2015; Bracis et al. 2018). This may lead preys to use areas with little or no predation risk (Swinkels et al. 2023) or adjust their activity to safer times (Riou & Hamer 2008; Rubolini et al. 2015).

The homing pigeon (*Columba livia*), selectively bred for its homing abilities (Jonston & Janiga 1995; Gazda et al. 2018), is considered a paradigmatic model species for uncovering the mechanisms underlying avian navigation (see Wallraff 2005; Bonadonna & Gagliardo 2021). In the last two decades the use of GPS tracking devices prompted investigations on the use of familiar visual landmarks by pigeons homing over familiar landscapes (for refs see Guilford & Biro 2014; Gagliardo & Bingman 2024). It has been frequently observed that repeated homing flights over the same areas may induce pigeons to develop fidelity to idiosyncratic homing routes (Meade et al. 2005; Guilford & Biro 2014), making at least part of their routes relatively predictable. In recent years, homing pigeons have also been used to study collective anti-predator responses. Specifically, it was documented how individuals in both small and large flocks maintain close alignment with nearby flock-mates to preserve a compact flight formation when exposed to a raptor-like drone (the

"RobotFalcon") (Sankey et al. 2021; Papadopoulou et al. 2022). Additionally, self-organized dynamics during flocking enhanced group consensus on escape direction and enabled coordinated turns as the predator approached (Papadopoulou et al. 2022). Nevertheless, to our knowledge the anti-predator strategies adopted by homing pigeons flying without companions have never been investigated. Yet, observations on wild rock doves (*C. l. livia*) during foraging flights showed that even in the presence of peregrine falcons (*Falco peregrinus*), a globally-distributed raptor frequently targeting pigeons, birds continued flying over the same area but reduced their flight altitude to stay closer to the vegetation, lowering the chances of successful predator attacks (Baldaccini et al. 2001).

We repeatedly exposed GPS-tagged homing pigeons to simulated attacks by a robotic predator mimicking a peregrine falcon, the RobotFalcon (Sankey et al. 2021; Storm et al. 2022) and assessed variation in their homing behaviour during solo flights. We then compared the response during these flights with the behaviour in a subsequent homing flight conducted without the presence of the RobotFalcon. All experimental pigeons had been extensively trained to return to the home loft from the same release site, and had developed highly consistent homing routes.

Based on previous studies on the collective responses of pigeons to RobotFalcon (e.g., Sankey et al. 2021), we expected experimental birds to change their flight behaviour or try to avoid the predator when in its proximity at first exposure to the RobotFalcon, indicating an immediate anti-predator response. We also tested whether pigeons response to the RobotFalcon included an anticipatory component by assessing whether they altered their flight behaviour and/or significantly changed path across repeated exposures, and particularly during a final release without the RobotFalcon.

This allowed us to evaluate whether pigeons behave as expected according to the ‘landscape of fear hypothesis’ (Laundrè 2001).

Methods

Fourty-five juvenile homing pigeons born and raised in the XXX field station (XX°XX′XX″N, XX°XX′XX″E; home loft site) of the Department of Biology, University of XXX, were used in the experiment. The individuals had access to food and water *ad libitum* and were free to perform spontaneous flights around the loft. Pigeons used in the experiment had previous homing experience consisting of seven homing flights performed from sites up to 12.9 km from home, in various directions. For the experimental flights a new release site located 13.1 km from home was selected (XXX; XX°XX′XX″N, XX°XX′XX″E; direction from home: 271°). This site was specifically chosen because in previous experiments pigeons released from XXX consistently followed several parallel linear features (XXX Road, the Imperiale Channel, and the Chiara Ditch) during the initial phase of homing (first 2 km from release site; XXX et al. 2021; XXX et al. 2024).

Selection of experimental subjects

Before the experimental flights, pigeons underwent 9 up to 13 consecutive training releases from the XXX release site between 27 June and 1 August 2023. When transported to the release site birds were held in a crate open to the air on the top and on one side. Pigeons were released singly (every 5–10 minutes) only in good weather conditions (sunny day with no or light wind, < 5 m/s). Each bird was released only once per day.

Homing routes were recorded using a GPS data logger (Mobile Action IgotU, https://www.mobileaction.com, weight 22 g, on average 5.6% ± 0.5 SD of pigeon's body mass). To habituate the pigeons to the logger weight, a few weeks before the start of homing releases birds were equipped with a PVC dummy weight (45 × 25 × 15 mm, ~30 g). Both the dummy weights and data loggers were mounted on the back of the bird using a Velcro strip (30 × 70 mm) glued to trimmed feathers with neoprene-based contact glue (Biro et al. 2002).

As expected, most pigeons (n = 44) tended to follow the local linear features during training flights. We selected a field regularly overflown by the birds as the area for the artificial predator attack during the experimental flights (RF-area, ~1.2 km from the release site, area: 11 ha; Figure 1, see section below). Twenty-three pigeons were selected for the experiment based on two criteria. For each training flight we recorded (1) whether the pigeon overflew the RF-area and (2) the time from release until the bird first passed beyond 2 km from the release site (virtual vanishing time; Gagliardo et al. 2009; Figure 1a). The pigeons that crossed the RF-area in > 50% of their training flights and had in the last four training releases a virtual vanishing time of < 10 min were used in the experiment.

Experimental procedures

The experimental flights were performed between 25 July and 4 August 2023. Experimental procedure consisted in exposing pigeons to the artificial predator in the RF area for three consecutive days (exposure flights) and then releasing the individuals one last time without the predator exposure (post-exposure flight). The last two homing flights from the training phase at XXX were used as control condition (pre-exposure flights). The artificial predator (RobotFalcon; 70 cm wingspan, 250 g flying weight) is a highly manoeuvrable radio-controlled drone designed to closely resemble in size, shape and coloration a common natural predator of pigeons, the peregrine falcon (see also Sankey et al. 2021; Storms et al 2022). The RobotFalcon was piloted from the ground by a certified operator (R.M.) using a viewer connected to a video camera mounted on the back of the drone's head, providing a real-time view from the perspective of the RobotFalcon (Figure S1 and Video S1 in Supplementary material).

During each exposure flight, the RobotFalcon was launched in the RF-area a few minutes before the start of the pigeons' releases and maintained a holding pattern at a constant altitude of 30–40 m above ground level (a.g.l.) while waiting for pigeons to approach. After releasing one pigeon, the experimenter followed the pigeon using binoculars and communicated the direction from which the bird was approaching the RF-area to a second experimenter positioned next to the drone pilot. This coordination helped the pilot to locate the approaching pigeon increasing the chances of successfully performing a simulated attack or a chasing action. The RobotFalcon's flight path was recorded with a GPS data logger (TechnosmartEurope srl, model Gypsy 6) with a sampling rate of 5 Hz placed inside the body of the drone. Given that pigeons' locations were recorded at 1 Hz, RobotFalcon's data were downsampled to have a comparable sampling rate.

Data preparation

GPS data from experimental birds were filtered to retain only segments where the individual was flying (flight speed > 5 km/h). The portion of the route considered for the analyses started when the pigeon crossed 750 m from the release site for the first time and ended when it crossed 1680 m from the release site for the first time.

The 750 m threshold was chosen to exclude the initial part of the flight, which could have been influenced by attraction towards two nearby farmhouses frequented by feral pigeons throughout the experimental period. The 1680 m threshold corresponded to a natural boundary (groove of trees where pigeons may find refuge and rest) at the far end of the RF-area (Figure 1b). We considered for the analysis only exposure flight when pigeons did not stop before entering the RF-area.

Flight altitude was obtained from GPS-recorded altitude values adjusted by using the mean of altitude values registered in the last 20 seconds before release as ground level. This correction was necessary because GPS-recorded altitude has an associated error which is mostly systematic and linked with the spatial configuration of available GPS satellites (Péron et al. 2020). The ground level estimates we used for correction were considered reliable as the pigeons remained in the carrier crate placed directly on the ground for at least 10 minutes prior to release (SD of altitude values in the last 20 seconds before release: median = 0.00 m, range = 0.00 - 1.62 m). Moreover, given that our experimental subject started to fly soon after release, we considered reliable the altitude registered in the first segment of their homing route.

Assessing pigeon-RobotFalcon interaction and route segmentation

To assess when and if the RobotFalcon interacted with the pigeon during the exposure flights, we analysed the segment of the pigeon’s track passing over the RF-area (Figure 1b) and associated at each timestamp the corresponding RobotFalcon location. Generally, the interaction with the RobotFalcon consisted in the drone either crossing the pigeon’s path or chasing the pigeon. The available field notes on the starting time of an attack or of a chasing action, which were collected when possible by the experimenter close to the RobotFalcon pilot during procedures, were used to validate the interactions identified from tracking data. At each timestamp, we estimated the distance between the RobotFalcon and the bird, the RobotFalcon's acceleration and the angle of the RobotFalcon movement in relation to the pigeon's position. Angles close to 0° indicated that the RobotFalcon was moving towards the pigeon, while angles close to ± 180° indicated that the RobotFalcon was moving away leaving the pigeon behind. We assumed that an interaction pigeon-RobotFalcon occurred if the RobotFalcon 1) was at a distance shorter than 100 m from the pigeon; 2) showed an acceleration of at least 2 m/s^2; 3) showed a directed movement towards the pigeon (within a range of ± 60°).

Flight routes were segmented into approach phase (AP), when the pigeon is getting close to the RobotFalcon, and it is likely to detect it, identify it, and potentially triggering "primary defence" behaviours (Kikuchi et al. 2023), and leaving phase (LP), after passing through the RobotFalcon's fly zone, where a predator attack might have had occurred (Figure 1b). The AP segment started at 750 m from the release site and ended when the pigeon reached its closest point to the RobotFalcon, while LP segment began after the last recorded interaction between the pigeon and the predator-like robot and ended at 1680 m from release site. Both segments were defined individually for each bird-release combination to take into account the spatial variability of the RobotFalcon position across the three exposure flights. Given the variability of pigeon responses, it was not possible for the RobotFalcon to interact with every bird in every release. When no interaction occurred, the starting point of the LP segment was defined as the first location where the pigeon crossed a reference boundary. This boundary was calculated as the mean longitude of the last interaction points from other exposure flights -either of the same individual or from other individuals- in which an interaction had occurred. For the six pigeon that never interacted with the RobotFalcon (Table S1), this same boundary was used consistently to define the start of LP segment across all their exposure flights.

Data analysis

Based on our initial hypotheses of immediate and/or anticipatory anti-predator responses, we predicted that the RobotFalcon would prompt pigeons to avoid the RF-area and/or alter their flight behaviour (Figure 2).

Fidelity to the familiar path

To evaluate whether pigeons avoided the RF-area (Figure 2), we considered the AP segment of the flight tracks. For this analysis, we delimited the end of the individually specific AP segment in the same way for pre-exposure and post-exposure flights by considering the longitude of the first interaction recorded in the last exposure flight where the pigeon interacted with the RobotFalcon. For the six birds that never interacted with the artificial predator in any exposure flights, we used the median longitude of RobotFalcon interactions from the other individuals. Avoidance of the RobotFalcon area was evaluated by estimating individual route fidelity, which represents the pigeon's tendency to follow a consistent path across successive releases. This fidelity typically increases with experience until reaching a plateau (Guilford & Biro 2014; Gagliardo et al. 2020). For each pigeon's exposure and post-exposure flights, we calculated a Fidelity Index (FI) as follows:

$$FI = \frac{\frac{\sum_{i=1}^{n} f_i}{n}}{r}$$

where f_i is the number of training and pre-exposure routes falling closer than 50 m from the i-th location of the focal track and n is the total number of locations of the focal track. The r corresponded to the total number of training and pre-exposure routes. FI values close to 0 indicate low individual fidelity to the routes established before the first exposure, while FI values close to 1 show a high degree of fidelity. Moreover, we estimated the FI for the last pre-exposure flight to obtain the information on the baseline level of individual fidelity to its route (before the RobotFalcon exposures). For this estimation, f_i and r refer to all the previous tracks.

Given that experimental subjects were specifically chosen for their preference to fly over the RF-area, we tested whether this preference was affected by being repetitively exposed to the presence of the RobotFalcon using a Linear Mixed Models (LMM) . FI values from exposure and post-exposure flights were used as the dependent variable. Release type, the FI baseline value (FI of the last pre-exposure flight) and their interaction were included as fixed factors. Bird ID was included as random intercept. To specifically test a possible RobotFalcon avoidance as immediate anti-predator response of the pigeons at 1st exposure, we performed a Welch's t-test comparing the baseline FI and the FI estimated for the 1st exposure. The analyses were performed in R version 4.5.0 (R Core Team 2025). Models were fitted using the package *glmmTMB* 1.1.11 (Brooks et al. 2017) and model assumption were tested using *DHARMa* 0.4.7 (Hartig 2024) and *performance* 0.13.0 (Lüdecke et al. 2021). The significance of predictors was tested using a type II Wald χ^2 test available in the package *car* 3.1-3 (Fox & Weisberg 2019). Pairwise comparisons were performed using the Post-hoc Tukey test by means of package *emmeans* 1.11.0 (Lenth 2025). Effect plots were obtained using the package *ggeffects* 2.2.1 (Lüdecke 2018).

Flight behaviour

Flight behaviour was evaluated for both AP and LP segments of each pigeon's track across the three release types: pre-exposure, exposure and post-exposure. For pre-exposure flights, the end of the AP segment was delimited by the longitude where the pigeon was at its closest distance from the artificial predator in its first exposure flight. For the post-exposure, the AP segment ended at the longitude where the pigeon was at its closest distance from the artificial predator in the last exposure flight.

Given that in most cases the RobotFalcon interacted with a specific pigeon during only one exposure out of three (Table S1), the start of the LP segment for the pre-exposure and post-exposure flights were delimited by the longitude where the artificial predator interacted with the pigeon. In the two cases where pigeons interacted more than one time with the RobotFalcon in their three exposure flights, the start of the LP segment for the pre-exposure flight was delimited by the longitude of their last interaction during their first encounter, while for post-exposure flight it was delimited by the longitude of their last interaction during their last exposure flight.

To evaluate whether birds reacted to the artificial predator by changing their flight behaviour, we considered three parameters: flight speed, flight altitude, and sinuosity index. The sinuosity index was used to quantify the tortuosity of the pigeons' flight path (Benhamou 2004). This index increases as the animal's paths becomes more meandering and sinuous and approaches 0 when the animal follows a straight and direct trajectory. The adjusted sinuosity index, designed to accommodate variable step lengths and a broader range of turning angles, was computed using the R-package '*trajr*' ver. 1.5.1 (McLean & Skowron Volponi 2018). For each individual AP and LP segment and type of release (pre-exposure, exposure and post-exposure), the sinuosity index and the mean flight speeds (km/h) were calculated. Flight altitude was evaluated using the median altitude over the final 10 seconds for the AP segment, and the first 10 seconds for the LP segment.

For the AP segment, we expected birds to change their flight behaviour (route sinuosity, flight speed and/or altitude) when exposed for the first time to the RobotFalcon (immediate anti-predator response, Figure 2). To test this expectation, we compared the flight parameters between the two pre-exposure flights and the 1st exposure flight. Additionally, we compared flight parameters across the three exposure flights to evaluate whether pigeons continued to respond to the predator's presence in successive exposures (immediate/anticipatory anti-predator response). Finally, to test whether pigeons altered their behaviour when approaching the RF-area even in the RobotFalcon absence (anticipatory anti-predator response, Figure 2), we compared flight parameters between two pre-exposure flights and the post-exposure flight. All analyses were performed using LMMs. The dependent variable was one of the three flight parameters (sinuosity index, mean speed or median altitude), while release type was included as fixed factor and individual identity as random intercept. Bird ID was included as random intercept. In the model testing the anticipatory anti-predator response in post-exposure releases, we included a binary variable indicating whether the pigeon had interacted with the RobotFalcon in at least one of the previous exposure flights, along with its interaction with release type.

Given that we observed a strong change in pigeon's flight altitude just before exiting the AP segment in response to the RobotFalcon, we further explored the time-course of altitude while pigeons were approaching the artificial predator. For this analysis, we considered only the portion of the AP route beginning from the last point at which the pigeon was 600 m from the RobotFalcon and ending at the location where the pigeon was at its closest distance from the RobotFalcon. To simplify the model, we considered only the last pre-exposure flight and set a common boundary for the end of AP segment in pre-exposure and post-exposure flight as the mean longitude of the closest locations to the RobotFalcon in the three individual exposure flights (dummy position of the RobotFalcon). For pre-exposure and post-exposure flights we estimated the distance from each location of the segment and the dummy position of the RobotFalcon. We applied a Generalized Additive Model with normal error distribution using the function *bam* in the R-package *mgcv* 1.9-1 (Wood 2017). The corrected altitude values at each second (see *Data preparation* section) was used as dependent variable. The interaction between distance to the RobotFalcon and release type was included as a smooth term using thin plate regression spline. Release type (five levels factor: pre-exposure, 1st exposure, 2nd exposure, 3rd exposure, post-exposure) was also included as a fixed factor. Bird ID was included as a random intercept along with an autoregressive correlation structure (AR1) to take into account the temporal autocorrelation of the data. The AR1 correlation parameter (*rho)* was estimated through the function *start.value.rho* in *mgcv* applied to the model including the AR1. Model diagnostics were assessed using the R-package *gratia* 0.10.0 (Simpson 2024) while graphical representation were produced with the R-package *marginaleffects* 0.26.0 (Arel-Bundock et al. 2024).

Since the expectations for the LP were the same as for the AP, we conducted the same comparisons of flight parameters across releases: 1) pre-exposure flights vs. 1st exposure flight (immediate anti-predator response); 2) across the three exposure flights (immediate/anticipatory anti-predator response); and 3) pre-exposure flights vs. post-exposure flight (anticipatory anti-predator response). Flight behaviour parameters (sinuosity index, flight speed and altitude) were used as dependent variables, with release type included as fixed factor and individual identity as random intercept. In model (2) we also included a binary variable indicating whether the pigeon had just interacted with the RobotFalcon, along with its interaction with release type. Moreover, to assess the effect of a pigeon's first ever interaction with the artificial predator, we compared each flight parameter in the first exposure flight between pigeons that had or had not interacted with the RobotFalcon using the Welch's t-test.

Ethical note

The experimental procedures employed in the present study were approved by the Scientific Ethics Committee of the University of XXX and authorized by the XXX Ministry of Health (permit no. 177/2022-PR). Pigeons were bred in large aviaries and were provided with food and water *ad libitum*. The experiments were carried out when birds were not reproducing and only animals that were in good physical condition were included.

Results

Homing routes across the entire experimental procedure were available for twenty-one individuals. A total of 114 homing flights were used in the analyses (Table S2). Detailed results of all models are reported in Table S3, S4, S5 and S6 in Supplementary Material.

Fidelity to the familiar path

Experimental pigeons showed a substantial inter-individual variability in baseline fidelity index (FI, mean ± SD: 0.40 ± 0.21). Route FI in exposure and post-exposure flights was strongly affected by the baseline FI ($\chi^2 = 52.13$, df = 1, $P < 0.001$, Table S3). Birds did not show any systematic avoidance of the area where the RobotFalcon was flying (i.e., reduction of route fidelity) both in exposure and post-exposure flights (Table S3; Figure 3 and S2). The t-test comparing baseline FI and 1st exposure FI did not highlight differences in fidelity ($t_{34.4} = 0.38$, $P = 0.70$).

Flight behaviour while approaching the predator

During the 1st exposure to the RobotFalcon (immediate anti-predator response), pigeons flew at a significantly lower flight altitude compared to pre-exposure flights (Table 1 and S4, Figure S3), while no significant effect of the RobotFalcon was observed on pigeon mean flight speed nor on route sinuosity (Table 1 and S4).

When comparing flight behaviour across the three exposure flights (immediate/anticipatory anti-predator response), no significant difference was observed in flight altitude nor in route sinuosity (Table 1 and S4). However, pigeons significantly increased their flight speed on the third day of exposure compared to the second day, while no differences in speed were observed between the 2nd and 3rd exposure and the 1st exposure flight (Figure S4).

The lack of effect of release type on flight altitude was indicative of a consistent anti-predator response as confirmed by the analysis of flight altitude over time in the AP segment. In fact, this analysis showed that during exposure flights pigeons kept a relatively constant altitude up to ~200 m from the RobotFalcon, then they drastically decreased it. In contrast, when the RobotFalcon was not present, pigeons constantly increased their flight altitude when approaching the target area (Table S5; Figure 4).

No evidence of an anticipatory anti-predator response was observed: flight parameters did no differ significantly between pre-exposure and post-exposure flights, indicating that pigeons returned to their usual flight behaviour in post-exposure flight when the RobotFalcon was absent (Table 1 and S4).

Flight behaviour while moving away from the predator (LP phase)

The first time pigeons met the RobotFalcon along their route (immediate anti-predator response), they did not alter their flight speed nor route sinuosity (Table S6), but kept flying at significantly lower altitudes in the presence of the artificial predator (Table 1 and S6; Figure S5). T-tests conducted on the first exposure flight did not highlight differences between birds experiencing an attack by the RobotFalcon ($n = 7$) and birds that did not ($n = 13$) in any of the flight parameters (flight altitudes $t_{10.9} = -1.79$, $P = 0.10$; flight speeds $t_{9.45} = 0.66$, $P = 0.52$; route sinuosity $t_{10.07} = -1.69$, $P = 0.12$).

While moving away from the RobotFalcon in the three exposure flights (immediate/anticipatory anti-predator response), pigeons did not show any variation in flight altitude nor route sinuosity across exposure flights (Table 1 and S6). Even if not significant, it is worth noting that pigeons that had just experienced an attack, tended to have a more tortuous route than those that did not interact with the predator (Table 1 and S6). Birds showed significant variation in flight speed across releases, with a marked increase in speed during the third exposure flight (Table 1 and S6, Figure S6). No effect of having just been attacked nor an interaction between release type and attack status emerged (Table 1 and Table S6).

No anticipatory anti-predator response was detected in the analysis of the LP segments, as no differences in flight parameters was found between pre-exposure and post-exposure flights (Table 1 and Table S6).

Discussion

We used a biomimetic raptor-like robot, the RobotFalcon, to investigate individual anti-predator strategies of highly experienced homing pigeons that repeatedly encounter a predator along their familiar homing route. We showed that pigeons did not avoid the area over-flown by the RobotFalcon. Nevertheless, pigeons altered their flight behaviour both when approaching and moving away from the predator. The anti-predator response of the pigeons was immediate and strictly connected to the presence of the RobotFalcon in the area (Figure 2).

The most evident response of the pigeons to the sight of the RobotFalcon was a significant reduction in flight altitude during the approach phase (AP). Notably, this effect occurred only when the Robotfalcon was present in the area (immediate anti-predator response), suggesting that pigeons were able to spot the potential predator from a distance of at least 200 m. The change in altitude, likely allowing to get closer to the vegetation (if present) or the ground, constitutes an effective anti-predator strategy against aerial predator specialized in hunting in open areas and attacking preys from above, such as peregrine falcons (Cramp & Simmons 1980; Ratcliffe 2010; Gowree et al. 2018; Mills et al. 2019; Garde et al. 2021). A similar strategy has been observed in wild rock doves departing from their colonies for foraging flights, where they reduced their flight altitude to fly closer to vegetation when detecting peregrine falcons (Baldaccini et al. 2001). During the leaving phase (LP), flight altitude remained at the same level as in the approach phase regardless of whether the pigeon just viewed the predator or was chased by it.

Differently from our initial expectations, none of the pigeons showed an avoidance response of the area over which they had experienced the RobotFalcon, as they kept retracing their preferred path. These data suggested that the risk of encountering a predator did not affect the tendency to retrace idiosyncratic homing routes, particularly when released multiple times from the same release site (Meade et al. 2005) and in presence of linear landscape features (Gagliardo et al. 2023). Ferrari et al. (2009) reviewed how prey animals might need to reduce the intensity of their anti-predator responses as it trades off with other activities; in the case of pigeons, they may gain an advantage in retracing their preferred homing route which allows them to reduce homing times (Biro et al. 2002; Holland et al. 2003) and cognitive effort required during the homing process (Meade et al. 2005). The high fidelity to the path observed in experimental subjects might be partially explained by the fact that homing pigeons are a domesticated species (Johnston & Janiga 1995) actively selected for homing performances (Gazda et al. 2018). Thus, artificial selection might play an additional role in favouring a more efficient homing over an intense anti-predator response (De Mestral & Herbinger 2013; Geffroy et al. 2020). This lack of avoidance of the area over which pigeons encountered the RobotFalcon persisted in the post-exposure flights. However, it must be considered that prey ability to memorise the area at which predators have been seen is beneficial only if predators are predictable (Bracis et al. 2018) which is not always the case for highly mobile predators (e.g., sharp-shinned hawk *Accipiter striatus*, Roth & Lima 2007). Under these circumstances, developing a memory of predator presence (“landscape of fear hypothesis”, Laundré et al. 2001), might constitute an ineffective survival strategy. Interestingly, it has been observed that wild rock pigeons belonging to a colony in Capo Caccia (Sardinia, Italy) mostly kept following the same familiar foraging route even if the presence of peregrine falcons regularly hunting in the area was highly predictable (Baldaccini et al. 2001).

Taken together, the results indicate that pigeons confronted with acute predation risk reduce their flight altitude, a tactic that may diminish the effectiveness of aerial predator strikes. These finding contrasts with predictions from the “landscape of fear hypothesis” (Laundrè 2001), suggesting that pigeons may prioritize energy-efficient travel through familiar terrain—where rapid, context-specific predator avoidance is facilitated—over selecting novel environments solely to reduce encounter risk.

Our study further supports the effectiveness of using emerging technologies, such as drones mimicking a real predator, to investigate prey-predator interaction and prey anti-predator strategies (Storms et al. 2019, 2022, 2024; Cerritelli et al. 2025; Vertua et al. 2025). For the first time, we investigated the anti-predator strategies of individual birds exposed to the artificial predator along their homing route. This new experimental framework could be applied to flocks for studying the pigeon collective response to a model predator encountered *en route* and investigating the relevance of relative role of individual route fidelity and tendency to fly in group when reacting to a model predator.

Data accessibility

All data and code used to perform the analyses are available from Zenodo (https://doi.org/10.5281/zenodo.16949191)

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Tables

			Approach Phase			**Leaving Phase**		
Model	**Parameter**	**Fixed parameters**	**Wald type II χ^2**	**df**	**P**	**Wald type II χ^2**	**df**	**P**
Immediate anti-predator response	Sinuosity Index	release type	0.12	2	0.94	3.38	2	0.18
	Flight speed	release type	1	2	0.61	0.86	2	0.65
	Flight altitude	**release type**	**10.88**	**2**	**0.004**	**17.11**	**2**	**<0.0002**
Immediate/ Anticipatory anti-predator response	Sinuosity Index	release type	2.39	2	0.30	4.92	2	0.08
		attacked	-	-	-	3.42	1	0.06
		release type:attacked	-	-	-	2.15	2	0.34
	Flight speed	**release type**	**13.07**	**2**	**0.001**	**18.99**	**2**	**<<0.001**
		attacked	-	-	-	0.43	1	0.51
		release type:attacked	-	-	-	0.18	2	0.91
	Flight altitude	release type	2.35	2	0.31	0.37	2	0.83
		attacked	-	-	-	0.34	1	0.55
		release type:attacked	-	-	-	4.40	2	0.11
Anticipatory anti-predator response	Sinuosity Index	release type	1.86	2	0.39	2.28	2	0.32
		attacked	0.01	1	0.91	-	-	-
		release type:attacked	2.34	2	0.31	-	-	-
	Flight speed	release type	3.70	2	0.15	1.55	2	0.46
		attacked	1.77	1	0.18	-	-	-
		release type:attacked	2.06	2	0.35	-	-	-
	Flight altitude	release type	1.63	2	0.44	3.80	2	0.15
		attacked	0.08	1	0.77	-	-	-
		release type:attacked	2.04	2	0.36	-	-	-

Table 1: Results (Wald type II χ^2 tests) of the Linear mixed models aimed at the testing the effect of release type and, in some cases, attacked condition (yes/no) in the Approach and Leaving phases on flight behavior parameters of homing pigeons exposed to the RobotFalcon. Three possible anti-predatory responses on Approach Phase and Leaving Phase route segments were tested: 1) immediate response; 2) immediate/anticipatory response; 3) anticipatory response. Release type is distinguished in six different release types: pre-exposure flight (1st and 2nd), exposure flights (1st, 2nd and 3rd), post-exposure flight. The variable 'attacked' was only used in two models: in the Approach Phase it indicates if the pigeon received at least an attack during the three exposure flights; in the Leaving Phase

indicates if the pigeon had just interacted with the RobotFalcon or not. Horizontal bars are reported in case the variable was not included in the model.

Figures

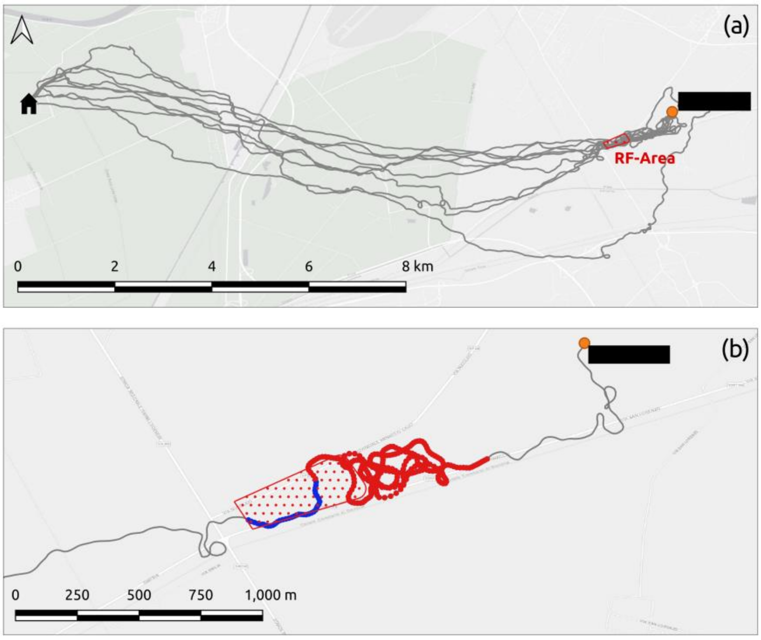

Figure 1: Example of homing routes for a sample individual (ID 049881). (a) Training and pre-exposure homing routes (n = 9) are shown in grey. (b) Zoomed in view of the experimental area, showing the initial part of the homing route for the 1st exposure flight; red dots represent GPS locations included in the approach phase (AP segment), which ends at the point of the closest distance to the RobotFalcon); blue dots indicate locations in the leaving phase (LP segment), starting after the last identified interaction with the RobotFalcon. The area where the RobotFalcon was flying (RF-area) is outlined in red with a dotted fill. The orange dot marks the XXX release site, and the black house symbol indicates the loft location.

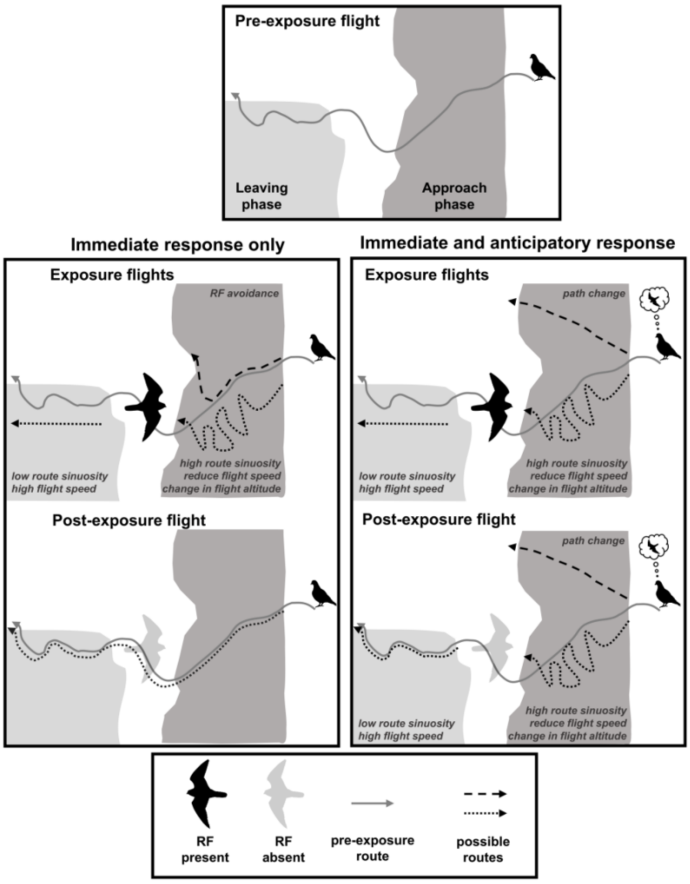

Figure 2: Graphical representation of the experimental expectations. In the top panel the grey arrow represents the route followed by the pigeon during pre-exposure flight, i.e., before its first exposure to the RobotFalcon (RF in figure). The same symbol is used in the panels illustrating exposure and post-exposure flights. The drawings on the left and on the right illustrate the expected effects of the RobotFalcon on the pigeon under two scenarios: an *immediate-only* (left) or *immediate plus anticipatory* anti-predator responses (right). In the first case, pigeons are expected to respond only when the RobotFalcon is present. In the second case, an anticipatory component is included and pigeons are expected to keep showing an anti-predator response even in the absence of the RobotFalcon (post-exposure flight). Black arrows represent potential changes in the pigeon's route: either a deviation from the familiar path to avoid the RF-area (dashed black line) and/or a change of flight behaviour during the approach or leaving phases (dotted black line). The pigeon symbol marks the release site. The black falcon icon indicates the releases when RobotFalcon was present in the area, while the grey icon indicates flights without RobotFalcon.

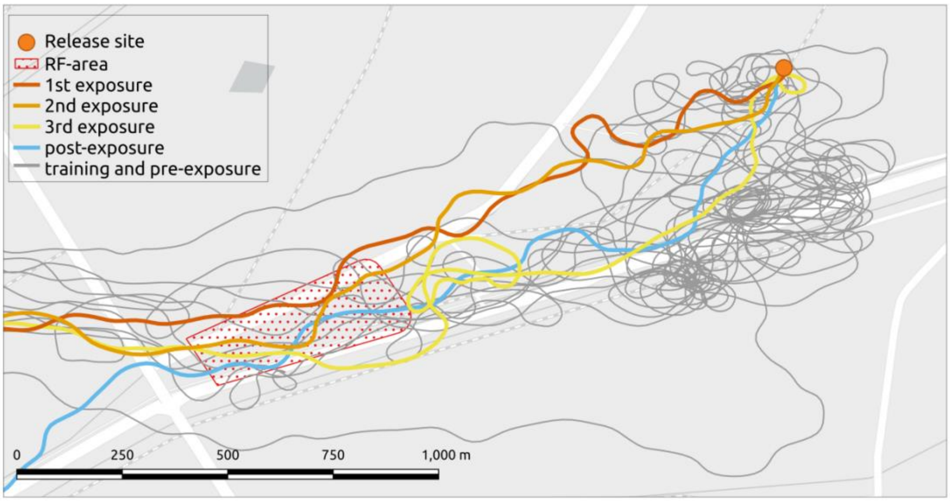

Figure 3: Example of routes for a sample individual (ID 049807) showing no avoidance of the area where the RobotFalcon was flying (RF-area) during exposure and post-exposure flights. Training and pre-exposure routes are shown in grey. The four coloured lines show the routes of the pigeon during the exposure and post-exposure flights. The red polygon with a dotted fill indicates the RF-area, and the orange dot marks the XXX release site.

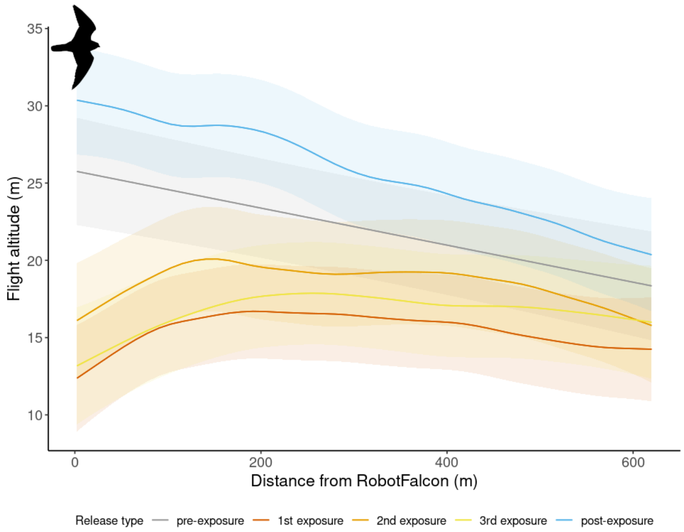

Figure 4: Plot of the effects (estimate ± CI) of release type and distance from the RobotFalcon on flight altitude in the approach phase (AP) segment of the route. Results of the Generalized Additive Model with normal error distribution, individual identity included as a random intercept along with an autoregressive correlation structure (AR1). Adjusted R^2 = 0.50, Deviance explained = 50.4%.

Old habits die hard: pigeons maintain route fidelity but reduce flight altitude when exposed to a raptor-like robot

Highlights

- Experienced homing pigeons faced repeated RobotFalcon attacks along familiar routes
- Immediate response to predator detection: pigeons dropped altitude by about 50%
- Birds lowered altitude starting ~200 m before reaching the simulated predator
- Pigeons did not abandon familiar flight routes after repeated predator encounters
- No anticipatory response to predator

Old habits die hard: pigeons maintain route fidelity but reduce flight altitude when exposed to a raptor-like robot

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Ethical statement

The experimental procedures employed in the present study were approved by the Scientific Ethics Committee of the University of Pisa and authorized by the Italian Ministry of Health (permit no. 177/2022-PR).

Author Contribution

Claudio Carere: Project administration, Funding acquisition, Conceptualization, Writing – review & editing; Giulia Cerritelli: Conceptualization, Methodology, Investigation, Formal analysis, Data curation, Writing – original draft, Writing – review & editing; Anna Gagliardo: Conceptualization, Methodology, Investigation, Writing – review & editing; Dimitri Giunchi: Supervision, Conceptualization, Methodology, Investigation, Funding acquisition, Formal analysis, Writing – review & editing; Luca Marinoni: Conceptualization, Methodology, Investigation, Formal analysis, Data curation, Writing – original draft, Writing – review & editing; Robert Musters: Investigation, Writing – review & editing; Diego Rubolini: Funding

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