Current Biology

Report

# Absence of “selfish herd” dynamics in bird flocks under threat

## Highlights

- Pigeons responded to a robotic falcon by turning away from its direction of flight
- Centroid attraction was not favored in the chased group over control conditions
- Fission or fusion responses were dependent on pigeons’ proximity to the robotic falcon

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## In brief

It is commonly thought that animals under threat crowd toward others in a selfish battle for the center. However, if instead of crowding the individuals in the group form into alignment, they may escape the predator as a group instead. Sankey et al. find a striking alignment response in pigeons chased by a remote-controlled robotic falcon.

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# Absence of "selfish herd" dynamics in bird flocks under threat

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## SUMMARY

The "selfish herd" hypothesis[1] provides a potential mechanism to explain a ubiquitous phenomenon in nature: that of non-kin aggregations. Individuals in selfish herds are thought to benefit by reducing their own risk at the expense of conspecifics by attracting toward their neighbors' positions[1,2] or central locations in the aggregation.[3–5] Alternatively, increased alignment with their neighbors' orientation could reduce the chance of predation through information sharing[6–8] or collective escape.[6] Using both small and large flocks of homing pigeons (*Columba livia*; n = 8–10 or n = 27–34 individuals) tagged with 5-Hz GPS loggers and a GPS-tagged, remote-controlled model peregrine falcon (*Falco peregrinus*), we tested whether individuals increase their use of attraction over alignment when under perceived threat. We conducted n = 27 flights in treatment conditions, chased by the robotic "predator," and n = 16 flights in control conditions (not chased). Despite responding strongly to the RobotFalcon—by turning away from its flight direction—individuals in treatment flocks demonstrated no increased attraction compared with control flocks, and this result held across both flock sizes. We suggest that mutualistic alignment is more advantageous than selfish attraction in groups with a high coincidence of individual and collective interests (adaptive hypothesis). However, we also explore alternative explanations, such as high cognitive demand under threat and collision avoidance (mechanistic hypotheses). We conclude that selfish herd may not be an appropriate paradigm for understanding the function of highly synchronous collective motion, as observed in bird flocks and perhaps also fish shoals and highly aligned mammal aggregations, such as moving herds.

## RESULTS AND DISCUSSION

We modified the predator context of both (1) small (n = 8–10) and (2) large (n = 27–34) homing pigeon flocks by introducing a remote-controlled robotic model of a male peregrine falcon (Figure 1). Homing pigeons are well known for their coordinated collective flights.[9–12] They are also regularly predated by peregrine falcons.[13] This makes them the ideal system to study collective prey responses to predators, as homing pigeons are the offspring of previously successful homers, stretching back over many generations.[14] By manipulating the perceived risk of predation across a series of 27 "predator" treatment flights and 16 control flights (totaling 628 individual pigeon GPS trajectories), we aimed to investigate the following questions: to benefit from "selfish herd" phenomena,[3–5] do individuals in flocks increase centroid attraction in favor of alignment with neighbors in the presence of an artificial predator? As selfish behavior could be more anonymous in larger groups,[15–18] do individuals in larger groups "free ride" and exhibit decreased alignment and increased centroid attraction relative to smaller groups? How does the relative proximity and orientation of an artificial predator influence whether individuals split from or stay with the group (i.e., the fission or fusion dynamics)?

During predator treatment flights, pigeons responded strongly to the RobotFalcon's orientation $\Theta_{rfo}$ (i.e., direction of RobotFalcon flight) by turning toward the opposite direction (Figures 2A and 3; linear mixed model [LMM]: DF = 4,079, $t = -14.018$, Cohen's D = $-0.439$, $p < 0.001$). Other social and environmental covariates (Figure 3) were positively associated with pigeon turning angle: pigeons in both control and predator treatments turned toward (1) direction to home $\Theta_h$, (2) the group's centroid $\Theta_{ca}$ (i.e., positive impact regardless of experimental treatment), and (3) the group's alignment angle $\Theta_{ali}$ (see STAR Methods for definitions; Figure 2A; LMM;

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**Figure 1. The "RobotFalcon" in flight-chasing pigeons**

Predator treatment flights (chased by the RobotFalcon) included up to 34 GPS-tagged homing pigeons (pictured). Photo credit: Marina Papadopoulou. See also Video S1.

$\Theta_{h}$—$t = 4.592$, Cohen's D = 0.131, $p < 0.001$; $\Theta_{ca}$—$t = 4.881$, Cohen's D = 0.122, $p < 0.001$; $\Theta_{ali}$—$t = 11.428$, Cohen's D = 0.291, $p < 0.001$).

## Does centroid attraction increase in favor of alignment in the presence of an artificial predator?

Individuals from groups that were chased by the RobotFalcon showed no greater "centroid attraction" $\Theta_{ca}$ than those in control groups but did show a significant decrease in "alignment" $\Theta_{ali}$ (Figure 2B; $\Theta_{ca}$: LMM—$t = -0.503$, Cohen's D = $-0.012$, p = 0.614; $\Theta_{ali}$: LMM—$t = -2.265$, Cohen's D = 0.056, p = 0.024). This drop in alignment is likely due to individuals splitting from the group upon close predator approaches (Figures 2C and 2D), because we do not find the same response when close predator approaches are removed from the data (closer than 40 m; 14.8% of all data points; Figure 2B; LMM: $t = -0.222$, Cohen's D = $-0.006$, p = 0.824).

Contrary to expectations from the "selfish herd" hypothesis,[1,3,5] pigeons in the half of the flock closer to the predator generally turned away from the centroid (i.e., the slope was negative; LMM: – $t = -1.716$, Cohen's D = $-0.080$, p = 0.086), whereas those on the side of the flock furthest away from predator turned positively toward the centroid (i.e., the slope was positive; LMM: – $t = 2.342$, Cohen's D = 0.106, p = 0.019). This was revealed by a significant interaction between the binary variable "flock half" and centroid attraction (LMM: – $t = -2.556$, Cohen's D = $-0.080$, p = 0.019). Again, this result can be explained by birds turning away from the flock when under pressure from the RobotFalcon at close proximity, as this result did not hold when close approaches where removed (<40 m as above; LMM: $t = -0.970$, Cohen's D = $-0.038$, p = 0.332).

A centroid attraction mechanism was not favored in the presence of the RobotFalcon. A theoretical flocking model by Wood and Ackland[6] has already demonstrated that groups of virtual prey fleeing a virtual predator can, over the course of many generations, evolve either high alignment or high centroid attraction mechanisms and that both are evolutionary stable strategies. This means that, in a group with a high degree of alignment, a tendency for centroid attraction will not necessarily invade the population and vice versa.[6] The benefit of alignment here is thought to be through enhanced information sharing, i.e., individuals can evade a predator without sensing it via alignment with a group member who has sensed and responded with evasive action.[7,8] It is also well known that highly "aligned" flocks are faster than highly "attracted" flocks,[8,22] which may be why alignment has further been shown to promote whole-group escape.[6]

## Is centroid attraction more pronounced in larger groups?

With regards to flock size, there was no evidence that small flocks (n = 8–10 individuals) attract to the centroid ($\Theta_{ca}$) less or align with neighbors ($\Theta_{ali}$) more than large flocks (n = 27–34 individuals; Figure 2B; $\Theta_{ca}$: LMM—$t = 1.005$, Cohen's D = 0.047, p = 0.314; $\Theta_{ali}$: LMM—$t = 1.005$, Cohen's D = 0.051, p = 0.280; full statistics for all models and covariates can be found in Table S1). As suggested above, selfish herd behavior may not be in the individual or the group's interest in highly aligned flocks,[6] regardless of flock size.

## How does the relative proximity and orientation of the RobotFalcon impact fission or fusion dynamics?

Individuals tended to split from the group (fission) at closer RobotFalcon approaches (Figure 2C; generalized LMM [GLMM] binomial: DF = 147, $t = -3.362$, Cohen's D = $-0.555$, p = 0.001; see STAR Methods for a sensitivity analysis). However, why would individuals split from the group, when staying with a group can offer individuals protection from predators?[1,23,24] Individuals may only split from a group (fission) at extremely close predator approaches, where they would otherwise likely be caught if they did not take immediate evasive action. Likewise, the decision to re-join (fusion) may correspond with moments after an immediate threat has passed, when grouping once again becomes favorable. Fission or fusion dynamics that fit this mechanistic hypothesis are observable in the flash expansion of starling murmurations, which may represent an example of the two processes above, performed in fast succession.[25]

Support for this hypothesis comes from our data, which show that, when individuals were faced with a conflict—i.e., when (1) turning away from the predator and (2) aligning with neighbors required opposite turning angles (see STAR Methods for further details on "conflict scenarios")—we found greater emphasis on

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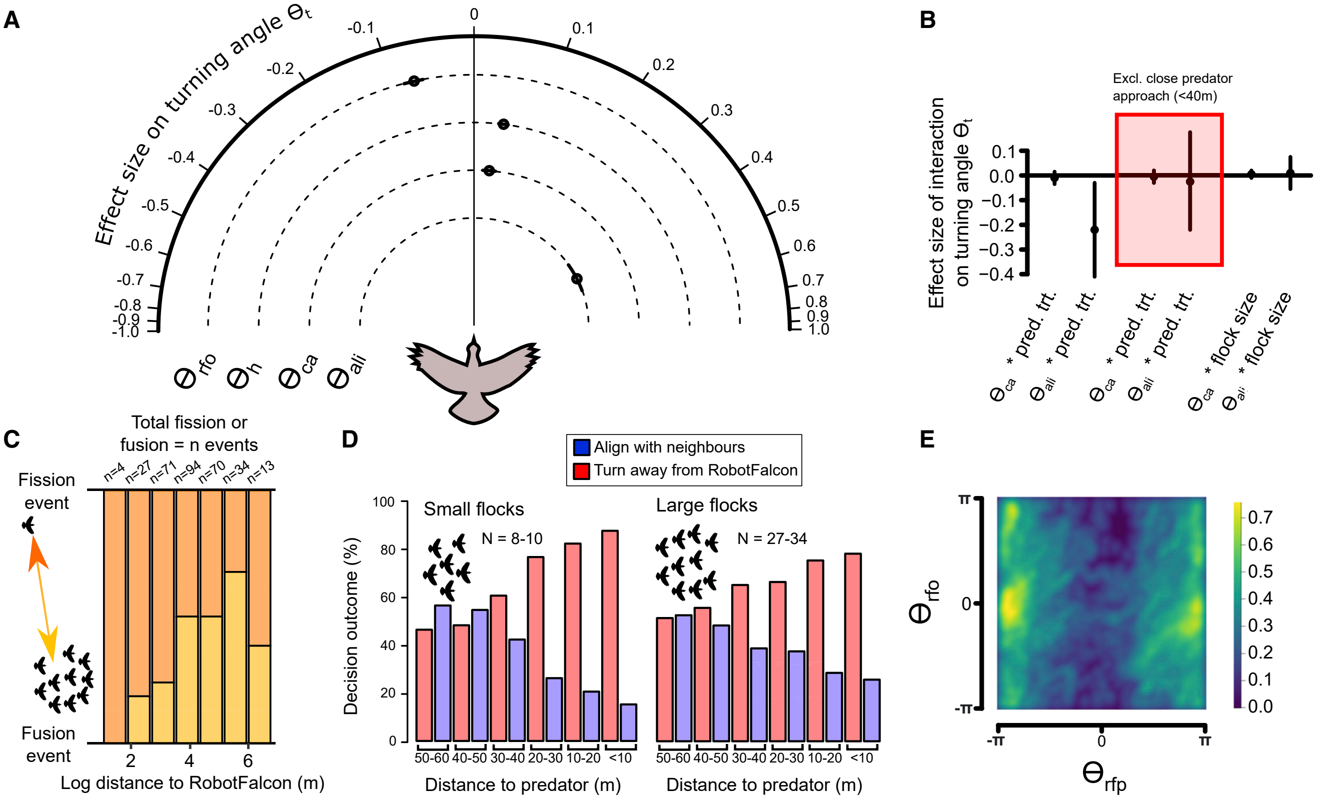

**Figure 2. Pigeon responses to the RobotFalcon**

(A) Mean estimate (black circles) and 95% confidence intervals (bars) of the effect size of predictor variables on turning angle $\Theta_t$ for both control and treatment flocks. Predictor variables are given from left to right (bottom left of A; [1] the RobotFalcon's orientation $\Theta_{rfo}$; [2] home $\Theta_h$; [3] centroid attraction $\Theta_{ca}$; [4] alignment $\Theta_{ali}$).

(B) Mean estimate for effect size and 95% confidence intervals for interaction terms (from left to right): (1) $\Theta_{ca}$ × predator treatment; (2) $\Theta_{ali}$ × predator treatment; (3) and (4) are the same as (1) and (2) but with close predator approaches (<40 m) removed from the data; (5) $\Theta_{ca}$ × flock size; and (6) $\Theta_{ali}$ × flock size.

(C) Fission or fusion dynamics. Bars indicate the relative number of fission (dark orange) or fusion (light orange) events at each binned distance to the RobotFalcon predator (logged) with number of events in each binned distance provided at the top. Both flock sizes are included in these data, as no difference was found between flock size treatment.

(D) Conflict decision outcome (as a percentage) binned by individual distance to the RobotFalcon, small flocks (left) and large flocks (right).

(E) Heatmap of the orientation of the RobotFalcon relative to the focal individual ($\Theta_{rfo}$) versus the RobotFalcon's relative position $\Theta_{rfp}$. Plot generated using smoothScatter in base R,[19] density scale using a two-dimensional kernel density estimate from function bkde2D in R package "KernSmooth,"[20] and using color scale "Viridis."[21]

See also Figure S1, Table S1, and Video S1.

avoiding the RobotFalcon than aligning at closer approaches (Figure 2C; GLMM binomial: $t = 4.170$; Cohen's D = 0.146; $p < 0.001$). There were no differences in conflict scenario outcomes between the two flock sizes (GLMM binomial: $t = 0.437$; Cohen's D = 0.046; $p = 0.662$), nor was there any evidence for an interaction between "distance to RobotFalcon" and flock size (GLMM binomial: $t = 1.054$; Cohen's D = 0.037; $p = 0.292$).

It is possible, alternatively, that fission could be driven by a need to reduce energy expenditure. Unlike V-formation flocks, which can benefit energetically by flying in a group, flying in a flock has been shown to come at a cost in pigeons.[26–29] Even the act of flying with a single other pigeon increases work rate by 18%.[27] That the pigeons are willing to pay this cost suggests anti-predator benefits are the primary driver of flocking, especially from familiar release sites, where the benefit from collective navigational information is reduced.[9,30] This is not to say all decisions will have an anti-predator focus. For example, if energy supplies have been almost or completely exhausted, energetic motivations may become more important. As an example, it was previously found that pigeons only prioritized energy conservation (fission) after 101 km of flight when a flock of pigeons took an unexpected and uneconomical route home from a flight release location 9 km from the home loft.[29] However, birds in the present study are unlikely to have favored energetic concerns just seconds after release.

## Fish shoals and selfish herds

Our findings thus lead to the question of why fish—which can move collectively with high alignment[8,31] (but see Katz et al.[32] and Herbert-Read et al.[33])—have been shown to behave accordingly with a selfish herd mechanism. (Note, this was when selfish herd was defined as minimizing approach time to neighbors[2] or responding to a greater number of neighbors' positions.[3]) Collision avoidance could potentially explain the differences between birds and fish, as centroid attraction movements may cause collisions in birds, the results of which are potentially more costly for

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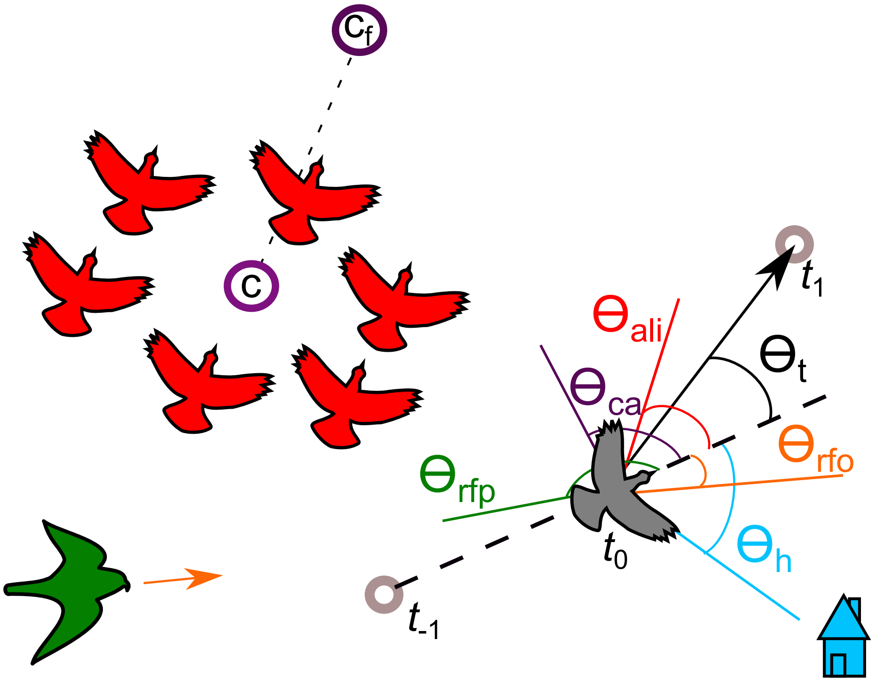

**Figure 3. Angular variables schematic**

The focal bird (gray) is turning at angle ($\Theta_t$) at time $t_0$, with respect to its previous orientation at $t_{-1}$, to reach the coordinates at $t_1$. The turning angles necessary to (1) align and (2) attract toward neighbors (red) are given by $\Theta_{ali}$ (red) and $\Theta_{ca}$ (purple), respectively. Centroid attraction is given to "predicted future centroid" ($C_f$; see STAR Methods) rather than instantaneous centroid (C) as it was more influential on turning angle ($\Theta_t$). Angle toward the RobotFalcon's position ($\Theta_{rfp}$; green) and orientation ($\Theta_{rfo}$; orange) are provided with respect to the falcon schematic and arrow. Angle toward home ($\Theta_h$; light blue) is also pictured. See also Figure S1.

airborne animals.[34] However, when we removed time steps where centroid attraction would likely cause collisions from our analysis (<0.8 m from seven nearest neighbors; see STAR Methods), thus focusing on time steps where centroid attraction could be seen as favorable (when following the logic of selfish herd theory),[1] we find no difference in the direction or significance of the statistics, and hence still find no evidence that centroid attraction is preferred in threatening situations (centroid attraction × predator treatment, LMM: $t = -0.424$, Cohen's D = $-0.013$, $p = 0.671$; close approaches <40 m: $t = -0.164$, Cohen's D = $-0.007$, $p = 0.869$).

Fish shoals have an additional option that airborne birds do not have, which is to decrease their speed and form a slow, barely moving aggregate, which could provide a shelter for those in the middle.[3,6] This approach is not possible for most birds, which would risk stalling and losing altitude rapidly if they ceased all locomotion. Therefore, we might expect fish to have a more flexible decision-making strategy, benefitting from selfish herd dynamics when ecological conditions are favorable to do so.[8] We suggest that the current results in support of selfish herd behavior may reflect such conditions. The impenetrable walls of fish tanks typically used in such studies may intrinsically favor centroid attraction over alignment, as alignment would be more likely to cause a group to speed up and produce collisions with the tank walls. Therefore, we suggest that centroid-based findings in fish shoals should be replicated in free-ranging environments, to investigate the potential flexibility of a selfish herd mechanism when no physical constraints are present. (A good starting point might be investigating the "attraction" properties of bait balls.[35]) It is important to test this hypothesis in free-ranging conditions, given that high speeds while maintaining high synchronicity—cf. alignment behavior[8,36]—are only possible in more wide-ranging, naturalistic spaces. Indeed, such a test is important in mammals too, whereby current evidence suggestive of selfish herd dynamics was conducted in relatively enclosed spaces.[5]

## Could a "cognitive load" hypothesis explain our results?

An alternative hypothesis for why a decrease in alignment is observed in our study is that simultaneously tracking neighboring flock mates and the predator becomes cognitively challenging for flocks under threat and that this cognitive demand leads to impediment of alignment. There is evidence that collective flocking behavior can be cognitively challenging in pigeons; Pettit et al.[37] demonstrated that pigeon "followers"—which need to pay more attention to the trajectories of other pigeons—were less efficient route learners than "leaders." They posited that the leaders may have more available cognitive capacity due to less attention being devoted to other pigeons' flight paths. Following this hypothesis, we might have expected that—in our study—smaller flocks would show less of a decrease in their alignment than larger flocks, as smaller flocks have less individuals to track from the start. However, we found no difference in alignment between small and large "predated" flocks. This is far from conclusive refutation of a cognitive load hypothesis,[38] as pigeons in larger groups may not need to pay attention to larger numbers of individuals than pigeons in small flocks. Indeed, local interactions can produce group level movements, independent of group size, and this is a reoccurring feature of collective motion.[22,39–41] Nevertheless, we found similar alignment decreases in both flock sizes, despite more birds to potentially obscure the view of the predator in larger flocks. Furthermore, the concordance of our results with theoretical models[6] suggests an adaptive benefit (of high alignment over high attraction) hypothesis is more consistent with our results. Altogether, whether or not a cognitive-load, or an adaptive-choice hypothesis, can better explain our findings or whether both hypotheses contribute in a non-mutually exclusive manner, our major conclusion would stand that selfish herd dynamics may be an inappropriate paradigm for the study of highly synchronous collective motion.

## Broader outlook

Our results suggest that pigeon collectives make use of an alignment mechanism, augmented by a fission or fusion response,

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depending on a predator's proximity to an individual. This result is consistent, regardless of flock size in the range that we tested ($n = 8–34$). Thus, we find no support for a selfish herd hypothesis in pigeon flocks. Original models of selfish herd theory assume the predator is always successful,[1] which is not always the case in nature.[7] If aligning with neighbors can increase the chance of a failed predator attempt—either via faster group speeds[36] or information transfer[6]—a ''high alignment'' mechanism could evolve instead. For example, in groups that face many predator strikes per day[42] or have a small total group size, a mechanism such as ''heading for the center and hoping one's neighbor gets predated upon'' is not likely to be a successful strategy for long, as the group size will diminish until all individuals are eaten. Overall, we question the usefulness of a selfish herd paradigm in moving animal groups and suggest that we should seek to understand which species actually benefit from selfish herd movements and which do not. When, instead, there is a high coincidence of individual and group-level interests,[43] we suggest species will favor alternatives, such as the mutualistically beneficial motivation to coordinate (align).[6–8]

## STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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## SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2021.05.009.

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## AUTHOR CONTRIBUTIONS

D.W.E.S., R.F.S., R.J.M., C.K.H., and S.J.P. conceived and designed the methods; D.W.E.S. conceived of, designed, and performed the analysis; T.W.R. contributed analysis tools; D.W.E.S., R.F.S., and R.J.M. collected the data; and D.W.E.S. wrote the paper with comments from all authors and extensive feedback from R.F.S., C.K.H., and S.J.P.

## DECLARATION OF INTERESTS

We declare no competing interests. R.J.M., who built the RobotFalcon, readily and willingly agreed to publish results (regardless of the findings) before the study took place.

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## STAR★METHODS

### KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|---|---|---|
| Experimental models: organisms/strains | | |
| Homing pigeons (*Columba livia*) | Louella pigeon world | Louella Pigeon WorldHall Farm, Copt Oak Road, Loughborough LE12 9XL |
| Software and algorithms | | |
| Inkscape | Inkscape | Retrieved from https://inkscape.org |
| R package multcomp | Hothorn et al.[44] | https://cran.r-project.org/web/packages/multcomp/index.html |
| R package EMAtools | Kleiman[45] | https://cran.r-project.org/web/packages/EMAtools/index.html |
| R package viridis | Garnier et al.[21,24] | https://cran.r-project.org/web/packages/viridis/index.html |
| R package mass | Ripley et al.[46] | https://cran.r-project.org/web/packages/MASS/index.html |
| R package KernSmooth | Krause and Ruxton[23] | https://cran.r-project.org/web/packages/KernSmooth/index.html |
| R package nlme | Pinheiro et al.[47] | https://cran.r-project.org/web/packages/nlme/index.html |
| Deposited data | | |
| Cleaned trajectory data | This paper | https://github.com/sankeydan/robofalcon |
| Other | | |
| GPS loggers | Qstarz International Co., Ltd.<br>Address: 6F-2, No. 160,<br>Ming Chuan E. Rd., Sec. 6,<br>Taipei 114, Taiwan, R.O.C. | Qstarz bt-q1300st |

### RESOURCE AVAILABILITY

#### Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Daniel Sankey (d.sankey@exeter.ac.uk).

#### Materials availability

Further information and requests regarding the RobotFalcon should be addressed to Robert Musters, who built the RobotFalcon.

#### Data and code availability

Combined bird trajectory data are available at https://github.com/sankeydan/robofalcon. Code used to combine the data are provided in the same location. As well as the scripts to run analyses in this paper.

### EXPERIMENTAL MODEL AND SUBJECT DETAILS

#### Subjects

Homing pigeons (N = 34) were housed at Royal Holloway University of London in purpose-built lofts. Birds were provided food (Johnstone & Jeff Four Season Pigeon Corn, Gilberdyke, UK), water, and grit (Versele-Laga – Colombine Grit and Redstone, Deinze, Belgium) *ad libitum*. At the time of the study, ten pigeons were aged at 27 months old, and formed the first group; the further 24 birds (all aged 15 months old) were assigned randomly into three groups of 8. Each group was housed separately. In the event of an individual going into a different group's loft, they were relocated back to their own group's loft within 24-hours.

#### Ethical guidelines

Experimental protocols were approved by Royal Holloway University of London Ethical Review Board. The data presented in this study form part of a larger ethical project to determine the value of the robotic falcon as a bird deterrent at airfields and ultimately reduce collisions with airplanes.

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## METHOD DETAILS

### Protocol, and release site

Body mass loss was used as a proxy for welfare[48,49]. There is ample evidence to suggest that body mass and corticosterone levels can covary in pigeons[50]. We weighed the birds with electronic scales (CoffeeHit: Coffee Gear Digital Bench Scale – 2kg/0.1g limit/accuracy) each day after the birds were flown with RobotFalcon treatment (1/10/18 – 12/10/18 and 17/10/18; see The RobotFalcon below), and most days after a control flight (except on 13/10/18, 18/10/18 and 22/10/18; control flight is the condition with RobotFalcon absent, see Release protocol below). In total, twelve mass measurements were taken per bird: three on days after control flights, and nine on days after the treatment or ‘‘mixed’’ (i.e., when the bird flew twice in a day, one flight being treatment and one control). On each day of weighing, we checked a pigeon’s body mass against its first recorded mass, to check for large reductions which may be indicative of stress[51]. We set this threshold at 90% of this first recorded mass, whereby if an individual were beneath this mass, it would be taken out of the study for a day and would join if and when the mass returned to above this threshold. We chose this threshold based on our knowledge (from careful monitoring of pigeons’ masses throughout the year) that both seasonal fluctuations and flight days often reduce mass by greater amounts than 10% over the space of two weeks[28,29]. This did not occur throughout the duration of the study for any individual, and pigeons were hence not rested, except on a specific rest day for all individuals on 06/10/2018.

### Release site and transit

Each flight in the present study was conducted from a release location in the southern area of Chobham Common (CC), England (latitude = 51.3712, longitude = $-0.5979$), which resides 5066 m in a southerly direction from the home loft at Royal Holloway University of London (trajectory = $-2.91$ radians). Permissions were granted from the landowners (Surrey Wildlife Trust, England). The exact release location within CC was chosen based on the minimization of potential obstructions (e.g., trees) and the centrality of the location within the common. Pigeons were transported to the release site by car in wicker boxes: either one box (dimensions = 80cm x 40 cm x 22 cm) for small flocks or two boxes (dimensions = 80cm x 40cm x 55cm) for large flocks (see Release Protocol below for definition of flock size). The total time in transit was 15 minutes by car, and then a further five-minute travel on foot to the release site.

### Training

Each bird was trained from a site just outside Chobham Common (CC) for a total of 10 flights prior to the study (latitude = 51.3625, longitude = $-0.5737$) between 15/9/18 and 1/10/18. This was to familiarise the birds with the surrounding area; a number of studies suggest that routes are learned by the 10th flight, as route efficiency improvements stabilize at this point[9,52]. The last two training flights were recorded with GPS, but given the large differences in topology (the training site was at a lower altitude in a heavily wooded area), we do not compare the data from the two sites; only between control and treatment flights (see Release protocol below) during the experimental phase at CC. Each bird had homing experience from multiple other sites, yet CC was novel to all pigeons in the present study.

### Release protocol

Bird groups were released either once or twice a day (morning and/or afternoon flights), either as small flocks (N = 8-10 birds) or large flocks with all groups combined (N = 27-34 birds). Flocks were flown either with the robotic falcon treatment (‘‘RobotFalcon’’; see The RobotFalcon below) chasing the pigeons, or absent (i.e., control flights with no robot present). The total number of flights in each of the four categories were as follows: small groups with predator – 20 flights; large groups with predator – 7 flights; small groups with control conditions – 12 flights; and finally, large groups with control conditions – 4 flights; providing N = 169, N = 229, N = 101 and N = 129 individual trajectories for each condition respectively (total pigeon trajectories N = 628).

The ‘‘predator’’ treatment period ran for 11 days, from 02/10/2018, to 13/10/2018 with a rest day on 6/10/2018. Each small flock (total groups N = 4) had four treatment flights during the treatment period, and three control flights: one during the treatment period (one group per day selected at random after the first two days using treatment, for pilot training and methodological purposes), and two following the RobotFalcon treatment period on 16/10/2018 and 19/10/2018. Large groups (N = 27-34 birds from all small groups combined) had seven treatment flights, and four control flights. These control flights consisted of two flights within the treatment period (10/10/2018 and 12/10/2018), and two following, on 18/10/2018 and 22/10/2018. Methodological protocol during pilot training (the first two days) was consistent with the methods from all other days, except that the pilot was closer to the release site (~50 m). Data from these days were analyzed alongside other data. See Methods S1 for the number of flights in each condition per individual pigeon.

### Wind measurements

Wind speed was recorded before each flight using a handheld anemometer (Windmaster2, Kaindl Electronics, Rohrbach, Germany). Wind direction was estimated with an approximate accuracy of ± 45 degrees. The wind vector (product of speed and direction) was combined with the pigeon’s orientation (heading between GPS locations) to estimate the impact of cross winds and support wind on the pigeons’ speed and turning angles (see methods in[53]).

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### Biologgers

To determine the positioning, trajectory, and speed of each individual within the group, we deployed GPS loggers (5 data points per second – 5Hz; QStarz BT-Q1300ST, Düsseldorf, Germany; mass = 12.5g) for each bird and the RobotFalcon for each flight throughout the duration of the study. Logger failures, through either logger or human error, were rare (1.2%). Significantly, GPS never failed during a flight with the RobotFalcon present and thus failed only on control flights. Total logger mass was 20.5g, which included accelerometers not used in the present analyses (AX3, Axivity Ltd, Newcastle upon Tyne, UK; 8g). The dimensions of the loggers were as follows: GPS loggers were 2.5cm length, 2.5cm width, 0.5cm depth; accelerometers were 3cm length, 2cm width, 0.5cm depth.

GPS loggers had their outer casing removed, so that only the circuit board and battery remained. They were then wrapped in generic duct tape (one layer) before having gaps at the top and bottom painted and filled in with liquid electrical tape (Performix, Liquid Tape – Electrical, Minnesota, U.S.A.) for waterproofing. Velcro strips (hoop side) were then attached to the battery side of the logger for deployment. The GPS loggers weighed 12.5 g each after this treatment. Accelerometers (AX3, Axivity Ltd, Newcastle upon Tyne, UK; 8g) did not need modification, except the Velcro strip (hoop side) on one side. For each flight, we attached one GPS logger, and one accelerometer logger, to another Velcro strip (hook side), which was attached to a trimmed 10 cm strip of feathers at the center each of the pigeons' backs with epoxy glue (Araldite Rapid Adhesive, Araldite, Basel, Switzerland)[9,52].

Given the initial mass of the birds (range 409.6 g – 533.1 g), the mass load as a proportion of body mass ranged from 3.8% for heaviest birds to 4.9% for the lightest individuals. This means that we did not surpass the commonly cited 5% rule[54]. When considering that biologging also has less welfare impact on captive animals, due to the relatively short-term attachment (< 1 day;[54]), and the provision of surplus food to restore their energy levels after deployment, we expect logger impacts on behavior should have been appropriately minimized.

### The RobotFalcon

The model, robotic falcon (or ‘‘RobotFalcon’’; Figure 1) was developed by RM, with key attention to copying the behavior as well as morphological likeness of a male peregrine falcon. The mass of the RobotFalcon was 0.245 kg. The RobotFalcon had a First-Person View camera (Runcam micro swift 2), which transmitted images (600TVL, 30fps) in real time to a set of goggles worn by the pilot (Video S1). The RobotFalcon's direction and speed were controlled by the pilot by commands sent via remote control. A GPS unit (5Hz), as described above, was attached to the inside of the body of the RobotFalcon casing with Velcro strips. We were granted informal permission from the UK's civil aviation authority (CAA) to conduct the flights. We did not require formal permission, because of the low mass of the RobotFalcon and the non-commercial nature of our study. Permissions were granted from the landowners (Surrey Wildlife Trust, England).

RM piloted the RobotFalcon. The final chase protocol was based on repeatable methods, from findings in the literature[55] as well as discussions among authors (DS, RS, RM). Wherever possible, the RobotFalcon would gain height before stooping[55]. Also, as we intended to investigate the impact of attacks on bird groups – not individuals – the RobotFalcon would always chase the largest group. Indeed, individuals which split from the group usually did so alone (see below: Grouping GPS data).

The RobotFalcon was launched by hand from a hill with good visibility of the release site, 500 m north-east of the release location (below). Just prior to this, we put a large dark mat over the wicker basket(s) which contained the birds, to prevent the pigeons getting an early visual on the RobotFalcon, and to minimize any differences between control and treatment conditions before release. When the RobotFalcon was in a good position to stoop for an initial attack (defined as approximately 50 m behind the wicker basket and 5 m above), the mat was taken off and the birds were released. The RobotFalcon stooped approximately two to three seconds after the birds were released, when they had already gained sufficient altitude and speed to be a cohesive flying group (all birds out of the box and flying with approximately 3 m altitude or more).

### Data treatment

After each flight, loggers were removed, recharged and the data downloaded. Erroneous GPS points were then removed, as well as duplicate timestamps, before trimming the dataset according to a defined site radius (see Site radius below; and Methods S1). Following this, pairwise distances between all pigeons' GPS locations were calculated (following[56]) at each timestamp (5Hz) for each flight. If a pigeon were less than ten meters from any neighbor, they were considered to be in the same group as one another, and a centroid of this group would be the mean of all individuals' x and y coordinates. Therefore, there is a potential scenario whereby two neighbors which are further than ten meters could be considered part of the same group if another neighbor (or set of neighbors) connected them together (see Methods S1 for a visual representation). Ten meters was chosen for several reasons. First, nearest neighbor distances of over 10 m were rare (between the 94th and 95th percentile of nearest neighbor distances: 9.73 m and 13.01 m). Second, given pigeon wingspans are roughly 62cm, ten meters is more than ten times the birds' wingspans, which would suggest the birds could fly much closer to their closest neighbor in the largest sub-flock if it were intended (or indeed, were possible). Finally, we also used visual observations of flock fission under a range of ‘‘fission distances’’ (5 m, 7.5 m, 10 m and 12.5 m, see Methods S1). Ten meters was chosen as it appeared to remove most of the erroneous splitting, while also not gathering too much data on birds which were in the process of leaving or joining a group (see Methods S1).

Data were grouped per flight from the point that the last individual in the group reached a speed of over 10 m/s, for a duration of over 10 s, i.e., to signify the birds were in flight. For this purpose of finding flight time only, speed was smoothed over ± 1 s, which is equal to 11 data points at 5Hz. This was to prevent erroneous allocation of flight start time, which may result from GPS error. Using these

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criteria, we found no flight where the last individual did not reach 10 m/s within two seconds of the first individual, and this matched observations: whereby the whole group would take flight concurrently (D.W.E.S., personal observation).

### Fission/fusion

The same grouping algorithm described in the previous section also provided binary data on splitting (fission) and re-joining (fusion) events. Specifically, the point at which an individual was not considered part of the largest group was considered a fission event; and vice versa re-entry of the individual to the group was considered a fusion event. If two (or more) individuals split from the group at the same time, this would count as two (or more) fission events. Therefore, fission is defined in terms of individuals splitting from the largest group. Events whereby two or more individuals split, were less common than solo splits: specifically, solo splits accounted for 76% of subgroup data in small flocks and 79% in large flocks (see Methods S1 for data plots on subgrouping). We made the criteria more stringent by including an ‘‘exclusion parameter,’’ ignoring fission/fusion events which occurred within *two* seconds of the last event per individual. We tested the sensitivity of this exclusion parameter, i.e., the threshold for fission/fusion events to be ignored, when occurring within *n* seconds of the last event. Having used *two* seconds in the main analysis (see Results and discussion), we then tested the effect of *one* and *three* seconds on the resulting statistics (see model output in Table S1). We found no differences in the direction or the significance of the statistics under any condition (Table S1).

### Site radius

To compare control and treatment (RobotFalcon) conditions, we needed to define an appropriate site radius, i.e., the area in which the RobotFalcon could come close and potentially cause a proximate response in the pigeons. First, we defined our release site coordinates by taking medians of the first recorded latitude and longitude for each flight (after release from the wicker box; see Release protocol). Then we measured the distance from the RobotFalcon to *i*) the release site coordinates and *ii*) the flock’s centroid (see Grouping GPS data). This enabled us to investigate the potential impact of the RobotFalcon at different distances to the release site (or, different potential site radii), using RobotFalcon distance to flock centroid as a temporary proxy for the impact of the RobotFalcon. Even at the RobotFalcon’s furthest distances from release site coordinates (> 450 m), RobotFalcon-to-flock-centroid distances as low as 46.1 m were still observed. We therefore included all RobotFalcon data (site radius = 451.7 m); further, we added an additional 50 m, as the pigeons may have responded beyond these limits. The site radius was, therefore, defined as 501.7 m, rounded down to an even 500 m, which captured the radius of Chobham Common (see data plot in Methods S1).

### Turning angle as a dependent variable to test predictions

As all pigeons in a cohesive group tend to fly at the same speed as one-another (see a data plot of individual speeds in Methods S1 and[28]), we restricted our major analyses to their turning angle $\Theta_t$. The difference in individual heading from one time-step to the next was termed turning angle $\Theta_t$ (Figure 3), ranging from sharp anticlockwise turns to sharp clockwise turns[10] given in rad/s. Our general approach was to test which polar coordinates have predictive power on an individual’s turning angle $\Theta_t$. I.e., what the birds are most likely responding to, whether it is their neighbors, the RobotFalcon, or home, or a combination of all of the above. Thus, we are investigating the *influence* of these social and environmental forces on individual turning angle.

This approach enabled us to test our first and second research questions using variations of the following example statistical method: If ‘‘centroid attraction’’ $\Theta_{ca}$ (below) was a greater predictor of turning angle $\Theta_t$ in predator treatment flocks than in control flocks, we would see this signal by running models of turning angle $\Theta_t$ against an interaction of ‘‘centroid attraction’’ $\Theta_{ca}$ and ‘‘predator treatment’’ (i.e., control or predator treatment as a factorial variable). Specifically, if there was a difference between groups, the $\Theta_t$ over $\Theta_{ca}$ slope would be different for the two treatments. See how angular covariates such as $\Theta_{ali}$ are regressed against turning angle in a hypothetical example in Methods S1.

### Centroid attraction, alignment, and other angular covariates

Centroid attraction ($\Theta_{ca}$) was given by the turn angle necessary to attract to the centroid of (*n*) nearest neighbors (Figure 3). Where optimal number of neighbors (*n*) is defined as the number that are most predictive of an individual’s turning angle in the next time-step (See below Topological range of interaction). We tried out both *i*) current centroid position, and *ii*) the ‘‘future predicted’’ centroid (below). Alignment ($\Theta_{ali}$) was given by the turn angle necessary to align with the mean orientation of (*n*) neighbors (Methods S1; Figure 3). Where, again (*n*) represents the optimal number of neighbors (though this time pigeon orientation vectors) which best predict individual turning angle. Other angular covariates measured were the angle to the ‘‘RobotFalcon’s position’’ ($\Theta_{rfp}$), ‘‘RobotFalcon’s orientation’’ ($\Theta_{rfo}$) and ‘‘home’’ ($\Theta_h$) with respect to the orientation of a focal individual (all visually represented in Figure 3). All angles $\Theta_{ca}$, $\Theta_{ali}$, $\Theta_{rfp}$, $\Theta_{rfo}$, $\Theta_h$ are calculated for each individual in each time step, with an aim to understand the subsequent movements of an individual in response to their local environment.

### Predicting future centroid

Individuals may be more likely to head toward a predicted future centroid than their present centroid[57]. To this end, we calculated where an individual might expect their neighbors’ centroid to be in timestep $t + 1$, by assuming that their neighbors combined turning angle, acceleration and speed will remain constant from the previous timestep (see Methods S1). As the ‘‘future predicted’’ centroid had a larger effect size on turning angle than current centroid, we used this metric as $\Theta_{ca}$ in all further analyses (Methods S1).

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### Topological range of interaction

To estimate how many neighbors each pigeon responded to, we found (for each successive neighbor iteratively (see[58]), *i*) the average orientation (*alignment*), and *ii*) flock centroid (*centroid attraction*). Here, each iteration adds another neighbor – in rank distance order – to the calculation. The relative difference between an individual’s orientation and the orientation denoted by centroid attraction/alignment ($\Theta_{ali}$ and $\Theta_{ca}$) from the previous time step was recorded for each time step (5 Hz) across all flights within the earlier denoted site radius.

To gauge which topological range had the greatest impact (effect size) on alignment and centroid attraction movements, we ran simple linear models between $\Theta_t$ and alignment/centroid attraction (for topological range: N = 1-7, or N = 1-33 for small and large flocks respectively) (Methods S1). This was performed separately for the ‘‘predator’’ treatment condition (N = 27 flights), and the control condition (N = 16 flights), and for large flocks (N = 11 flights) and small flocks (N = 32 flights). The optimum number of neighbors (*n*) (alignment = 4 and 8; centroid attraction = 7 and 29, for small flocks and large flocks respectively) was given as the largest effect size (*t*) after an equally weighted mean of treatment and control conditions (i.e., mean average not biased by the unequal lengths in the initial calculation; Methods S1). In cases where group size was less than the chosen topological range, we took the value for the closest number of neighbors possible (which was the highest). This approach is justified in that it was only necessary for $\Theta_{ca}$, where the slope for *t*-value for increasing topological structure is mostly continuous and positive (Methods S1). Thus, implying that the closest number of neighbors (to 7 or 28 neighbors; for small or large flocks) will reflect the strongest impact of $\Theta_{ca}$ on $\Theta_t$ anyhow.

### Conflict scenarios

As both *i*) aligning with the group and *ii*) avoiding the RobotFalcon had a strong impact on individual turning angle in the subsequent time step (see: Results and discussion), when these motivations clash it is likely that the pigeons were often faced with a genuine conflict regarding their directional preference. We thus demarcated ‘‘conflict scenarios’’ as situations whereby individuals would need to decide either to *i*) align with the group, or *ii*) turn away from the predator orientation, when both could not be achieved with the same direction of turn. We recorded the decision outcome (either *i or ii*) as a binomial variable. For *i*), ‘‘alignment’’ with neighbors was chosen instead of ‘‘centroid attraction’’ as this had a stronger effect on turning angle $\Theta_t$, and thus a more motivating force. For *ii*), turning-away-from-predator-orientation was chosen instead of turning-away-from-predator-position, as this had a stronger, negative effect on $\Theta_t$.

### Artificial position manipulations

#### *To test a collision avoidance hypothesis*

Birds may pay a particularly high cost from colliding[34]. Therefore, it was important to assess timesteps where all possible decisions (i.e., centroid attraction, alignment, avoiding falcon) are available, and not likely to cause collisions with neighbors. To do this we took an individual’s seven nearest neighbors (following[58]) and calculated where they were likely to be in the future ($t + 1$) timestep, using the same algorithm as the future predicted centroid calculation (above and Methods S1), but instead for each of these seven nearest neighbors (rather than a centroid as is performed in future centroid predictions). This is done by adding turning vector of these individuals to their trajectory path (plus the previous acceleration, which is speed at *t* minus speed at *t*-1). If any of the neighbors resulting trajectories were within 0.8 m of the focal after our artificial ‘‘decision’’ to either *i*) attract, *ii*) align or *iii*) avoid RobotFalcon. Then we discard this timestep from the analysis because we consider that decision not to have been available to the focal individual. 0.8 m was chosen as it was the mode nearest neighbor distance in small flock sizes and suggests individuals are comfortable at these inter-individual distances. Large flocks had a mode nearest neighbor distance of 0.5 m, though this was disregarded as it is more likely an artifact of the greater depth of the flock’s 3D nature. All artificial headings were given a maximum turning angle of 0.8rad/s, a high but not highly unusual value for turning angle from the data (between the 94th and 95th percentile).

#### *To test cost/benefit assumptions*

We broadly assume that (*1*) turning away from the falcon may minimize risk, and that (*2*) heading to the centroid could mitigate risk to individuals relative to their flockmates. To assess these questions, we used the proxy for risk ‘‘distance to predator’’ for the first question, and ‘‘distance to predator, relative to flockmates’’ for the second question. Again, we use artificial position manipulations to assess the outcome of different movements. We took each individual for each timestep in each predator treatment flight and moved them either *i*) toward centroid, *ii*) toward alignment vector or *iii*) avoid RobotFalcon. As in the section above, we removed timestamps where decisions may have caused collisions. From the new, updated position, we measured the ‘‘distance to predator’’ and ‘‘distance to predator, relative to flockmates,’’ using data from the proceeding timestep for neighbors and RobotFalcon. We applied an ANOVA with Tukey HSD on repeated-measures (timesteps), with Bonferroni corrected statistics in R package ‘‘multcomp’’[44] to assess differences in the (*1*) ‘‘distance to predator’’ and (*2*) ‘‘distance to predator, relative to flockmates’’ provided by decisions: *i*), *ii*) or *iii*). Repeated-measures were *timesteps*, because each timestep represents a distinct and unique context. By ‘‘freezing’’ each timestep and looking at differences in distance measures provided by each decision, we control for all other present conditions. Autocorrelation was accounted for using the autocorrelation methods (as described below in Autocorrelation for ‘‘conflict scenarios’’).

We assume broadly throughout this paper that ‘‘distance to predator’’ is an appropriate proxy for risk. However, an important caveat is that maximizing their ‘‘distance to predator’’ would require individuals to always turn faithfully away from the RobotFalcon’s position. In our study, we found that – while individuals turned away from the RobotFalcon’s orientation $\Theta_{rfo}$ (Figure 2A) – there was actually a significantly positive relationship between turning angle and RobotFalcon position $\Theta_{rfp}$ (Table S1; LMM: DF = 4079, $t$ = 16.712, Cohen’s D = 0.522, $p < 0.001$). It seems counter-intuitive that birds would turn *toward* the threat. However, the RobotFalcon

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was more often behind the birds (with respect to bird heading, as is clearly seen in Figure 2E), with RobotFalcon position $\Theta_{rfp}$ only occupying a narrow range of angles, mostly behind the focal bird. Here, slight movements toward the RobotFalcon's position may not result in collision, especially when there were many other variables that positively predicted turning angles (e.g., "home" $\Theta_h$, "alignment angle" $\Theta_{ali}$).

Notwithstanding the issue with using "distance-to-falcon" as a measure of risk, we performed artificial position manipulations, to assess whether movements *i*) toward centroid $\Theta_{ca}$, *ii*) toward alignment vector $\Theta_{ali}$ or *iii*) away from RobotFalcon's orientation $\Theta_{rfo}$ would optimize an individual's "distance-to-falcon" in a given moment. We found surprising results that, first, turning away from a predators' orientation can bring an individual closer to the predator's position (relative to the group) compared to alignment, when direct comparisons were made in our artificial position manipulations (ANOVA with Tukey HSD on repeated-measures[44]: estimate = $-0.027$, Std. Error = 0.001, $z = -16.245$, $p < 0.001$). This may be seen as risky, however, this behavior (turning away from predator's orientation) can result in the predator overshooting the individual performing the maneuver[59]. This is thought to be an optimal strategy for prey which are slower than their predator, which is the case for pigeons and their predators (sparrowhawks *Accipiter nisus* and peregrine falcons) during attacks[13,59,60]. Additionally, sharp turns have been shown to interrupt goshawks' (Accipiter gentilis) visual tracking of their prey[61], which would not be possible if an individual tried to maximize their distance to the predator involving solely forward, non-turning flight[59].

Additionally, when artificially updated individuals (see STAR Methods) were made to "attract to the centroid" their resulting position put them no further from the RobotFalcon (relative to the group) than if they had aligned with the group (LME with Tukey HSD on repeated-measures[44]; *N* observations = 400, estimate = $-0.071$, Std. Error = 0.390, $z = -0.183$, p = 1). This overturns an assumption that "selfish herd" movements would be beneficial to the individual, but nevertheless fits well with the observation of Wood and Ackland[6], that locally perceived centroid attraction becomes unfavorable in highly aligned modeled flocks.

### Agent-based model

We employed an agent-based model to test the assumption that net-positive centroid-attraction across a group is not an impossible outcome for cohesive moving flocks of animals. The reasoning here is that if all individuals in a group had positive centroid attraction, then potentially the group would collapse in on itself, and hence slow down to minimal speeds, and cease to fit the definition of a *moving* group. For this, we employed an agent based model, mimicking Couzin et al.'s[22] flocking model, with parameters set in the range tested in the original model (see a parameter table in Methods S1). Each iteration of the model (n = 1000) ran for 1000 time-steps, but we removed the first 500-time steps to reduce any bias of initial conditions. Initially, individuals were normally distributed about the same point, and were given the same starting velocity. With zones of attraction, alignment and repulsion defined as in[22], the group moved across the virtual world successfully as a cohesive unit.

Our agent-based model revealed that in a moving flock, mean "instantaneous $\Theta_{ca}$" was greater than zero in every simulation we ran (N = 1000). Where "instantaneous $\Theta_{ca}$" is defined as turning angle toward the centroid, relative to the alignment angle $\Theta_{ali}$. Thus, positive centroid attraction is possible in a moving group, without the collapsing in on itself. Because agents (like birds) are limited in their maximum turn angle per unit time[10,22], it was possible for all individuals in the group to make more movements toward a locally perceived centroid than away from it, while remaining mobile. James et al.[62] have criticized studies that have looked for net-positive "selfish herd" behavior, because domains of danger (the angle of an animal's body exposed to the outside, which is vulnerable to attack) cannot decrease "on average" when considering all individuals in a group[62]. Instead, it is suggested that average "instantaneous $\Theta_{ca}$" would be zero, but, individuals could attempt to outcompete one another with differential success (i.e., some have positive "instantaneous $\Theta_{ca}$" and some have negative)[62].

To answer this valid criticism, we ran two models of empirical "instantaneous $\Theta_{ca}$" 1) including pigeon ID as random intercepts, whereas in 2) we dropped this variable. (In both models, unique flight ID and group number were also included as random intercepts.) The rationale is that if some pigeons had high $\Theta_{ica}$ and some pigeons had low "Instantaneous $\Theta_{ca}$," the model with pigeon ID as a random intercept would better fit the data. In actuality, when pigeon ID (as a random intercept) was taken out the model had a *lower* AIC value ($-13819.72$ versus $-13817.72$), so the model was a better without these random intercepts. This suggests that $\Theta_{ica}$ was similar across all individuals. Together we have strong evidence that "selfish herd" dynamics, while *possible* as a component of collective motion, were *not present* in our data at the group or individual level.

## QUANTIFICATION AND STATISTICAL ANALYSIS

### Linear mixed models

To test our first research question – whether "alignment" decreased in favor of "centroid attraction" in "predated" flocks – we used the following model: A linear mixed model[47] of turning angle ($\Theta_t$) against an interaction of "centroid attraction" ($\Theta_{ca}$) with predator treatment (i.e., control or "predated" flocks), and an interaction of "alignment" ($\Theta_{ali}$) with predator treatment. Turn angle to "home" coordinates ($\Theta_h$) and crosswind component (see Wind measurements) were also added as covariates to this model. As our study system contains repeated-measurements of the same individuals and groups, pigeon ID, group ID, were added with random intercepts. Additionally, unique flight ID was added as a random variable, this is a crucial addition to not "boost" findings from large flock flights above that of small flock flights where more data (in the former) are inevitable. All statistical tests were two-sided. Effect size (Cohen's D) was calculated for each covariate or interaction, using R-package "EMAtools"[45].

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Then considering just data from the treatment (''predated'') flocks, we tested whether ''centroid attraction'' was higher, and ''alignment'' was lower in larger flocks (our second research question). Similar to our first research question, the method was to regress $\Theta_t$ against interactions of $\Theta_{ca}$ and $\Theta_{ali}$, but this time with ''flock size'' (i.e., large, or small flocks). As this model only contained predator treatment flocks, covariates: ''RobotFalcon's position'' ($\Theta_{rfp}$), and ''RobotFalcon's orientation'' ($\Theta_{rfo}$) were added to the model, as well as a binary variable ''flock half'' describing whether individuals were on the side of the flock closer or further to the RobotFalcon. The primary differences between this model and the first model were these interaction terms (hence the removal of experimental treatment, i.e., RobotFalcon presence/absence) and the addition of the three ''predator'' covariates (above). Other fixed and random covariates were kept the same.

### Binomial models

To test our third research question regarding fission/fusion events, and their relationship with the distance to the artificial predator, we constructed GLMMs with binomial error family ''glmmPQL''[46]. The dependent variable: fission (binary-0) or fusion (binary-1) event, was regressed over log-transformed ''distance to RobotFalcon,'' in an interaction with flock size. Random variables were pigeon ID, group ID and unique flight number. We also analyzed binomial ''conflict scenario'' outcomes (either 0 ''align with group''; or 1 ''avoid RobotFalcon'') in the same manner as ''fission/fusion'' models with the same random and fixed variables.

### Transformations

Turning angle data $\Theta_t$ were first trimmed by removing turn rates of over 0.3 radians per second (both anticlockwise and clockwise), which were over the 99% quantile range (1% = −0.22 rad/s; 99% 0.294 rad/s), and likely reflects slight errors in the GPS coordinates[57]. We further trimmed turning angle to remove movement in a straight-line (turning angle less than 0.02 rad/s). This was necessary to satisfy the assumptions of the model, however this removed 29.9% of the data representing flight in a relatively straight line. Our models, therefore, predict turning decisions of the pigeons, but cannot be interpreted to predict decisions to fly straight ahead. A model was run on all of the data, i.e., with straight line flight also, and here the major statistics reported in the main text did not change in their direction or significance (Table S1), however, this model did not satisfy the assumption of normally distributed residuals. The removed 29.9% were generally at greater distances from the site coordinates than the remaining 69.9%. The median distance of the removed data was 258 m from the site, compared with 169 m from time steps in turning flight. Removed data were also at generally greater distances from the RobotFalcon (median = 107 m compared with 68 m), and therefore possibly less important to our conclusions.

### Autocorrelation

We calculated temporal autocorrelation (using ''acf()'' function in base R[19]) for turning angle $\Theta_t$. For each autocorrelation curve (i.e., one per unique trajectory), the point at which the curve passed below the 95% confidence interval was noted, and all such points collated. A median value of all these ''autocorrelation end points'' was used instead of a mean value as the distribution was non-normal, and thus due to greater accuracy at estimating central tendency in skewed distributions[63] (Shapiro-Wilks test; turning angle: $W = 0.808$, $p < 0.001$). The final autocorrelation estimate for turning angle was 1.8 s, and this was used to subsample data (every 1.8 s) in statistical models describing this variables.

Temporal autocorrelation in turning angle $\Theta_t$ for ''conflict scenarios'' (see Conflict scenarios) was treated differently to other larger models described above. As this variable is already staggered in time (subset according to conflict criteria). Here, all data were treated together for autocorrelation (not per flight and in variables described above). All together this gave an estimate of 1.8 s autocorrelation for both ''conflict scenarios'' and ''no conflict.''

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# Supplemental Information

# Absence of “selfish herd” dynamics

# in bird flocks under threat

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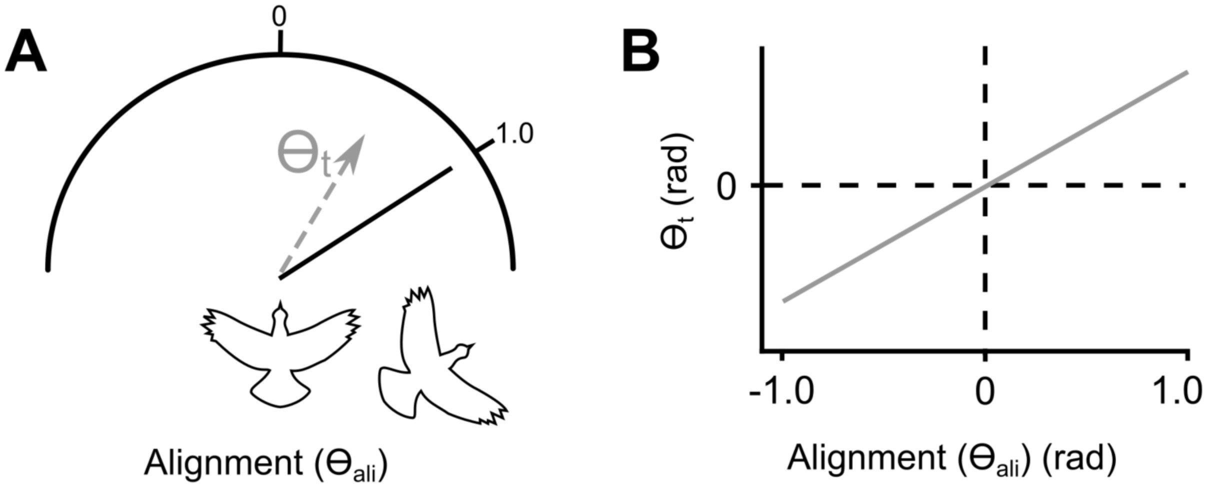

**Figure S1. The influence of angular covariates on turning angle $\Theta_t$. Related to Figures 2 & 3.**

Angular covariates which may influence turning angle $\Theta_t$ were defined as the angle between the focal individual's orientation and the angle in question (here using alignment $\Theta_{ali}$ as an example). **(A)** A schematic where a focal individual's (centre) neighbour (right of centre) is facing one radian clockwise**.** $\Theta_{ali}$ is thus equal to 1, and the turning angle $\Theta_t$ of the focal individual (centre) is less than this. Both angles are recorded, and after being corrected for autocorrelation, would be used in regression**. (B)** An example of such a regression. Here, a potential relationship between alignment $\Theta_{ali}$ (black line **(A)**) on turning angle $\Theta_t$ (grey arrow in **(A)**) is plotted. This is only to provide a visual example of our dependent and independent variables used in statistical models and should not be taken as *a priori* prediction of linearity, or the magnitude of the effect (hence there are no labels on the y-axis other than zero).

| Dependent variable - data treatment | Independent variable | Value | CI 2.5% | CI 97.5% | DF | *T*-value | Cohen's D | p-value |
|---|---|---|---|---|---|---|---|---|
| Model of turning angle | (Intercept) | 0.022 | 0.019 | 0.026 | 6445 | 12.533 | NA | 0 |
| | conditionp | -0.009 | -0.013 | -0.005 | 562 | -4.042 | -0.341 | 0 |
| | futatt | 0.007 | 0.003 | 0.011 | 6445 | 3.654 | 0.091 | 0 |
| | align | 0.127 | 0.094 | 0.16 | 6445 | 7.506 | 0.187 | 0 |
| | cross.wind | 0 | -0.001 | 0.001 | 6445 | -0.576 | -0.014 | 0.565 |
| | turn2home | 0.008 | 0.007 | 0.01 | 6445 | 10.429 | 0.26 | 0 |
| | conditionp:futatt | -0.002 | -0.007 | 0.003 | 6445 | -0.934 | -0.023 | 0.35 |
| | conditionp:align | -0.044 | -0.082 | -0.006 | 6445 | -2.265 | -0.056 | 0.024 |
| Model of turning angle, excluding interaction terms | (Intercept) | 0.017 | 0.015 | 0.019 | 6447 | 15.504 | NA | 0 |
| | futatt | 0.006 | 0.003 | 0.008 | 6447 | 4.881 | 0.122 | 0 |
| | align | 0.093 | 0.077 | 0.109 | 6447 | 11.429 | 0.285 | 0 |
| | cross.wind | 0.000 | -0.001 | 0.000 | 6447 | -0.707 | -0.018 | 0.479 |
| | turn2home | 0.009 | 0.008 | 0.011 | 6447 | 11.687 | 0.291 | 0 |
| Excluding 40m closest to RobotFalcon | (Intercept) | 0.025 | 0.022 | 0.028 | 4946 | 15.499 | NA | 0 |
| | conditionp | -0.024 | -0.029 | -0.02 | 537 | -10.939 | -0.944 | 0 |
| | futatt | 0.01 | 0.006 | 0.013 | 4946 | 5.388 | 0.153 | 0 |
| | align | 0.144 | 0.114 | 0.174 | 4946 | 9.364 | 0.266 | 0 |
| | cross.wind | -0.001 | -0.002 | 0 | 4946 | -2.669 | -0.076 | 0.008 |
| | turn2home | 0.004 | 0.002 | 0.005 | 4946 | 4.592 | 0.131 | 0 |
| | conditionp:futatt | -0.001 | -0.006 | 0.004 | 4946 | -0.492 | -0.014 | 0.623 |
| | conditionp:align | -0.005 | -0.044 | 0.035 | 4946 | -0.222 | -0.006 | 0.824 |
| Including RobotFalcon variables | (Intercept) | 0.022 | 0.016 | 0.027 | 4079 | 7.390 | NA | 0 |
| | futatt | 0.005 | 0.001 | 0.010 | 4079 | 2.282 | 0.071 | 0.023 |
| | small.bigs | -0.014 | -0.022 | -0.006 | 33 | -3.675 | -1.279 | 0.001 |
| | binary.closestTRUE | 0.004 | -0.003 | 0.012 | 4079 | 1.128 | 0.035 | 0.259 |
| | align | 0.121 | 0.069 | 0.173 | 4079 | 4.575 | 0.143 | 0 |
| | turn2falchead | -0.013 | -0.015 | -0.011 | 4079 | -14.018 | -0.439 | 0 |
| | turn2falcpos | 0.009 | 0.008 | 0.010 | 4079 | 16.712 | 0.523 | 0 |
| | cross.wind | 0.001 | 0.000 | 0.002 | 4079 | 2.061 | 0.065 | 0.039 |
| | turn2home | 0.008 | 0.006 | 0.010 | 4079 | 8.077 | 0.253 | 0 |
| | futatt:small.bigs | 0.022 | 0.016 | 0.027 | 4079 | 7.390 | NA | 0 |
| | small.bigs:align | 0.005 | 0.001 | 0.010 | 4079 | 2.282 | 0.071 | 0.023 |
| | futatt:binary.closestTRUE | -0.013 | -0.023 | -0.003 | 4079 | -2.556 | -0.080 | 0.011 |
| | small.bigs:binary.closestTRUE | -0.005 | -0.015 | 0.006 | 4079 | -0.918 | -0.029 | 0.359 |
| | small.bigs:align | -0.040 | -0.100 | 0.019 | 4079 | -1.323 | -0.041 | 0.186 |
| | binary.closestTRUE:align | -0.043 | -0.106 | 0.021 | 4079 | -1.323 | -0.041 | 0.186 |
| | futatt:small.bigs:binary.closestTRUE | 0.005 | -0.008 | 0.018 | 4079 | 0.738 | 0.023 | 0.461 |
| | small.bigs:binary.closestTRUE:align | 0.079 | -0.001 | 0.158 | 4079 | 1.941 | 0.061 | 0 |
| Speed Variance | (Intercept) | 1.675 | 1.497 | 1.852 | 432 | 18.548 | NA | 0 |
| | conditionp | -0.115 | -0.272 | 0.042 | 36 | -1.486 | -0.495 | 0.146 |
| | small.bigs | 0.195 | -0.13 | 0.519 | 3 | 1.911 | 2.207 | 0.152 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | abs(cross.wind) | 0.002 | -0.011 | 0.015 | 432 | 0.266 | 0.026 | 0.791 |
| | support.wind | -0.008 | -0.016 | 0 | 432 | -1.946 | -0.187 | 0.052 |
| | conditionp:small.bigs | -0.049 | -0.23 | 0.131 | 36 | -0.556 | -0.185 | 0.582 |
| Centripetal acceleration | (Intercept) | 0.959 | 0.948 | 0.97 | 16556 | 174.414 | NA | 0 |
| | conditionp | 0.007 | -0.002 | 0.016 | 558 | 1.507 | 0.128 | 0.132 |
| | small.bigs | -0.041 | -0.063 | -0.019 | 3 | -5.851 | -6.756 | 0.01 |
| | abs(cross.wind) | 0.007 | 0.005 | 0.008 | 16556 | 9.148 | 0.142 | 0 |
| | support.wind | 0 | -0.001 | 0.001 | 16556 | -0.685 | -0.011 | 0.493 |
| | conditionp:small.bigs | 0.046 | 0.033 | 0.06 | 558 | 6.676 | 0.565 | 0 |
| Speed | (Intercept) | 18.153 | 17.504 | 18.802 | 3145 | 54.847 | NA | 0 |
| | conditionp | -0.493 | -1.014 | 0.027 | 512 | -1.862 | -0.165 | 0.063 |
| | small.bigs | 0.286 | -1.01 | 1.583 | 3 | 0.703 | 0.812 | 0.533 |
| | abs(cross.wind) | 0.164 | 0.082 | 0.246 | 3145 | 3.906 | 0.139 | 0 |
| | support.wind | -0.173 | -0.226 | -0.121 | 3145 | -6.455 | -0.23 | 0 |
| | conditionp:small.bigs | -1.518 | -2.265 | -0.771 | 512 | -3.993 | -0.353 | 0 |
| Distance to centroid | (Intercept) | 1.241 | 1.041 | 1.442 | 2815 | 12.135 | NA | 0 |
| | insta.grp.size | -0.008 | -0.014 | -0.002 | 2815 | -2.777 | -0.105 | 0.006 |
| | conditionp | 0.057 | -0.038 | 0.153 | 576 | 1.177 | 0.098 | 0.24 |
| | abs(cross.wind) | 0 | -0.01 | 0.01 | 2815 | 0.072 | 0.003 | 0.943 |
| | support.wind | 0.003 | -0.003 | 0.009 | 2815 | 1.021 | 0.039 | 0.307 |
| | insta.grp.size:conditionp | -0.004 | -0.008 | 0.001 | 2815 | -1.55 | -0.058 | 0.121 |
| Nearest neighbour distance | (Intercept) | 0.657 | 0.59 | 0.725 | 2954 | 19.128 | NA | 0 |
| | insta.grp.size | 0.008 | 0.005 | 0.012 | 2954 | 4.698 | 0.173 | 0 |
| | conditionp | -0.078 | -0.14 | -0.016 | 572 | -2.452 | -0.205 | 0.014 |
| | abs(cross.wind) | -0.004 | -0.011 | 0.003 | 2954 | -1.131 | -0.042 | 0.258 |
| | support.wind | -0.003 | -0.008 | 0.001 | 2954 | -1.446 | -0.053 | 0.148 |
| | insta.grp.size:conditionp | 0.005 | 0.002 | 0.008 | 2954 | 3.401 | 0.125 | 0.001 |
| Proportion of time separated from group | (Intercept) | 0.21 | 0.15 | 0.27 | 591 | 6.881 | NA | 0 |
| | conditionp | 0.051 | -0.01 | 0.112 | 591 | 1.645 | 0.135 | 0.1 |
| | flock.sizes | -0.183 | -0.256 | -0.11 | 591 | -4.894 | -0.403 | 0 |
| | conditionp:flock.sizes | 0.053 | -0.04 | 0.145 | 591 | 1.123 | 0.092 | 0.262 |
| Conflict scenario outcome | (Intercept) | -1.826 | -2.219 | -1.432 | 3233 | -9.101 | NA | 0 |
| | log(dist2pred) | 0.377 | 0.291 | 0.462 | 3233 | 8.606 | 0.303 | 0 |
| | small.bigs | 0.661 | 0.093 | 1.228 | 363 | 2.287 | 0.24 | 0.023 |
| | log(dist2pred):small.bigs | -0.133 | -0.256 | -0.01 | 3233 | -2.118 | -0.074 | 0.034 |
| Fission/fusion “exclusion parameter” one second | (Intercept) | 1.774 | 0.766 | 2.782 | 257 | 3.443 | NA | 0.001 |
| | log(dist2pred) | -0.367 | -0.603 | -0.131 | 257 | -3.041 | -0.379 | 0.003 |
| | small.bigs | 1.757 | -0.91 | 4.425 | 19 | 1.37 | 0.629 | 0.187 |
| | log(dist2pred):small.bigs | -0.46 | -1.099 | 0.178 | 257 | -1.41 | -0.176 | 0.16 |
| Fission/fusion “exclusion parameter” two seconds | (Intercept) | 2.53 | 1.253 | 3.807 | 147 | 3.878 | NA | 0 |
| | log(dist2pred) | -0.505 | -0.798 | -0.211 | 147 | -3.362 | -0.555 | 0.001 |
| | small.bigs | 2.33 | -1.377 | 6.037 | 19 | 1.303 | 0.598 | 0.208 |
| | log(dist2pred):small.bigs | -0.568 | -1.423 | 0.287 | 147 | -1.301 | -0.215 | 0.195 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Fission/fusion “exclusion parameter” three seconds | (Intercept) | 4.541 | 2.515 | 6.568 | 101 | 4.387 | NA | 0 |
| | log(dist2pred) | -0.96 | -1.417 | -0.503 | 101 | -4.108 | -0.818 | 0 |
| | small.bigs | 0.267 | -4.034 | 4.568 | 17 | 0.129 | 0.063 | 0.899 |
| | log(dist2pred):small.bigs | -0.054 | -1.016 | 0.908 | 101 | -0.11 | -0.022 | 0.913 |

**Table S1. Model output. Related to Figure 2.**

The dependent variable, turning angles, here are turn rate per time step, not per second (= turn rate per timestep x 5), as is reported in Figure 2. Dependent variable, and brief description of data treatment, are listed in the furthest left column. The next column describes independent variables: “conditionp” is “predator” treatment; “futatt” is centroid attraction (to the future predicted centroid); “align” is alignment; “dist2cent” is distance to centroid; “dist2pred” is distance to the RobotFalcon; “cross.wind” and “support.wind” are cross- and support-wind components respectively; “turn2home” is the angle from focal individual’s current orientation to home; “turn2falchead” and “turn2falcpos” are angles between focal individual’s current orientation and RobotFalcon’s orientation and position respectively; “small.bigs” is small flocks “small.bigb” is large flocks; “flock.size” is the number of individuals in the largest cohesive part of the flock. Colons “:” represent interactions between independent variables. Other columns provide slope estimate, 2.5% confidence interval, 97.5% confidence interval, degrees of freedom, *T*-value, Cohen’s D, and *p*-value (two-tailed) respectively. All numbers are rounded to three decimal places.