Animal Behaviour xxx (xxxx) xxx

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Personality composition affects group cohesion of homing pigeons in response to novelty and predation threat

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ARTICLE INFO

Article history:
Received 1 October 2024
Initial acceptance 31 October 2024
Final acceptance 10 December 2024
Available online xxx
MS. number: 24-00609R

Keywords:
behavioural consistency
collective behaviour
collective escape
homing pigeon
personality
predation

Understanding how and why animal groups behave collectively is a central question in behavioural and social sciences. Variation in the phenotypic composition of the individuals within a group can lead to differences in group attributes and performance. However, whether and how individual personalities translate into group performance is not yet fully understood because experiments that test such hypotheses in realistic set-ups are still scarce. We explored how between-group variation in personality composition affected flock cohesion during homing flights of homing pigeons, *Columba livia*. Based on consistent individual differences, we established flocks of either 'more reactive' (MR flocks) or 'less reactive' (LR flocks) pigeons naïve to homing. Cohesion of flocks was tested in three distinct challenges: (1) first-ever collective homing experience (novelty); (2) release from a novel site (novel site homing); and (3) hunt by a robotic peregrine falcon (predation threat), with the latter two challenges performed with flocks trained for homing. MR flocks were more cohesive than LR flocks in the novelty challenge, but showed similar levels of cohesion during the novel site homing challenge. Predation threat decreased cohesion in both flock types, with a stronger effect in LR flocks. These results indicate that differences in the composition of personalities of group members can produce detectable differences in collective performance, and highlight the importance of accounting for individual-level behavioural variation when studying collective patterns in nature.

In social species, individuals within groups may exhibit phenotypic or genotypic differences that can potentially influence how the group performs. Differences in collective behaviours have been widely observed in the animal kingdom (e.g. in ant colonies: Bengston & Dornhaus, 2014; bird flocks: Carere et al., 2009; Papadopoulou et al., 2023; fish shoals: Jolles et al., 2018; Kareklas et al., 2018; honey bee colonies: Wray et al., 2011; beetles: Cook et al., 2022). Theoretical and empirical studies suggest that the phenotypic traits of group members significantly influence group formation and functioning (Farine et al., 2015; Killen et al., 2017; Martin et al., 2024; O'Shea-Weller et al., 2020; Sankey & Portugal, 2023). A fundamental question is whether the behavioural traits of individuals within a group, which also appear in social contexts such as collective behaviours, are linked to their responses to functional challenges as suggested by the 'behavioural type hypothesis' (Jolles et al., 2020; Laskowski & Bell, 2014).

Animal personality, defined as a systematic behavioural tendency of an individual that is consistent over time and across different situations and contexts (Wolf & Weissing, 2012), may constitute a major source of individual behavioural variation leading to group-level differences. For instance, groups composed of half shy and half bold guppies, *Poecilia reticulata*, were faster to explore a novel environment and to sample potential foraging sites than monotypic groups composed of shy or bold fish only (Dyer et al., 2009). In addition, it was shown that the personality trait of even a few key individuals within the shoal affected the overall group performance, with the most social members boosting the exploration activity of the entire group (Brown & Irving, 2014). In colonial ants, *Aphaenogaster senilis*, groups of highly exploratory

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https://doi.org/10.1016/j.anbehav.2025.123122

workers were more aggressive towards intruders, more efficient in collecting prey, faster in nest relocation and more prone to use tools than groups of less exploratory workers (Martin et al., 2024). Most of these studies have been carried out under controlled laboratory settings, as have studies on social arthropods (e.g. Carere et al., 2018; Martin et al., 2024; Modlmeier & Foitzik, 2011), fish (e.g. Brown & Irving, 2014; Cook et al., 2022; Dyer et al., 2009; Jolles et al., 2017) and primates (e.g. Koski & Burkart, 2015). To date, experimental studies are scarce, especially in natural settings and in highly mobile social species such as birds, with most studies focusing on social foraging (e.g. great tits, *Parus major*: Aplin et al., 2014) or exploring the link between personality and survival during predator attacks in group flights (e.g. homing pigeons, *Columba livia*: Santos et al., 2015). A recent study on homing pigeons by Sankey and Portugal (2023) showed that homogeneous flocks consisting solely of leader pigeons were faster, maintained a more compact formation and were more goal-oriented than flocks consisting only of follower birds. Given that boldness seems to predict leadership in homing pigeons (Sasaki et al., 2018), these results suggest that personality may influence collective movement, even though this aspect has not been specifically investigated. This is largely due to the technological complexity of accurately tracking individual behaviour within a group and of simulating realistic challenges that elicit functional collective responses.

Many bird species form flocks during specific phases of their life cycle, such as migration, the nonbreeding season, or while performing specific activities, like commuting flights between breeding/roost sites and foraging areas. As in other collective systems, during flocking many group properties emerge from local interactions between individuals (self-organization; e.g. Hildebrandt et al., 2010). These properties might provide some fitness advantage in several ecological contexts, such as predation or novel situations. Yet flocks may show variation in their response to different ecological challenges. One source of variability in flock responses is the extent of cohesiveness among flocking individuals during collective manoeuvres, which may have crucial fitness payoffs under aerial predation threat. For example, in the highly gregarious European starling, *Sturnus vulgaris*, when flocks show a high degree of cohesiveness and perform a variety of coordinated collective escape responses, they tend to deter attacks by peregrine falcons, *Falco peregrinus*, and reduce its success (e.g. Carere et al., 2009; Procaccini et al., 2011; Storms et al., 2019; Zoratto et al., 2010). When attacked by a robotic aerial predator, homing pigeons in flocks tended to remain in a mutualistic alignment condition, which is advantageous for successful collective escape responses and, at the same time, allows individuals to avoid accidental collisions while flying together; for example, during quick turns (Papadopoulou et al., 2022; Sankey et al., 2021).

Here, we asked how consistent individual differences in personality traits affect collective performance in a highly gregarious species, the homing pigeon, through an experimental set-up comparing the responses of flocks that were homogeneous in terms of personality types. Homing pigeons have been previously shown to display consistent individual personalities (e.g. Portugal et al., 2017; Santos et al., 2015). We characterized consistent individual personality traits and then we established experimental flocks composed either of more reactive (MR flocks) or less reactive (LR flocks) birds. By GPS-tracking flocking individuals, we tested whether MR and LR flocks vary in flock cohesion during homing flights upon exposure to three different functional challenges, namely: (1) their first-ever collective homing experience (novelty challenge); (2) when released from a novel site after a collective homing training period (novel site challenge); (3) when threatened by aerial attacks performed by a robotic predator mimicking a peregrine falcon, a common aerial predator that frequently targets pigeons (Storms et al., 2022, 2024), upon collective homing training (predation threat challenge).

It has been predicted and empirically shown, at least in social insects, that the average behavioural phenotype of a group reflects the behavioural phenotypes of its group members (Carere et al., 2018; Martin et al., 2024; Pinter-Wolman, 2012). Given our experimental set-up comparing homogeneous flocks with different personality composition, we expected that cohesion would differ between them. Specifically, assuming that achieving and maintaining cohesion is the primary goal for individuals facing a challenge, we expected higher cohesion in flocks consisting of MR individuals in both the novelty and the predation challenges, as these individuals should be faster in achieving and maintaining it.

METHODS

Study Site and Subjects

One hundred and fifty-five homing pigeons, hatched and bred at the Arnino Field Station (43°39′26″N, 10°18′14″E; home loft site) of the University of Pisa, Italy (Department of Biology), were used in the experiment. The experiments were performed during the period from 25 July to 30 August 2022. All experimental birds were naïve individuals (<1 year old) with no previous homing experience. The birds were housed in three lofts at the Arnino Field Station (each loft measuring 10 × 3.40 m and 2.60 m high) and were fed a mixture of grains supplemented with grit, which was provided ad libitum. The pigeons were allowed to perform spontaneous flights around the loft, usually moving <800 m from the loft (Gagliardo et al., 2007).

Individual Personality Assessment

Each bird was subjected to three behavioural tasks to define its personality traits: Flight Initiation Distance (FID), Escape Reaction Time (ERT) and Exploration Propensity (EXP). To assess the consistency of individual responses over time, we performed two replicas of each test. The second replica took place 1 week after the completion of the first one. The sequence of tests was randomized for each individual in each replica. The individual characterization of personality traits was performed from 30 May to 18 July 2022. Detailed descriptions of each test and the results of the analysis of the repeatability of individual behavioural responses to these tests are reported in the Appendix.

For each test of the first replica, individual responses were ranked based on their reactivity, assigning the lowest rank to the least reactive individual. An individual was considered more reactive if it took off at a greater distance from the experimenter in the FID test, took less time to escape from the wooden box in the ERT test and exhibited more extensive exploration in the maze during the EXP test. For each test, the ranks were then transformed into a three-level score based on the tertiles of the rank distribution. The first, the second and the third tertiles were scored as 0, 1 and 2, respectively. The scores of the three tests were then summed to obtain an Overall Personality Score (OPS). Subjects with OPS ≥ 4 were classified as ‘more reactive’ (MR pigeons, $N = 50$), provided that the FID score was greater than 0 (i.e. took off at greater distances from the experimenter). We included this condition because the FID test mirrors better than the other two the expected response of individuals to the predation threat challenge, a key component of our experimental procedure. Subjects with OPS ≤ 2

were classified as 'less reactive' (LR pigeons, $N = 56$), provided that the FID score was ≤ 1 (i.e. individuals seemed less intimidated by humans and took off only when the experimenter was close to them, at a distance of 1.10 m or less). In cases where these criteria were not fulfilled (i.e. intermediate individuals) the birds were excluded from subsequent homing trials ($N = 38$).

Experimental Set-Up

For the homing trials, we established flocks of four pigeons belonging to the same personality category (MR or LR). Overall, we could establish 11 MR flocks and 12 LR flocks. Birds were transported to the release site in crates containing 12 pigeons each (three flocks). At the release site, the crates were placed on the ground and covered with a white cloth to prevent the birds from observing their surroundings. Flocks were released from a box placed on the roof of a car. The box (66 × 24 cm and 44 cm high) was screened on all sides to prevent birds from viewing their surroundings. The box had a guillotine door (62 × 24 cm) and a movable wall on the other side of the door. Each flock was kept for 1 min inside the release box before being released. At release, one experimenter removed the guillotine door while another simultaneously pushed the opposite wall forward to force all pigeons to exit simultaneously. Both experimenters remained out of the pigeons' sight until they began their homing flight.

Each flock was first released six consecutive times from the same release site located south of the home loft (R1; 43°35′58.2″N, 10°18′46.4″E, direction and distance from home loft: 353°, 6.3 km; Fig. A1). These six releases took place on consecutive days (once or twice a day). After these releases, which were meant to consolidate collective homing behaviour, flocks were released from a novel release site (see Novel site homing challenge in Experimental challenges section). All releases were performed on sunny days with no or light wind.

Individual homing tracks were recorded by equipping individuals with GPS data loggers (1 Hz location sampling rate) shortly before the homing trials (Mobile Action I-gotU, https://www.mobileaction.com: mass 22 g; Technosmart Europe SRL, model Gypsy 6, https://www.technosmart.eu: mass 12.9 g). For each release, we used only data loggers of the same type. Birds were equipped with a dummy GPS logger (similar in size and mass to I-gotU loggers) 1 week before beginning the homing trials, to accustom them to flying with an additional mass. Loggers (both dummy and real ones) were attached on the pigeon's back using a Velcro strip (30 × 70 mm). One side of the strip was glued to trimmed feathers using a neoprene-based contact adhesive glue (BOSTIK S.p.A, https://www.uhubostik.it), while the opposite side was affixed to the bottom part of the logger, following attachment procedures described in Biro et al. (2002). This method allowed for an easy and quick removal of the loggers from the birds once they had returned to the loft. The mass of the heavier logger used (I-gotU) was on average 5.6% (± 0.5 SD) of a pigeon's body mass (range 309.6−476.7 g).

Experimental Challenges

Novelty challenge

At the initial release of a newly established flock, each individual was exposed to a novel condition, as it had never previously performed a homing flight from a location far from the loft, either alone or with the other individuals. Hence, this initial release was considered a 'novelty challenge' to which flocks with different personality compositions were exposed, similar to the widely used 'open field' paradigm in animal personality research (e.g. Carere et al., 2005; Perals et al., 2017).

Novel site homing challenge

Upon consolidating flock behaviour by repeated homing flights from site R1 (up to 11 releases per flock, median = 11, min = 5; including also the predator threat flight; see Predation threat challenge, below), flocks were released from a different site, thereby constituting a second novelty challenge. Each flock was randomly released from one of two novel sites (Fig. A1). Specifically, four MR and four LR flocks were released from site R2 (43°43′40.8″N, 10°21′22.9″E, direction and distance from home loft: 209° and 9.0 km, respectively), while six MR and five LR flocks were released from site R3 (43°38″29.0″N, 10°27′39.2″E, direction and distance from home loft: 278°, 12.7 km).

Predation threat challenge

After completing six consecutive releases, each flock was subjected to an additional homing trial from R1, during which a robotic falcon (RobotFalcon) was flying over the release site. The RobotFalcon has fixed wings and mimics the size, shape and coloration of the peregrine falcon, with a wingspan of 70 cm and a flying weight of 250 g (Fig. A2). It is radio controlled and highly manoeuvrable, allowing it to be piloted from the ground to effectively chase bird flocks by imitating the hunting behaviour of a real falcon. More details on the RobotFalcon, which has been shown to be efficient in eliciting competent collective escape responses among flocks of several wild bird species, are described in Storms et al. (2022, 2024). A certified operator (R.M.) steered the RobotFalcon on sight to target flocks. It was launched a few minutes before the release of the pigeons and it was left hovering around the release site (<100 m) at a height of 30−40 m above ground level. The pigeons could not see the RobotFalcon before their release because they were inside the release box with screened view (see Experimental set-up, above). The flock was released when the falcon was around 30 m behind the box and moving in its direction. As soon as the flock was released, it was attacked by the RobotFalcon from above. Hence, all flocks were exposed to the RobotFalcon at the release site and, depending on their flight speed upon departure, some were actively pursued by the RobotFalcon (within a radius of 200 m from the release site).

Data Analysis

Assessing flock cohesion

Flock cohesion was assessed only for flocks with complete GPS recording for all four birds until at least one pigeon entered a 100 m buffer around the home loft. For each flock in each homing trial, the number of GPS locations used for assessing cohesion was the number of data points of the track of the bird that homed first. A cohesion index was computed for each homing trial as follows. The distance of each pigeon from all the others in the group was computed for each sampling step. If the distance between two individuals was equal to or higher than 500 m, we set a cutoff value of 500 m. These distances were summed, and this sum was divided by the sum of the theoretical maximum distances if the pigeons were flying alone (3000 m; i.e. all six pairwise distances were at the cutoff value of 500 m). The resulting value was then subtracted from 1. Therefore, the cohesion index varies from 0, when pigeons fly separately, to 1, when pigeons fly in group.

To examine potential differences in flock splitting between flock types, we measured the time elapsed since a flock's release (TR) and the distance to home (DH) when the first split occurred (if any). A split was defined as at least one pigeon leaving the flock, with a separation threshold of 20 m, based on a previous study that found an average distance of 24 m between two pigeons flying together (Biro et al., 2006). This analysis was performed using a custom script on R version 4.4.1 (R Core Team, 2024) implemented with functions of R package wildlifeDI version 0.5.1 (Long et al., 2014, 2022). To assess the effect of the threshold value, we performed the analysis also considering 40 m instead of 20 m, showing that no marked difference in the results was observed when using a higher distance threshold to identify a split event (see Appendix, Tables A1–A3). We considered two types of splits: (1) to stop and rest before completing the journey ('split-to-rest'); (2) to follow a different homing path from the rest of the flock ('split-to-fly'). In the novelty challenge we performed the analysis considering both types of split behaviour in order to detect potential biases due to stress or physical fatigue potentially affecting flight performances. In the other two challenges, we considered only 'split-to-fly' individuals, given that an individual showed 'split-to-rest' behaviour in only two cases (one for the novel site challenge and one for the predation threat challenge).

Furthermore, we analysed flock composition along the entire track, computing the number of locations at which the pigeons were flying in two main conditions: (1) No Flock (i.e. all pigeons were distant from each other); (2) Flock (i.e. at least two pigeons flew together). Within the Flock condition we distinguished between Full Flock (all pigeons close together) and Partial Flock (one or two pigeons separated from the flock, with the remaining pigeons flying together). The group composition (which pigeons were flying together and which were flying as singletons) at each second was evaluated in the following way: for each location of each pigeon (focal individual), we measured its distance from the location of all other flock companions (individuals to compare) collected at the closest time to the location of the focal individual, within an interval of $\leq$10 s (median = 0 s). When an individual was more than 20 m away from all other group members, it was considered separated from the flock.

Statistical Analyses

For analysing cohesion responses to the novelty challenge and the novel site homing challenge in relation to flock type, we fitted a generalized linear model (GLM) with beta error distribution, with the cohesion index as the response variable and flock type (two-level factor: MR and LR) as predictor. The effect of flock type on the time since release (TR, log-transformed) and distance to home (DH) at the location of the first split was tested using linear models (LM). For the novelty challenge, the analyses were performed both including and excluding those groups containing 'split-to-rest' individuals. Flock cohesion of MR and LR flocks during the predation threat challenge was assessed using a generalized linear mixed model (GLMM) with beta error distribution. The cohesion index of each flock during the homing flight after exposure to the RobotFalcon (RobotFalcon flight) was compared to the cohesion index of the last available training release without predator exposure (control flight). Predictors included predator treatment (control versus RobotFalcon flight), flock type (MR versus LR) and their interaction as fixed effects, and flock identity as random intercept. Similar GLMMs were fitted to test the effect of the RobotFalcon on first flock split after release (TR and DH), using a negative binomial and a Gaussian distribution, respectively, and flock identity as random intercept.

Regarding the pattern of group composition along the entire track, for each challenge the proportion of locations in No Flock and Flock conditions for each track was compared between MR and LR groups by fitting a binomial GLMM. Moreover, the proportion of locations in Full and Partial Flock conditions for each track were compared between MR and LR flocks using a similar binomial GLMM. In both models on patterns of group composition, flock identity was included as an observation-level random effect to control for overdispersion (Harrison, 2015).

All analyses were performed using R version 4.4.1 (R Core Team, 2024). Models were fitted using the package glmmTMB 1.1.8 (Brooks et al., 2017) and model performance was tested using DHARMa 0.4.6 (Hartig, 2022) and performance 0.10.8 (Lüdecke et al., 2021). The significance of predictors was tested using a type II Wald χ^2 test available in the package car 3.1–2 (Fox & Weisberg, 2019). In cases of significance of the interaction term, a Tukey post hoc analysis was performed using the package emmeans 1.8.9 (Lenth, 2023). Effect plots were obtained using the package ggeffects 1.6.0 (Lüdecke, 2018). The sample size (number of flocks) of different analyses could vary because in some cases the GPS logger failed in recording the track of one or more pigeons in a flock. Given that the analyses were made at a group level, in these cases the flock had to be excluded from the analysis. Overall, four LR pigeons were lost during the consecutive homing flights from site R1 while no MR pigeon was lost during the experiments.

Ethical Note

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). Pigeons were bred in large aviaries at the Department of Biology of the University of Pisa, where they 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. Between the personality test phase and the homing trials phase, birds were free to fly around the home loft with dummy weights to get used to the additional weight of the GPS devices during homing flights.

RESULTS

Novelty Challenge

MR and LR flocks did not differ in their cohesion index considering all data from flocks performing all types of splitting ('split-to-rest' and 'split-to-fly'; Table A4). However, MR and LR flocks exhibited different behaviours during the first flock split event, with LR pigeons separating from the flock earlier and at greater distances from the loft compared to MR birds (Table A4). When considering only flocks with 'split-to-fly' individuals, MR flocks were significantly more cohesive than LR ones (cohesion index; Table 1, Figs. 1a and 2). Moreover, MR individuals separated from the flock at significantly closer distances to the home loft (DH;

Table 1
Generalized linear models of flock cohesion parameters in relation to flock type for the first ever collective homing flight of experimental pigeons (novelty challenge)

		$\beta \pm$ SE	z	P
Cohesion index	(Intercept)	0.77 ± 0.37		
	Flock type	−1.38 ± 0.52	−2.65	0.008
TR	(Intercept)	4.50 ± 0.15		
	Flock type	0.91 ± 0.21	4.20	<0.001
DH	(Intercept)	5.99 ± 0.29		
	Flock type	−1.68 ± 0.41	−4.10	<0.001

Flock type is expressed as MR (more reactive) or LR (less reactive). The parameters used to assess flock cohesion are: cohesion index, TR (time since release when the first pigeon(s) separates from the flock) and DH (distance from home when the first pigeon(s) separates from the flock). The models included only data for the flocks that performed a 'split-to-fly' type of splitting. Model coefficients ($\beta \pm$ SE) and relative significance are reported. Sample size: LR = 6, MR = 6.

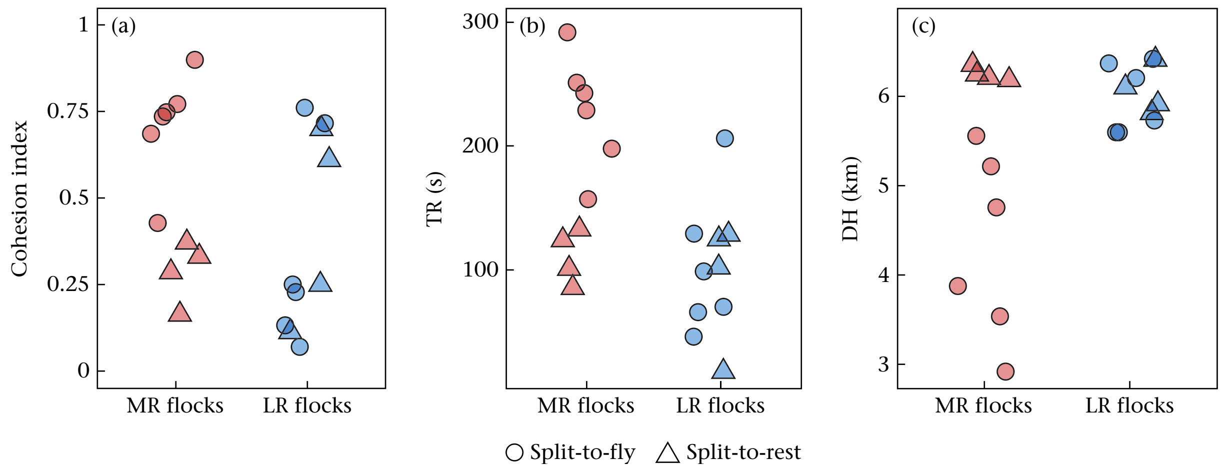

Figure 1. Flock cohesion in the 'novelty challenge': (a) cohesion index, (b) time since release (TR) when the first pigeon(s) separates from the flock and (c) distance from home (DH) when the first pigeon(s) separates from the flock, estimated for the first release for MR and LR flocks. Different symbols indicate the two conditions that led to the split of the first pigeon(s) from the flock: "split-to-fly" as circles and '"split-to-rest"' as triangles.

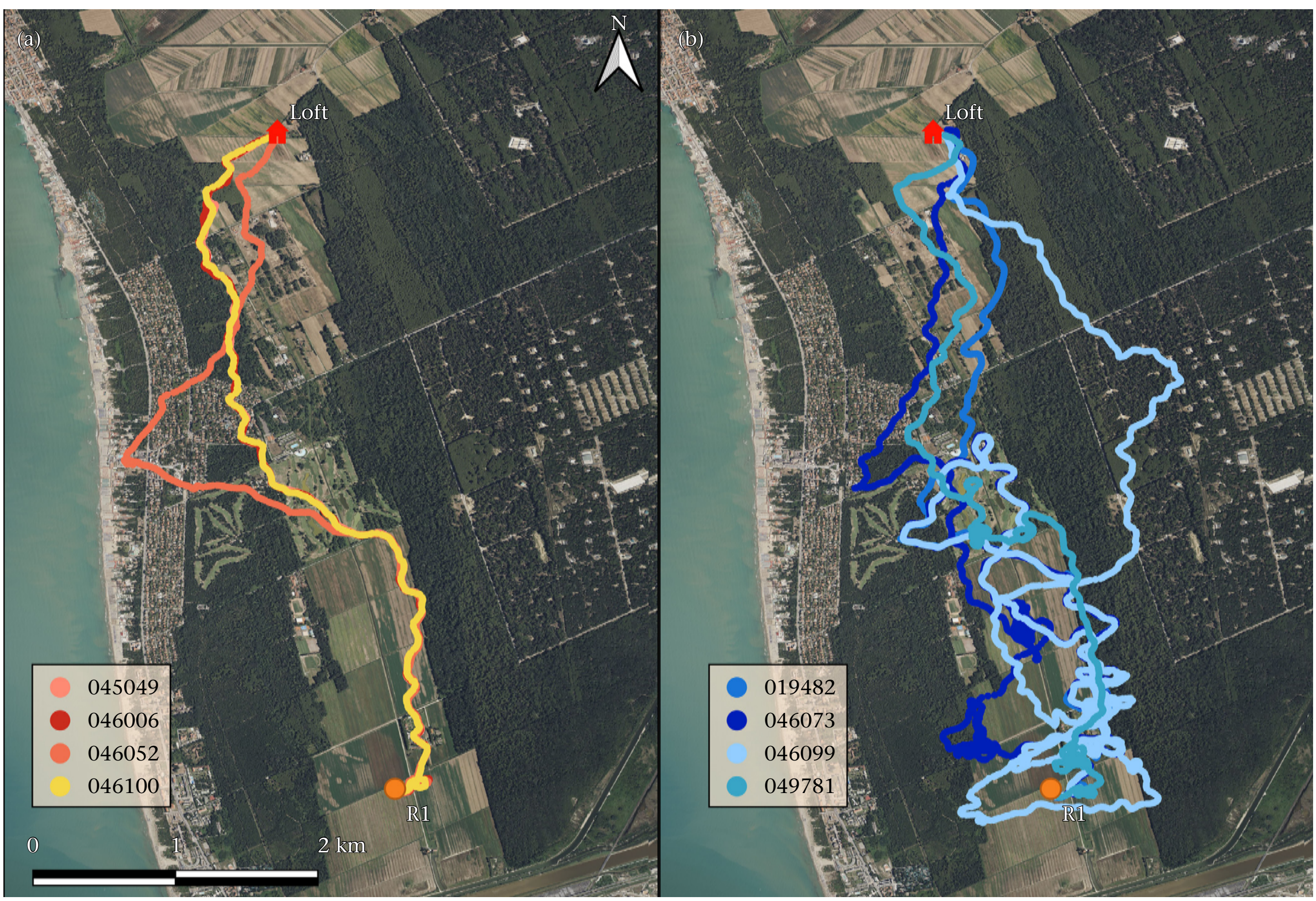

Figure 2. Examples of the first homing routes with pigeons released as a flock (novelty challenge) for one (a) more reactive (MR) flock and one (b) less reactive (LR) flock. Each flock was composed of four pigeons. The red house and orange dot are the location of the pigeons' loft and R1 release site, respectively. In panel (a) the yellow route of one pigeon overlaps with two other routes because the three pigeons were flying together.

Table 1, Fig. 1c) and remained together for a longer time than LR individuals (TR; Table 1, Fig. 1b). When considering the subsequent five training homing trials, LR flocks progressively increased flock cohesion and reached the same cohesion level of MR flocks (analysis reported in the Appendix).

Considering the composition of the flocks during the first homing flight, no significant difference in the proportion of time spent in No Flock or Full Flock conditions was found between LR and MR flocks (binomial GLMM, $\beta \pm SE$: -2.70 ± 1.53, $z = -1.75$, $P = 0.08$ and 0.67 ± 0.59, $z = 1.13$, $P = 0.25$).

Please cite this article in press as: Cerritelli, G., et al., Personality composition affects group cohesion of homing pigeons in response to novelty and predation threat, Animal Behaviour (2025), https://doi.org/10.1016/j.anbehav.2025.123122

Table 2
Generalized linear models of flock cohesion parameters in relation to flock type for the novel site homing challenge

		β ± SE	z	*P*
Cohesion index	(Intercept)	0.12 ± 0.45		
	Flock type	0.24 ± 0.61	0.39	0.69
TR	(Intercept)	5.23 ± 0.38		
	Flock type	−0.14 ± 0.54	−0.25	0.8
DH	(Intercept)	7.60 ± 1.10		
	Flock type	3.10 ± 1.62	1.91	0.05

Flock type is expressed as MR (more reactive) or LR (less reactive). The parameters used to assess flock cohesion are: cohesion index, TR (time since release when the first pigeon(s) separates from the flock) and DH (distance from home when the first pigeon(s) separates from the flock). In the models were included only data for the flocks that performed a 'split-to-fly' type of splitting. Model coefficients (β ± SE) and relative significance are reported. Sample size: LR = 7, MR = 6.

Novel Site Homing Challenge

No significant difference between flock types was detected for the cohesion index and TR (time since release when the first pigeon split from the flock; Table 2). However, MR pigeons tended to split from the group at longer distances from the loft than LR pigeons (Table 2). The proportion of time spent in No Flock or Full Flock conditions did not significantly differ between LR and MR flocks (respectively, binomial GLMM, β ± SE: 1.54 ± 2.51, z = 0.61, *P* = 0.54 and −0.23 ± 0.92, z = −0.26, *P* = 0.79.

Predation Threat Challenge

Exposure to the RobotFalcon significantly reduced cohesion compared to control flights, regardless of flock type (Table 3, Fig. 3a). Apart from one LR flock that remained compact, the pursue/attack of the RobotFalcon produced a rapid flock split shortly upon release in both flock types, with different pigeons (mostly one or two) homing separately from the other flock members. The time and the distance from home of the first split event were significantly affected by both flock type and RobotFalcon exposure (Table 3). For MR flocks, TR and DH did not vary significantly between the two tests (post hoc Tukey test, control versus RobotFalcon flight: TR, estimated marginal mean difference ± SE, 0.03 ± 0.3, *P* = 0.9; DH, −0.48 ± 0.60, *P* = 0.41; Fig. 3b and c). In contrast, LR flocks showed a significant reduction in TR and increase in DH after

Table 3
Generalized linear mixed models of flock cohesion parameters in relation to flock type for the predation threat challenge

		β ± SE	χ^2	*P*
Cohesion index	(Intercept)	1.11 ± 0.41		
	Predator treatment	−0.84 ± 0.32	15.56	<0.001
	Flock type	0.60 ± 0.62	0.63	0.42
	Predator treatment x Flock type	−0.28 ± 0.49	−0.31	0.58
	Random effects SD	0.91		
TR	(Intercept)	5.45 ± 0.21		
	Predator treatment	−1.46 ± 0.37	5.53	0.02
	Flock type	−0.85 ± 0.32	1.65	0.19
	Predator treatment x Flock type	1.43 ± 0.45	9.99	0.002
	Random effects SD	0.33		
DH	(Intercept)	3.63 ± 0.56		
	Predator treatment	2.70 ± 0.65	11.65	<0.001
	Flock type	1.70 ± 0.76	0.92	0.33
	Predator treatment x Flock type	−2.21 ± 0.88	6.24	0.01
	Random effects SD	0.77		

The effect of flock type (MR: more reactive; LR: less reactive), predator treatment (control or RobotFalcon flight) and their interaction on cohesion index, TR (time since release when the first pigeon(s) separates from the flock) and DH (distance from home when the first pigeon(s) separates from the flock) were included as fixed factors. Only data for the flocks that performed a 'split-to-fly' type of splitting were included in the models. Model coefficients (β ± SE) and significance predictor estimated with Wald II χ^2 test are reported (*df* = 1 in all tests). Number of observations = 26, Number of groups = 13.

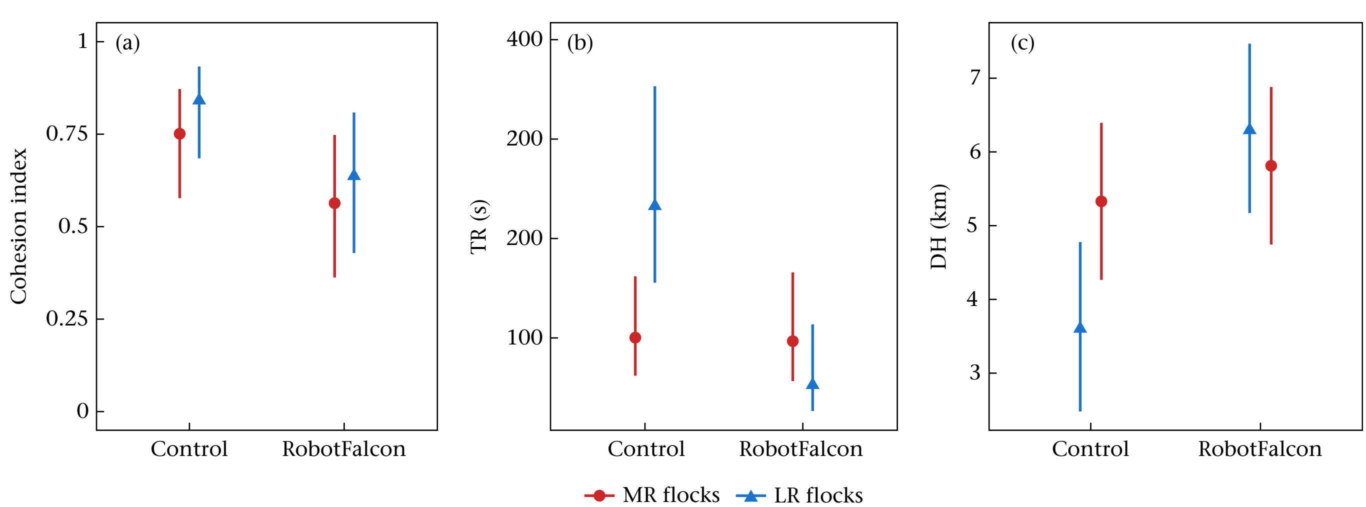

Figure 3. Plots of the effects (estimate ± 95% CI) of flock type (more reactive, MR, versus less reactive, LR) and predator treatment (Control versus RobotFalcon flight) on (a) cohesion index; (b) time since release (TR) when the first pigeon(s) separates from the flock and (c) distance from home (DH) when the first pigeon(s) separates from the flock. Number of MR flocks = 7; Number of LR flocks = 6.

Please cite this article in press as: Cerritelli, G., et al., Personality composition affects group cohesion of homing pigeons in response to novelty and predation threat, Animal Behaviour (2025), https://doi.org/10.1016/j.anbehav.2025.123122

the exposure to the RobotFalcon (TR, 1.49 ± 0.37, $P < 0.001$; DH, −2.69 ± 0.65, $P < 0.001$; Fig. 3b and c). As for the previous homing challenges, also in this case no significant differences between LR and MR flocks were found in the composition of the flocks along the whole homing flight (No Flock condition, binomial GLMM, β ± SE: 3.57 ± 1.91, z = 1.87, $P = 0.06$; Full Flock condition: −0.42 ± 0.80, z = −0.52, $P = 0.60$).

DISCUSSION

The aim of this study was to assess whether individual personality traits played a role in the flock cohesion of homing pigeons while facing different challenges, namely the first homing experience, the release at a novel site after gaining homing experience and the exposure to predation threat. We found evidence that homogeneous personality composition of flocks affected group cohesion in two out of the three challenges the flocks faced. Specifically, during the first homing experience, MR flocks were more cohesive than LR flocks, while under predation threat LR flocks exhibited less cohesion compared to MR flocks.

Investigations into the collective behaviour of social species have increasingly focused on the role of individual personality in shaping group-level responses, including both theoretical and empirical approaches (e.g. Pinter-Wollmann, 2012; Sankey & Portugal, 2023; see also references in the introduction, above). However, these findings have often provided unclear or contradictory results. Some studies provided clear evidence of a direct effect of individual personality (e.g. Carere et al., 2018; Laskowski & Bell, 2014; Martin et al., 2024), while others suggested that individual differences are buffered within social contexts (e.g. McDonald et al., 2016; Rands & Ioannou, 2023). For homing pigeons, most of the studies on collective movements have focused on flight hierarchies and the position of individuals within their flock during the homing flights, revealing that boldness is a predictor of leadership (Sasaki et al., 2018). This finding, combined with the observation that groups composed entirely of leaders performed better in homing tasks, suggested a possible relationship between personality traits and collective movements (Sankey & Portugal, 2023). Our study confirms that personality plays a role in collective behaviours performed by homing pigeons, since homogeneous flocks that differed in personality composition clearly showed different cohesion levels in response to realistic functional challenges.

Response to Novelties

During their first ever collective homing experience, pigeons in LR flocks were more likely to split from the group and follow their own individual homing route, while MR flocks exhibited higher cohesion. The cohesive behaviour of MR flocks likely facilitated close flying among companions, whereas LR pigeons were more prone to lose contact with the other group members, remaining alone. However, after several training homing flights, both MR and LR flocks displayed comparable cohesion levels (see Appendix), suggesting that the LR pigeons progressively learned to stay with the group during repeated releases from the same site.

The tendency of LR pigeons to become isolated during their first homing experience could be due to impaired synchronization of the group's movements. This is supported by the timing and distance from home at which the first split occurred: LR flocks split significantly earlier and at greater distances from home than MR flocks during the first homing flight. Taken together, these findings suggest that the separation of a pigeon from its flock might be due to different reasons: LR birds may experience a passive separation from the flock, while MR pigeons that split may do so by intentionally choosing an individual route after a prolonged group flight. Given that boldness is a predictor of leadership (Sasaki et al., 2018), this idea is corroborated by the finding that leaders were the individuals showing higher route fidelity when flying alone (Freeman et al., 2010).

Our results partly align with previous observations of homing behaviour in pigeon groups consisting exclusively of leaders or followers, extensively trained to home from a specific release site (Sankey & Portugal, 2023). Specifically, groups of leaders were found to fly in more compact flock formations and were more goal oriented than followers-only flocks. The different cohesion of MR and LR flocks during the first release was probably due to novelty of group composition rather than the novel release site per se. When the same flocks, after gaining repeated homing experience from the same release site, were displaced to a new site, they displayed a comparable level of cohesion regardless of personality composition.

Response to Predation

The exposure to the RobotFalcon at the release site had a clear, disruptive effect on flock cohesion, regardless of personality composition. The collective reaction to the attack of the RobotFalcon, consistent with what was previously observed (Sankey et al., 2021), suggested that the pigeons recognized the artificial model as a real predator. Also, a recent computational study on pigeons showed that, under predation attack, early splits can emerge alongside collective turns from similar individual behaviour depending on the specifics of information transfer through the group (Papadopoulou et al., 2022). It is worth noting that, when considering the whole of the individual tracks during homing, the exposure to an initial predator attack diminished overall cohesion, but in no case was a complete fragmentation of the group observed (i.e. four pigeons flying home individually). The finding that the reduction in time to the first split was less pronounced in MR flocks than in LR flocks suggests that the former flock type might be less vulnerable to predation. In the only study relating actual predation to personality in homing pigeons, individuals that were more tolerant to humans in a FID test were those more likely to be predated by raptors during homing flights, and the same pattern emerged with pigeons that were slower to escape from a confined environment (Santos et al., 2015).

Conclusion

Our study suggests a link between individual personality and collective responses in pigeon flocks, supporting the ‘behavioural type hypothesis’. Specifically, the collective response of a group may be predicted by the personality types of its members, particularly in novel contexts, where individual personalities are most likely to emerge, as well as in antipredator contexts. Overall, these results have important implications for future empirical studies and theoretical models of social/collective behaviour. In particular, our findings could be useful for predicting the most efficient features to elicit collective escape responses in a flock, such as splitting and merging events. The fact that these behavioural decisions can be personality dependent adds an important layer of variation and complexity that should be considered in future models. A future area of exploration would be to test group performance under varying degrees of homogeneity by assembling flocks with heterogeneous personality compositions; this was unfeasible in our case given the limited availability of experimental individuals. Finally, it would be highly relevant to investigate the level of within-group variability of individual personality in spontaneously formed flocks and test their performance. A final line of investigation, also with practical implications in the applied use of the RobotFalcon, should be to test the habituation rate of the exposed flocks given the common conflicts pigeons and other species of birds create in urban areas.

Please cite this article in press as: Cerritelli, G., et al., Personality composition affects group cohesion of homing pigeons in response to novelty and predation threat, Animal Behaviour (2025), https://doi.org/10.1016/j.anbehav.2025.123122

Author Contributions

Claudio Carere: Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Conceptualization. **Giulia Cerritelli:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Anna Gagliardo:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Dimitri Giunchi:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Robert Musters:** Writing – review & editing, Methodology, Investigation. **Diego Rubolini:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Lorenzo Vanni:** Writing – review & editing, Methodology, Investigation. **Irene Vertua:** Writing – review & editing, Methodology.

Data Availability

The data set and R code used for the analyses are available via the following link: http://datadryad.org/stash/share/KlX_Xmoy-uSUeh9_SzfAWBvosxgd9mKpXyRplFiEXdA.

Declaration of Interest

The authors have no competing interests.

Acknowledgments

Funding was provided by the Italian Ministry of University and Research under the funding programme PRIN2020 (grant no. 2020H5JWBH, awarded to C.C., D.R. and D.G.). S. Benedetti, B. Bianchi, S. A. Cafiero, S. Cioccarelli, J. M. L. Goyet, A. Guidi, R. Mencacci and E. Pollonara are acknowledged for the logistical help during releases of homing pigeons and at the Arnino field station. V. Jennings is acknowledged for her help in developing one of the custom functions used in the analysis. M. Papadopoulou is acknowledged for her feedback on a previous version of the manuscript and for her assistance with English proofreading. We also thank two anonymous referees for their constructive comments, which helped improve the final version of this paper.

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Appendix

Descriptions of Personality Tests

Flight initiation distance (FID)

A cardboard box (size: 40 × 40 cm and 40 cm high) was placed over the bird, on top of a table (70 cm high). After 1 min, the box was raised and an experimenter started to walk at constant speed towards the bird from a starting distance of 2.50 m. The distance between the experimenter and the pigeon at which the bird flew away (fled) was measured. The experimenter was different at each repetition of the test. Reactive birds flew at greater distances from the experimenter, while less reactive birds waited until the experimenter got closer to them.

Escape reaction time (ERT)

The bird was placed in a wooden box (size: 40 × 40 cm and 40 cm high) that had a sliding opening on top. The box was placed on top of a table (120 cm high), positioned far from buildings so that no landmarks were visible from inside the box when opened. After 1 min of acclimatization, the top of the box was opened and the time taken by the pigeon to escape was recorded. If after 15 min the pigeon did not fly out of the box, the test ended, and the bird was released by the experimenter. Less reactive pigeons tended to remain for more time inside the box before escaping than more reactive pigeons, or did not escape at all before the end of the test.

Exploration propensity (EXP)

Each pigeon was tested in a wooden eight-arm radial maze. Each corridor of the radial maze was 71 cm long and 17 cm wide. The walls of each corridor were 32 cm high. The maze was placed in a room void of objects and with homogeneous walls. Before the beginning of the test, each bird was placed at the end of one arm (the starting point), and prevented from walking around by the presence of a removable screen placed 34 cm from the terminal wall. After 1 min, the screen was removed so that the pigeon was free to explore the maze. All tests were video recorded (Hyundai camera, model HYU-761). We assigned scores to represent the level of maze exploration. For each arm of the maze, birds received a score of 0 if they did not enter the arm, 1 if they explored half of the arm and 2 if they explored more than half of the arm. The total score for each bird was the sum of the scores from all arms, ranging from 0 (if the bird stayed at the starting point) to 16 (if all arms were fully explored). The test duration was 10 min. More reactive individuals showed a higher propensity to explore the maze compared to less reactive birds.

Repeatability of the behavioural response to personality tests

Overall, 145 pigeons were exposed twice to all tests (FID, ERT, EXP) to assess behavioural consistency to personality tests. We were unable to assess the repeatability of the response of 13 individuals in the EXP test due to technical issues with video recordings. The repeatability of the response of the birds to the first and second replicas of each test was assessed using mixed effect models through R 4.4.1 and the package rptR 0.9.22 (Stoffel et al., 2017) with 1000 bootstraps. The repeatability was adjusted taking into account the level of experience of tested birds, which could affect the response. The level of experience was thus included in the model as independent variable and bird identity as random intercept. The dependent variables 'time to escape' for the ERT and 'fled distance' for the FID were included as log and cubic exponentially transformed variables, respectively. Model assumptions were checked using the package DHARMa 0.4.6 (Hartig, 2022) and the significance of repeatability was tested using a likelihood ratio test (LRT; Stoffel et al., 2017).

Individual responses were significantly consistent across the first and second replicas of each test (LRT; ERT: $N = 145$, repeatability ± SE = 0.75 ± 0.04, 95% CI = 0.67–0.81, $P < 0.001$; FID: $N = 143$, repeatability = 0.43 ± 0.07, 95% CI = 0.29–0.55, $P < 0.001$; EXP: $N = 107$, repeatability = 0.29 ± 0.09, 95% CI = 0.11–0.45, $P < 0.001$).

Analysis Using a Different Distance Threshold to Evaluate Split Events

In order to evaluate whether a pigeon in the flock was flying together with its companions or not, we had to choose a distance threshold; that is, the minimum interindividual distance at which a pigeon would be considered separated from the flock. From literature (Biro et al., 2006) the average distance of two pigeons flying together is 24 m (SD ± 14 m, $N = 35$). Therefore, we analysed the data using a distance threshold of 20 m. However, to explore the effect of the choice of the threshold on our results, we also conducted the analysis considering a 40 m threshold. The results obtained with the two thresholds were mostly comparable, with a few exceptions. The Results section reports results using the 20 m threshold, while below are reported the results for the 40 m threshold.

Novelty challenge

Even considering a higher distance threshold, the main outcomes did not change when considering the performances of the two groups in the novelty challenge. More reactive (MR) and less reactive (LR) flocks still showed different behaviour in terms of when the flock split the first time, with LR flocks splitting sooner after being released and at longer distances from the home loft when compared to MR flocks (Table A1). Regarding flock composition, MR pigeons spent a smaller proportion of time in a No Flock condition than LR pigeons (binomial GLMM $\beta \pm$ SE: −6.58 ± 2.98, z = −2.21, $P = 0.03$), while no difference was found in the proportion of time spent in the Full Flock condition (binomial GLMM: 1.13 ± 0.67, z = 1.69, $P = 0.09$).

Novel site homing challenge

The change of distance threshold used to evaluate the split event did not highlight any difference between groups on the distance from home at which the first split occurred from that observed in the analysis using a 20 m threshold (Tables 2, A2). Apart this difference in the two analyses, they produced similar results also when considering the flock composition. No significant differences between MR and LR groups were found in time spent in a particular flock composition, neither considering a No Flock condition (binomial GLMM $\beta \pm$ SE: 1.36 ± 3.84, z = 0.35, $P = 0.72$) nor a Full Flock condition (binomial GLMM: −0.01 ± 1.26, z = −0.01, $P = 0.99$).

Predation threat challenge

The only significant effect on TR (time since release when the first pigeon(s) separates from the flock) was the presence/absence of the RobotFalcon (predation treatment). Neither the flock type nor the interaction between predation treatment * flock type significantly affected the TR (Table A3), as was observed in the model using a distance threshold of 20 m (Table 3). When considering the model on DH (distance from home when the first pigeon(s) separates from the flock) no factor tested significantly affected the DH except for predator treatment, as in the model using a distance threshold of 20 m (Table 3). Finally, no significant differences between MR and LR groups were found in time spent in a particular flock composition, either considering a No Flock condition (binomial GLMM $\beta \pm$ SE: 1.36 ± 2.86, z = 0.47, $P = 0.63$) or a Full Flock condition (binomial GLMM: −0.77 ± 1.03, z = −0.75, P = 0.45).

Analysis of Development of Flock Cohesion During Training Homing Flights

To assess how group cohesion evolved with experience, we compared the cohesion index among less reactive (LR) and more reactive (MR) pigeons by using a generalized linear mixed model with a beta error distribution, with personality (LR and MR), experience level (factor with 6 levels: exp1 to exp6) and their interaction as fixed factors, and group ID as random factor. Moreover, differences in personality in TR (time since release when the first pigeon(s) separate from the flock, log-transformed) and DH (distance from home when the first pigeon(s) separate from the flock) were tested with a linear mixed model with the same fixed and random effects as above. In cases where the interaction term was significant, a post hoc analysis was performed by testing the effect of personalities across successive training flights using linear and quadratic interaction contrasts. For this analysis, only groups for which the entire tracks of each of the four pigeons were available were considered. Groups comprising 'split-to-rest' pigeons were excluded. All models were fitted using the package glmmTMB 1.1.8 (Brooks et al., 2017) and model checking was carried out using the package DHARMa 0.4.6 (Hartig, 2022). The significance of predictors was tested using type II Wald χ^2 test available in car 3.1−2 package (Fox & Weisberg, 2019). Effect plots were obtained using the package ggeffects 1.6.0 (Lüdecke, 2018). Post hoc analyses were also carried out using the package emmeans 1.8.9 (Lenth, 2023). The statistical analysis on the cohesion index revealed a significant interaction between personality and experience level (Wald $\chi^2_5 = 18.11$, $P = 0.003$). While the LR pigeons showed a low cohesion index at the first release (exp1 in Fig. A3) and then their cohesion index tended to increase in subsequent releases, the MR pigeons tended to show a high cohesion index at the first release but did not show a significant trend across successive releases (linear trend contrast LS versus MR pigeons, estimate ± SE: 11.47 ± 4.04, $P = 0.004$; Fig. A3).

The distance from home at which the first pigeon(s) left the flock (DH) was not affected by experience level ($\chi^2_5 = 3.53$, $P = 0.62$), personality ($\chi^2_1 = 0.80$, $P = 0.37$) or their interaction ($\chi^2_5 = 8.77$, $P = 0.12$). However, the statistical analysis on TR revealed a significant interaction between personality and experience level ($\chi^2_5 = 12.25$, $P = 0.03$). The LR pigeons tended to split quite soon after their first release (exp1 in Fig. A4), increasing their TR across successive releases. Conversely, the MR pigeons remained a compact flock for a longer time after the first release (higher TR in exp1 than in LR pigeons), but then tended to decrease their TR in the following releases (linear trend contrast MR versus LR pigeons: −11.39 ± 4.32, $P = 0.01$; Fig. A4).

Figure A1. Location of the pigeons' loft (red symbol) and of the three release sites (orange dots). R1 was the main release site used in the present experiment, the flocks were repeatedly released from this site (novelty challenge and other five consecutive releases) and were exposed to the RobotFalcon also from this site (predation threat challenge). After completing the first two challenges, the flocks were then released from a new release site, R2 or R3 (novel site homing challenge). Each flock was assigned randomly to be released from one site or another.

Figure A2. Image of the RobotFalcon used in the experiment for the predation threat challenge. Photos: Robert Musters.

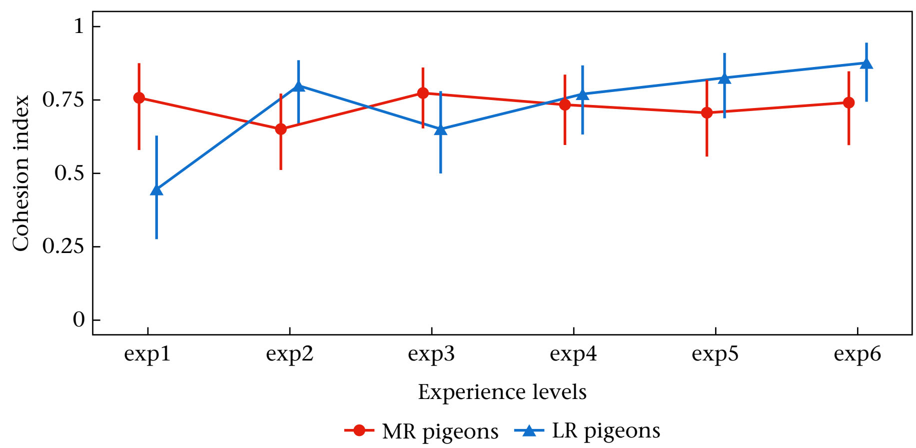

Figure A3. Plot of the effects (estimate ± CI 95%) of personality and experience level on group compactness expressed as cohesion index (values go from 0 to 1, indicating that the four pigeons flew home all independently or all together, respectively). Results of the GLMM with beta distribution, including personality (MR/LR), experience level (exp1– exp6) and their interaction as independent variable and group ID as random intercept. Number of observations = 88, Number of groups = 19.

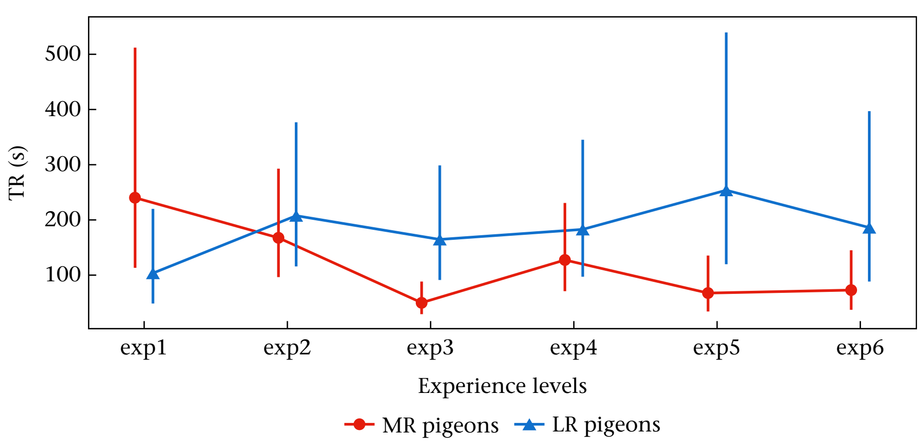

Figure A4. Plot of the effects (estimate ± CI95%) of personality and experience level on the time since release (TR) when the first pigeon(s) leaves the flock. Results of the GLMM with normal distribution, including personality (MR or LR), experience level (exp1–exp6) and their interaction as independent variable and group ID as random intercept. Number of observations = 73, Number of groups = 19.

Please cite this article in press as: Cerritelli, G., et al., Personality composition affects group cohesion of homing pigeons in response to novelty and predation threat, Animal Behaviour (2025), https://doi.org/10.1016/j.anbehav.2025.123122

Table A1
Generalized linear models of flock cohesion parameters in relation to flock type for the first ever collective homing flights of experimental pigeons (novelty challenge), when using a 40 m distance threshold

		β ± SE	*z*	*P*
TR	(Intercept)	4.71 ± 0.24		
	Flock type	0.94 ± 0.33	2.87	0.004
DH	(Intercept)	5.43 ± 0.52		
	Flock type	−2.01 ± 0.73	−2.74	0.006

Flock type is expressed as MR (more reactive) or LR (less reactive). The parameters used to assess flock cohesion are: cohesion index, TR (time since release when the first pigeon(s) separates from the flock) and DH (distance from home when the first pigeon(s) separates from the flock). The models included only data for the flocks that performed a 'split-to-fly' type of splitting. Model coefficients (β ± SE) and relative significance are reported. Sample size: LR = 6, MR = 6.

Table A2
Generalized linear models of flock cohesion parameters in relation to flock type for the novelty site homing challenge, when using a 40 m distance threshold

		β ± SE	z	*P*
TR	(Intercept)	5.31 ± 0.37		
	Flock type	−0.12 ± 0.55	−0.23	0.82
DH	(Intercept)	7.36 ± 1.47		
	Flock type	1.97 ± 2.17	0.91	0.36

Flock type is expressed as MR (more reactive) or LR (less reactive). The parameters used to assess flock cohesion are: cohesion Index, TR (time since release when the first pigeon(s) separates from the flock) and DH (distance from home when the first pigeon(s) separates from the flock). In the models were included only data for the flocks that performed a 'split-to-fly' type of splitting. Model coefficients (β ± SE) and relative significance are reported. Sample size: LR = 7, MR = 6.

Table A3
Generalized linear mixed models of flock cohesion parameters in relation to flock type for the predation threat challenge, when using a 40 m distance threshold

		β ± SE	χ^2	*P*
TR	(Intercept)	5.04 ± 0.31		
	Predator treatment	−1.03 ± 0.22	29.62	<0.001
	Flock type	−0.13 ± 0.42	0.0003	0.99
	Predator treatment x Flock type	0.47 ± 0.27	2.87	0.09
	Random effects SD	0.64		
DH	(Intercept)	4.85 ± 0.71		
	Predator treatment	1.40 ± 0.78	8.47	0.004
	Flock type	−0.68 ± 0.96	0.49	0.48
	Predator treatment x Flock type	−0.22 ± 1.05	0.04	0.83
	Random effects SD	0.77		

The effect of flock type (MR: more reactive; LR: less reactive), predator treatment (control or RobotFalcon flight) and their interaction on TR (time since release when the first pigeon(s) separates from the flock) and DH (distance from home when the first pigeon(s) separates from the flock) were included as fixed factors. In the models were included only data for the flocks that performed a 'split-to-fly' type of splitting. Model coefficients (β ± SE) and significance predictor estimated with Wald II χ^2 test are reported (*df* = 1 in all tests). Number of observations = 26, Number of groups = 13.

Table A4
Generalized linear models of flock cohesion parameters in relation to flock type for the first ever collective homing flights of experimental pigeons (novelty challenge)

		β ± SE	*z*	*P*
Cohesion index	(Intercept)	0.17 ± 0.29		
	MR vs LR	−0.65 ± 0.42	−1.53	0.12
TR	(Intercept)	4.42 ± 0.17		
	MR vs LR	0.70 ± 0.24	2.91	0.004
DH	(Intercept)	6.02 ± 0.28		
	MR vs LR	−0.93 ± 0.39	−2.39	0.02

Flock type is expressed as MR (more reactive) or LR (less reactive). The parameters used to assess flock cohesion are: cohesion index, TR (time since release when the first pigeon(s) separates from the flock) and DH (distance from home when the first pigeon(s) separates from the flock). The models included data from flocks performing all types of splitting ('split-to-rest' and 'split-to-fly'). Model coefficients (β ± SE) and relative significance are reported. Number of observations: LR = 10, MR = 10.