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Boldness traits, not dominance, predict exploratory flight range and homing behaviour in homing pigeons

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Research

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Group living has been proposed to yield benefits that enhance fitness above the level that would be achieved through living as solitary individuals. Dominance hierarchies occur commonly in these social assemblages, and result, by definition, in resources not being evenly distributed between group members. Determinants of rank within a dominance hierarchy can be associated with morphological characteristics, previous experience of the individual, or personality traits such as exploration tendencies. The purpose of this study was to investigate whether greater exploration and positive responses to novel objects in homing pigeons (*Columba livia*) measured under laboratory conditions were associated with (i) greater initial exploration of the local area around the home loft during spontaneous exploration flights (SEF), (ii) faster and more efficient homing flights when released from further afield, and (iii) whether the traits of greater exploration and more positive responses to novel objects were more likely to be exhibited by the more dominant individuals within the group. There was no relationship between laboratory-based novel object exploration and position within the dominance hierarchy. Pigeons that were neophobic under laboratory conditions did not explore the local area during SEF opportunities. When released from sites further from home, neophobic pigeons took longer routes to home compared to those birds that had not exhibited neophobic traits under laboratory conditions, and had spontaneously explored to a greater extent. The lack of exploration in the neophobic birds is likely to have resulted in the increased costs of homing following release: unfamiliarity with the landscape likely led to the greater distances travelled and less efficient routes taken. Birds that demonstrated a lack of neophobia were not the dominant individuals inside the loft, and thus would have less access to resources such as food and potentially mates. However, a lack of neophobia makes the subordinate position possible, because subordinate birds that incur high travel costs would become calorie restricted and lose condition. Our results address emerging questions linking individual variation in behaviour with energetics and fitness consequences.

This article is part of the themed issue 'Physiological determinants of social behaviour in animals'.

1. Introduction

Group living has been proposed to yield benefits that enhance fitness above the level that would be achieved through living as solitary individuals [1]. Such benefits can include reduced predation risk through enhanced vigilance and predator detection [2–4], energetic saving through positive aero- or

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hydro-dynamic interactions [5–7] and increased foraging efficiency [8–10]. Within single-species groups, individual differences in physiology, morphology and personality can lead to conflicts, and a common outcome of these can be the emergence of dominance hierarchies [11]. These dominance relationships are a frequently documented characteristic of group living, observed within a variety of animal taxa. A dominance hierarchy can confer benefits to all group members, by reducing incidences of agonistic interaction [12]. These reductions result from individuals within the group having evaluated their chances of winning or losing such conflicts with particular individuals [13]. By reducing the time and energy devoted to agonistic encounters, individually beneficial behaviours such as maintenance, vigilance, and foraging can be invested in more heavily [11]. The exact drivers that determine positioning within a dominance hierarchy have been traditionally assumed to include body mass and structural size (reviewed in [14]), but more recently, individual personality traits of group members have been demonstrated to affect dominance [15]. Accordingly, different personality traits may confer different benefits and costs, depending on how they interact with position within a dominance hierarchy.

Individual differences in personality can have profound implications for decision making by animal groups, particularly in unpredictable scenarios and environments. Boldness (defined as the tendency to take risks for potentially higher rewards) is one component of animal personality, and lies on what is typically referred to as the bold–shy continuum. Bolder individuals typically arrive at new resources first, are more aggressive, take more risks, learn more quickly and are generally more active [16]. However, by being bold, individuals can also put themselves at a higher risk of being predated upon, or sustaining injury during exploration [16]. To persist within natural populations, personality types must have an equal average pay-off [17], and the benefits of each are likely to become apparent under different environmental conditions and contexts [18]. In many species, bolder individuals are typically leaders, initiating successful movements and group decisions [19]. Neophobic behaviour, a component of the bold–shy continuum, can also be an integral determinant of leadership. A lack of neophobia has been shown to be associated with leadership in barnacle geese (*Branta leucopsis*), with bolder individuals exhibiting an influence over more neophobic flock mates, making them bolder and less neophobic [20]. Similarly, bolder fish (measured as a willingness to explore a novel arena) have been shown to increase overall activity levels within shoals, and sample novel foraging patches faster than shoals comprising shy individuals [21,22]. How personality traits such as boldness and neophobia (or their absence) determine (if at all) social positions such as dominance is still unclear. Spontaneous exploration may differ from the traditional shy–bold continuum [17], due to the possibility that individuals recorded as bold in laboratory conditions may potentially be looking for conspecifics for safety. This in turn may be an artefact of personality traits being assessed under laboratory conditions when animals are alone, the effects of which may be exacerbated for social species. Exploration of a novel environment through free choice may be more indicative of a propensity to learn and explore, rather than looking for safety or a group mate (i.e. the individual chooses to leave a group and explore). Similarly, however, exploration in an environment with conspecifics may also reflect a lower desire to be close to others, leading Jolles *et al.* [23] to conclude that the interaction between exploration and boldness or general activity is context-dependent. Therefore, whether such natural exploration is linked to personality traits determined in the lab, and how in turn this is associated with position within a dominance hierarchy, are not fully established. Can personality traits measured within a laboratory setting be used to predict the likelihood of voluntary exploration from the safety of home and the group, and is there a link between a willingness to explore and individual positioning within a ground-based dominance hierarchy?

An ideal model system for studying such questions about natural exploration and personality traits is homing pigeons (*Columba livia*). Homing pigeons are purported to use a variety of mechanisms and sensory cues for homing, including deriving 'map' information from olfaction [24,25], directional ('compass') information from the position of the sun [26] and from the Earth's magnetic field [25,26], and, once highly familiar with the landscape, pilotage by landmarks [27]. Pigeons home more quickly as groups when compared to solo releases [28], and there is much evidence for a collective intelligence element ('wisdom of the crowd') in their route learning and route optimization [29,30]. Leadership in pigeon flocks during homing exercises is driven by individual preferred speeds, with individuals flying faster when solo leading the flock when flown as part of a group [28]. On the ground, however, different hierarchies are seemingly evident, where dominant individuals that exert authority via direct physical aggression are not the same as those that act as leaders in flight, leading to the suggestion that multiple context-dependent hierarchies exist in pigeon societies [31,32]. Therefore, it is still unclear what drives dominance, how personality traits affect leadership and rank within a hierarchy, and how these traits influence an individual's route learning and propensity to explore. Naive pigeons that have never left the loft or undergone a homing flight, offer an intriguing opportunity to examine the relationships between laboratory-based personality traits and dominance, and how these translate to spontaneous exploratory flights (SEF), and subsequent success at homing. Does a lack of exploratory behaviour come at a price when it comes to then homing for the first time, due to a lack of knowledge of the home area? Thus, our hypotheses are that (i) greater exploration and a lack of neophobia under laboratory conditions determine a bird's willingness to explore during SEF, and that in turn, greater exploration then results in, (ii) a higher position within the ground-based dominance hierarchy due to the combination of personality traits and perceived knowledge accrued from exploratory flights, and (iii) greater distance covered during SEF results in quicker homing, thus reducing the time out of the loft and the chances of being predated upon.

2. Material and methods

(a) Birds and housing

A group of homing pigeons (*Columba livia*) (hereonin referred to as pigeons) were housed at Royal Holloway University of London (Egham, UK). All birds were three months old, had lived together since hatching, and had never flown outside of the loft. Nine birds were used for experimental trials. The exact

Table 1. Personality testing and dominance in nine homing pigeons. Rank refers to the individuals' position within the dominance hierarchy as determined by David's score (see §2). Novel object score refers to the amount of time spent in the zone closest to the novel object versus time in zones closer to safety (with a higher score denoting less neophobic behaviour). Novel object latency refers to the time (in seconds) taken to first enter the zone (figure 1) containing the novel object (with a lower time denoting less neophobic behaviour). 'P' refers to woodpigeon as the novel object, and 'J' to jackdaw as the novel object. Exploration score denotes time spent in the furthest zone versus time closer to safety (with a higher score denoting a greater willingness to explore).

pigeon ID	body mass (g)	tarsus length (mm)	rank	novel object (P) (score)	novel object (P) (latency)	novel object (J) (score)	novel object (J) (latency)	exploration (score)
1	440	36	7	2.33	4.18	7.83	0.40	21.18
2	420	36	2	3.73	3.51	0	0	5.22
3	500	41	9	2.09	0	1.73	2.28	29.17
4	420	34	5	0	0	0	0	7.92
5	510	43	8	1.50	0	1.56	23.47	0
6	370	34	4	13.05	9.08	9.04	6.17	20.88
7	560	45	3	30.77	5.01	10.83	0	20.45
8	590	45	1	5.77	6.45	8.60	13.17	14.46
9	590	44	6	0	0	0	0	8.34

sex of the birds was not known, although at least four birds were known to be males based on display behaviour to four birds assumed to be females. Birds were kept in a pigeon loft (dimensions 3.6 m (long), 2.4 m (wide)) with *ad libitum* access to food and water. Wooden perches ($n = 20$) were attached to the sides of the loft, in arrangements of six perches in horizontal rows at three heights (1 m, 1.30 m, 1.60 m), plus two additional single perches (1.30 m). Birds were weighed regularly, and tarsus length measured (table 1).

(b) Determination of dominance

Dominance hierarchies in the pigeons were studied between November (2015) and March (2016), and involved 10 separate trials (two per month, spaced two weeks apart). Food was removed at 17.00 the day before each recording session. The following morning (10.00 GMT), all the pigeons were individually labelled via a back-mounted sticker, and put into a pigeon carrier within their home loft. A single feeder was placed at the opposite end of the loft on the ground. The feeder had a roof and had limited space available for feeding (three birds at any one time). Birds were released from the basket simultaneously, and their behaviour recorded using video. The video focused on interactions taking place within a square metre of the feeder, where birds were fighting for access to the food. The first 30 min of agonistic interactions between all individuals following release from the carrier were analysed [32]. Interactions recorded were: pecking, chasing, beak grabbing, neck grabbing and wing slapping (see [32]). The total number of interactions between individuals was recorded in a matrix, as initiators of aggressive acts (winner) or receivers of aggressive acts (loser) from each interaction.

Agonistic interaction matrices were used to produce a dominance hierarchy based on David's score [33–35]. David's score is a measure of an individual's success in agonistic interactions, considering the relative strength of the other individuals with which that individual interacts. Large positive values of David's score identify individuals that are successful against many individuals, including against those that are themselves relatively successful. Large negative values, on the other hand, identify individuals that are unsuccessful against many individuals, including against other individuals that are themselves usually unsuccessful. Rank was assigned based on David's score.

(c) Laboratory-based exploration trials

Exploration in the laboratory was quantified as the time to emergence from a familiar box into an unfamiliar environment. Each bird was caught in their home loft and transported to a laboratory in a pigeon carrier (1 m long × 60 cm wide). After the initial move, the solo bird was left for 5 min in the carrier to recover and settle from being caught. The floor of the laboratory was divided into 3 × 1 m zones radiating from the entrance to the pigeon carrier (figure 1). The carrier was placed against the wall so as to allow the birds to only move in one direction (i.e. not behind the box). The following variables were measured: (i) time to first emergence, (ii) time to enter each zone for the first time, and (iii) total time spent in each zone overall. Trials ran for 15 min, and commenced after the 5 min recovery time. Birds were observed via a small peep hole, so that there were no observer effects on the pigeon's behaviour. Each individual could choose to stay in the box for the entirety of the trial, and birds were immediately caught and returned to the home loft following the 15 min of observations. Each pigeon was tested three times, with a minimum of 5 days between each test. All birds completed each laboratory exploration trial in each round (during June and July 2016) before the next set of trials began. The order in which the birds were tested was randomly assigned for each trial, through the use of a random number generator, which in turn was linked to the identification number on each pigeon's leg ring. All laboratory-based exploration trials were completed before any trials for response to novel objects began.

(d) Laboratory-based responses to novel objects

Novel object trials followed a similar format to the laboratory exploration trials: they used the same setting as the exploration trials in order to remove the novelty of the environment and focus the novelty on the foreign object. The same box and floor set-ups were used. Trials took place six weeks after completion of the exploration trials (August–September 2016). Two novel objects were used, both stuffed birds, common woodpigeon (*Columba palumbus*), and Eurasian jackdaw (*Corvus monedula*). The pigeons used in this study had not yet been flown nor left the loft and laboratory facilities, and thus had never come into contact with either wild bird species. Novel objects were selected based on the potential for intrinsic responses to a species that looks similar to (woodpigeon) or very different from (jackdaw)

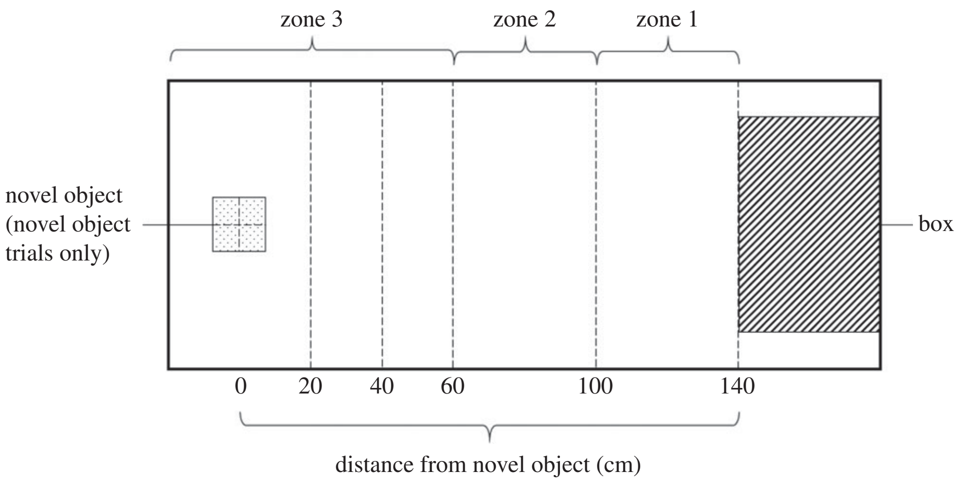

Figure 1. Simplified representation of floor space of laboratory for personality testing in the pigeons.

conspecifics. As with the laboratory exploration trials, birds were left for 5 min to settle following capture. After the 5 min recovery period, the door to the carrier was opened and the 15 min trial began. Time to first emergence from the carrier was recorded, followed by the time to enter each initial zone, total time spent in each zone and time to walk within 15 cm of the novel object. Pigeons were observed through a peep hole. For each pigeon, three trials of each novel object type (woodpigeon and jackdaw) were undertaken, and the order of these trials was randomized. For both laboratory-based exploration and novel object trials, scores were calculated following $1^1 + 2^2 + 3^3$, where the numbers refer to time spent in each zone (figure 1), with 3 being the zone furthest from the safety box, and the zone incorporating the novel object [36]. For analytical purposes, novel object score incorporated both woodpigeon and jackdaw data combined. Only latency to approach the woodpigeon is presented.

(e) Flight experiments

The birds were tracked using 5 Hz GPS loggers (BT-Q1300ST, Qstarz International Co., Ltd., Taipei, Taiwan; 12 g). The loggers were attached to the pigeons using Velcro strips that were glued using epoxy to trimmed feathers on the back of the birds. In total, the full logger attachment weighed 13 g, approximately 2.5% of mean body mass of the birds. One week prior to the start of the experiment, self-adhesive iron motorbike wheel-balancing weights (12 g) were attached to the birds' backs to accustom them to carrying the additional mass. GPS data were downloaded using QTravel (QStarz; v. 1.48(T)).

First, birds were tested for their natural willingness to explore the area around their home, through spontaneous exploration flights (SEF). For SEF, birds were captured individually and placed in a pigeon carrier. The carrier was then placed on the roof of the pigeon loft with the door open. The birds were allowed to exit at will and explore the local environment, and return inside the loft when they wished. This step was repeated three times for each bird, each time with a week between flights. All flights for one round of trials were completed for all birds, before a second round of trials began. Birds were released singly, and birds were only released after the preceding bird had returned to the loft. Key parameters measured were (i) distance travelled, (ii) furthest point reached from loft, and (iii) total time out of the loft. Furthest point and time out of the loft were included to differentiate between those individuals that had undergone long flights from those individuals that had simply sat on the roof of a nearby building.

Once all birds had completed three releases from the pigeon loft for measures of SEF, they were then released individually from six release sites at increasing distances from the loft (electronic supplementary material, table S1) over successive days to study their homing behaviour. All birds were released on the same day from a release site, allowing a minimum gap of 30 min between individual releases. The first site was just *c.* 500 m from the home loft, and the sixth release 6 days later was 3 km. Each of these six releases was only performed once, as the primary interest was initial homing behaviour, not route learning and recapitulation. A key extra parameter measured in addition to those recorded for SEF was route efficiency (measured as the beeline route between home and release divided by distance flown to reach home). No releases took place during rain or on overcast days. For homing flights, the time taken to return home ended when the bird was within 10 m of the loft, and any additional circling after that was not included in distance flown. For three of the trials, birds did not return home within the battery life of the GPS loggers. For these individuals, a nominal figure of 0.02 was used for route efficiency. At the point of logger failure, the birds had been static for some time, and the loggers had remained recording until past dusk.

(f) Statistics

The relationships between morphological parameters (body mass and structural size) and personality traits (laboratory-based exploration score and neophobia) were investigated using linear regression. Relationships between mean furthest point reached during SEF and route efficiency during homing release sites were also investigated using linear regression. The repeatability of traits during SEF (furthest point reached, total distance travelled and total time away from the loft) and route efficiency ($N = 6$ homing flights) were assessed by calculating the intraclass correlation coefficient (the proportion of variance explained by the random effect of individual identity in a model with no fixed predictors) using the *rptR* package v. 0.9.1 of R v 3.3.2 [37,38]. The significance of repeatability was assessed using likelihood ratio tests and the 95% of repeatability was estimated using 10 000 parametric bootstraps.

3. Results

Body size (tarsus length, mm) and body mass (g) were significantly correlated in the nine homing pigeons ($y = 0.056x + 12.21$, $r^2 = 0.92$, $F = 0.027$, $p > 0.001$) and thus body mass only is used for investigating the interactions between behavioural traits and size (table 1). Body mass was a not a significant predictor of any behavioural measure under either laboratory conditions (laboratory-based exploration and novel object response, or dominance rank position) or during SEF of the environment around the loft (furthest point reached during SEF; see electronic supplementary material, table S2).

Pigeons' latency to respond to the two novel objects (woodpigeon and jackdaw) varied at the individual level, and there was no relationship between the latency to approach the woodpigeon and the latency to approach the jackdaw (electronic supplementary material, table S3). In contrast, novel object scores for woodpigeon and jackdaw were positively correlated ($y = 1.597x - 0.44$, $r^2 = 0.54$, $F = 8.12$, $p = 0.02$), with individuals that were more likely to spend time close to the woodpigeon also more likely to spend time close to the jackdaw. Laboratory-based exploration score or dominance hierarchical rank were not correlated to either novel object score or latency to approach the novel object (electronic supplementary material, table S3).

The mean furthest point (metres) reached during SEF ($N = 3$) was significantly repeatable ($R = 0.86 \pm 0.09$ (s.e.), 95% CI: 0.60–0.94, $p < 0.001$), and was used as a measure of degree of exploration behaviour prior to homing flights (electronic supplementary material, table S2). Furthest point reached and total distance covered were highly correlated when all three SEF trials were combined ($F = 45.5$, $R^2 = 0.65$, $p < 0.0001$), so only furthest point reached was used for investigations into SEF. For some birds, the furthest point reached was minimal, as the birds went no further than the roof of the building opposite their home loft. In contrast, other individuals' (for example, individuals 1, 6 and 7; electronic supplementary material, figures S1 and S2), furthest point reached was considerably further than the immediate surroundings.

Novel object score was positively correlated with mean furthest point reached of three exploratory flights ($y = 30.94x + 256.71$, $r^2 = 0.71$, $F = 16.65$, $p < 0.01$), demonstrating that individuals who spent more time in zones further away from safety and closer to novel objects under laboratory conditions travelled further during exploration flights (figure 2). Conversely, however, there was no association between latency to approach novel objects and the furthest point reached during SEF ($y = 111.79x + 245.96$, $r^2 = 0.56$, $F = 8.94$, $p = 0.02$, figure 2), suggesting that novel object score and latency to approach the novel object test different tendencies, with only novel object score being related to furthest point reached during exploration flights. It is possible that latency to approach a novel object can be misleading, as on occasion birds would exit the box rapidly, seemingly in an escape response, but then rapidly return to the box upon realizing no other pigeons were present. There was no relationship between dominance rank and furthest point reached (electronic supplementary material, table S3). Laboratory-based exploration score was also positively correlated with mean furthest point reached during SEF (figure 2), with birds that exhibited more exploratory behaviour under laboratory conditions also exploring further from the loft ($y = 36.22x + 82.91$, $r^2 = 0.46$, $F = 6.06$, $p = 0.043$). Noticeably, there was no overall trend for individuals to improve their flight parameters over successive SEF ($N = 3$), with birds not generally increasing their furthest point reached over sequential successive flights.

Route efficiency was significantly repeatable ($R = 0.86 \pm 0.09$ (s.e.), 95% CI: 0.60–0.94, $p < 0.001$), varied greatly among individuals (electronic supplementary material, table S4), and as would be predicted, did not increase over time, as each bird was released just once from each release site, thus providing no opportunity to learn and refine homing routes from any given site. Mean furthest point reached during SEF was positively correlated with mean route efficiency during homing releases ($y = 2872.1x + 30.05$, $r^2 = 0.86$, $F = 43.722$, $p < 0.001$) (figure 3), demonstrating that birds that had explored more during SEF from home were able to home more efficiently when released from novel sites (see also figures 4 and 5). Similarly, mean route efficiency (electronic supplementary material, table S4) was positively correlated with laboratory exploration score ($y = 42.45x + 5.81$, $r^2 = 0.53$, $F = 7.96$, $p = 0.03$) (figure 3), novel object score (table 1) ($y = 75.68x + -3.944$, $r^2 = 0.81$, $F = 30.60$, $p < 0.001$) (figure 3) and latency to approach the novel object ($y = 0.0365x + 0.083$, $r^2 = 0.57$, $F = 9.03$, $p < 0.01$). Repeatability was significantly greater than zero for total distance travelled ($R = 0.63 \pm 0.18$ (s.e.), 95% CI: 0.13–0.85, $p < 0.001$, electronic supplementary material, figure S3), but low and with a bootstrapped 95% CI that abutted zero for total time out of loft ($R = 0.32 \pm 0.20$ (s.e.), 95% CI: 0–0.68, $p = 0.001$).

4. Discussion

Individual birds that demonstrated less neophobic tendencies and more extensive exploration under laboratory conditions exhibited greater exploration during SEF and subsequently homed more quickly. There was no relationship between dominance rank and degree of exploration, and there was no clear trend to suggest that laboratory-based exploration or a lack of neophobia measured under laboratory conditions resulted in individuals being highly ranked within the dominance hierarchy.

(a) Exploration

It is likely that birds were gathering information during exploratory flights, which resulted in faster homing from novel release sites, despite the sites being outside the area that was explored. Information gathered during early exploratory flights is an important component of the development of the navigation system in young birds [39]. The greater the area covered and explored, the more accurate the bird's navigational map of the local area [39], and in this instance, birds that are more willing to explore are developing larger maps. As the initial early flights and associated experiences are the beginnings of map formation, it is fascinating that a personality trait—neophobia, or lack thereof—seemingly dictates the size of the navigational map that will be developed in young birds. As has been identified in many species, young animals initially learning to forage, for example, will start out exploring a wide range of choices, before either narrowing down these options through experience, or through trial and error learning [40]. The tendency to exhibit such exploratory behaviour has been linked to natural ecological conditions at the species level (e.g. in 61 parrot species, [41]). In the present study, the tendency to exhibit such exploratory behaviour demonstrates variation at an individual level too. Typically, intra-specific variation in neophobia has been linked to factors such as perception of predation pressure (e.g. Trinidadian guppies (*Poecilia reticulata*) [42]) or exposure to urban environments (e.g. common mynahs (*Acridotheres tristis*) [43]). Until the initial release for

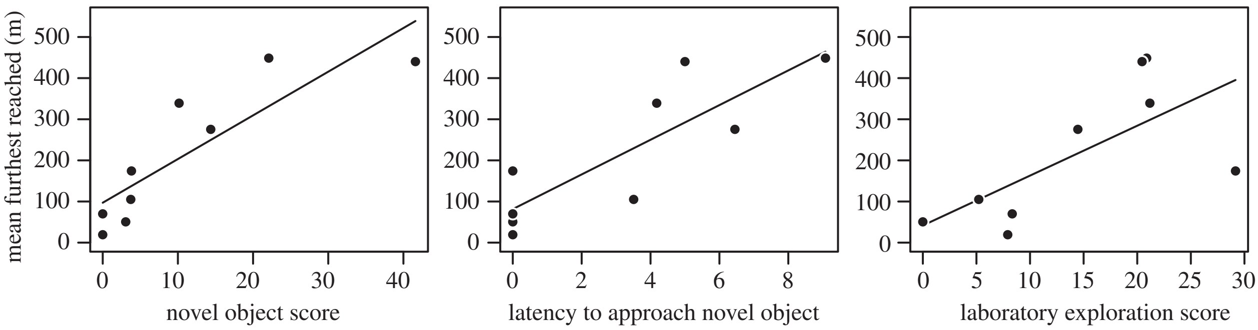

Figure 2. Laboratory-based personality tests in nine homing pigeons versus spontaneous exploration flight (SEF) from the loft. (Left) Novel object score (measured as time spent in respective zone close to novel object, table 1) versus mean ($n = 3$, full details in electronic supplementary material, table S2) furthest point reached (in metres) during SEF from the home loft. (Middle) Mean furthest point reached during SEF versus latency to approach novel object. (Right) Mean furthest point reached during early exploratory flights versus laboratory-based exploration score. Regression details: (left) $r^2 = 0.66$, $F = 16.65$, $p = 0.004$, $r^2 = 0.72$, $F = 21.15$, $p = 0.002$, (middle) $r^2 = 0.50$, $F = 8.94$, $p = 0.02$, and (right) $r^2 = 0.39$, $F = 6.06$, $p = 0.043$ (see §3 for regression equations).

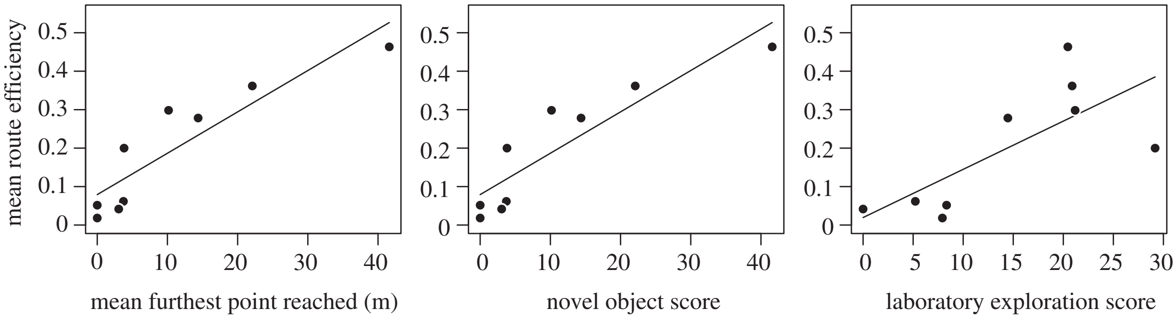

Figure 3. (Left) Mean furthest point reached (metres) during free-choice natural exploration flights versus mean route efficiency in nine homing pigeons. Mean route efficiency (see electronic supplementary material, table S4 for s.e.) versus (middle) novel object score (measured as time spent in respective zone close to novel object, figure 1 and table 1), and (right) exploration score (see §3). Regression details: (left) $r^2 = 0.86$, $F = 43.72$, $p = 0.0003$, (middle) $r^2 = 0.81$, $F = 30.80$, $p = 0.0008$, and (right) $r^2 = 0.53$, $F = 7.96$, $P = 0.03$ (see §3 for regression equations).

the first exploratory flight, all individual pigeons had experienced the same conditions in terms of life history. As dominance rank was not related to personality traits or morphological features, it is difficult to ascertain what determined the inter-individual differences in neophobia, or indeed in dominance rank, observed in the pigeons. It is possible that early life events during fledging could be a determining factor, and future work tracking individuals from the moment of hatching would provide insight into the effects of early life experiences on general boldness traits and dominance, versus genetic effects.

(b) Home range development and subsequent homing

During SEF, very young pigeons are thought to use route reversal during homing, which is later replaced, over the course of development, by a ‘map-and-compass’ mechanism that relies on various position-fixing and directional cues learnt through experience [44,45]. The necessary knowledge of the local area (the ‘navigational’ or ‘mosaic’ map) is presumably acquired through exploration [46,47]. In the present study, the non-neophobic birds that explored significantly larger areas during early exploration were likely creating larger navigational maps prior to any homing flights being undertaken, in comparison to their neophobic conspecifics. The greater knowledge of their local area and landmarks—a more detailed and/or expansive navigational map—is likely to be the mechanism by which these individuals home faster, and along more efficient routes (electronic supplementary material, table S4). Pigeons’ short-range navigation, in the immediate home loft area or close to it, is thought to rely on prominent landmarks and their memorized directional relationship to home [45]. Schiffner *et al.* [39] proposed that the range of the mosaic map would be limited by the degree of information obtained and subsequently retained during exploratory flights (see also [48]), and this mosaic range expansion is likely to be around and up to 10 km from the home loft [46]. The variability in the present study of the range of exploration and thus creation of a local mosaic map, is seemingly dictated by a lack of neophobia and exploration tendencies as measured in the laboratory. Given the context-dependency observed in pigeon social behaviour [31] it is perhaps surprising that non-neophobic individuals who explore more around the local loft area are also seemingly more efficient at homing from longer distances that lie outside the mosaic map region that has been collated. It is possible, however, that these birds may be flying at higher altitudes, allowing them to potentially see landmark features much further afield than the ground distance they have actually covered. This suggests that traits within such individuals both encourage exploration and make for more efficient homers, the latter perhaps through an enhanced ability to extrapolate navigational information to outside areas with which they have direct experience.

When released from further away, the pigeons that had explored more returned home more quickly, and by a more efficient route. This suggests they were better at ‘pilotage’

Figure 4. Initial homing flight from release site 2 (electronic supplementary material, table S1). Six pigeon GPS traces are shown: pigeons 1 (green), 2 (black), 4 (yellow), 6 (red), 7 (blue) and 9 (brown). The black triangle denotes the home loft, and the release site is represented by a black square. Route efficiencies are detailed in electronic supplementary material, table S4. Bird 4 did not return home within the battery life of the logger (*c*. 6 h), and returned approximately 7.5 h following release. Some initial circling has been removed for presentation purposes. Background images taken and owned by UK Ordnance Survey™.

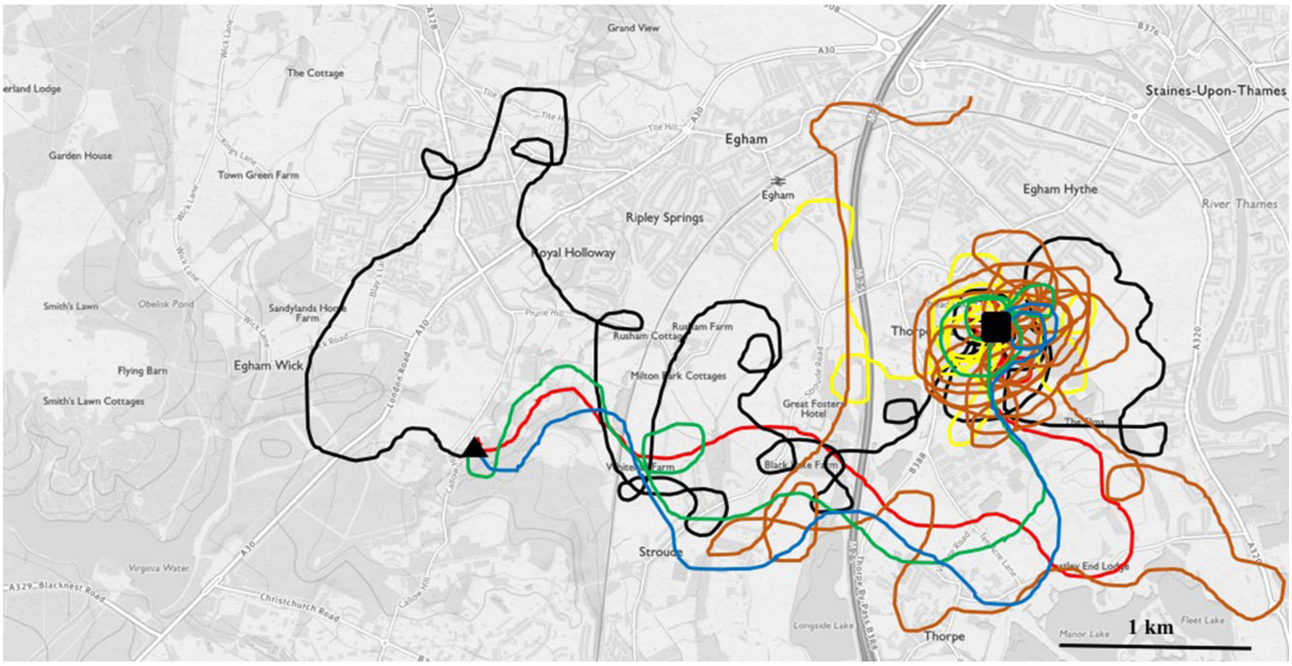

Figure 5. Initial homing flight from release site 6 (electronic supplementary material, table S1). Six pigeon GPS traces are shown: pigeons 1 (green), 2 (black), 4 (yellow), 6 (red), 7 (blue) and 9 (brown). The black triangle denotes the home loft, and the release site is represented by a black square. Route efficiencies are detailed in electronic supplementary material, table S4. Birds 4 and 9 did not return home within the battery life of the logger (*c*. 6 h) and did not return until the next day. Some initial circling has been removed for presentation purposes. Background images taken and owned by UK Ordnance Survey™.

(navigation by familiar landmarks alone) or at using a map-and-compass strategy [44,49–53]. Both mechanisms are dependent on building up knowledge of local familiar landmarks, with respect to which the non-neophobic birds were at an advantage. Schiffner *et al*. [39] found great variability between young pigeons in their initial route choices, but suggested that due to every individual showing significant orientation to the home loft after 2.5 km of flight, all birds had some idea about their position relative to the loft (see also [48]). In the present study, all birds came home eventually, but at least some birds, when released from the furthest point (Site 6, figure 5), did not show significant orientation towards their home loft within the first hours of release, and indeed two birds doubled back on themselves, with the logger battery failing after eight hours. This suggests the variability in these individuals is greater than in those previous studies [39,48].

It is feasible that the findings in the present study could be interpreted differently. Even those pigeons that came home via a route with high efficiency still had numerous deviations from the beeline and took tortuous paths. Schiffner *et al*. [39] interpreted such behaviour in their birds as being opportunistic, and a way of increasing knowledge of routes and the area in general. Schiffner *et al*. [39] noted that different landmarks seemed to hold different levels of interest to different individual birds, and that they lingered for some time at certain locations. Is being out of the loft and being released from a site a few km away perceived by the birds as being an opportunity to further develop their map and obtain information about the area? If this is the case, flights that are highly convoluted and extremely inefficient (e.g. bird 2, figures 4 and 5) could be interpreted as the individual being exploratory, rather than being 'lost', and potentially unrelated to their laboratory-based neophobia and SEF behaviour from the loft. If this was the case, those individuals are exhibiting latent learning and building up a detailed mosaic map for future use. The fact that they made it home eventually demonstrates the desire and motivation to home, and hence deviations could indeed be interpreted as exploratory and 'intentional', termed 'exploration refinement' by Guilford *et al*. [54]. However, the long periods of time that the birds spent perched as opposed to in active flight would suggest this is an unlikely explanation.

(c) Future directions

It is established that individual variation in personality can have fitness consequences [55], with, for example, personality dictating overwinter survival in female red squirrels (*Tamiasciurus hudsonicus*) [55] and reproductive fitness in fish [56], birds [57] and mammals [58]. Similarly, Santos *et al*. [59] demonstrated that laboratory assays of homing pigeons' boldness behaviour could predict an individual's likelihood to be predated by raptors. Further studies with homing pigeons should investigate the long-term fitness trade-offs between exploratory behaviour and dominance. Biro and Stamps [60] proposed the 'life-history productivity' hypothesis, which states that proactive individuals express behaviours that provide them with the necessary traits to sustain high productivity, and these traits are associated with high metabolic rates [60–62]. When flying in a flock, pigeons tend to form a cluster, where flying at the back of the flock comes at a cost, in terms of increased flap frequency [63,64]. Metabolic rates may both be dictating certain personality-based behaviours, along with flock positioning within group flights. Future work tracking metabolic rate of each individual over the course of a year may reveal that birds with high metabolic rates preferentially place themselves at the front of cluster flocks, while simultaneously exhibiting greater exploratory behaviour. Similarly, changes in hormone levels and physiological condition throughout the annual cycle may result in changes to personality traits that in turn may alter willingness to explore [65,66], or cause perturbation to social networks [67,68].

In summary, pigeons that were neophobic under laboratory conditions did not explore the local area during SEF opportunities. When released from sites further from home, neophobic pigeons took longer routes to home compared to those birds that had not exhibited neophobic traits under laboratory conditions, and had spontaneously explored to a greater extent. The lack of exploration in the neophobic birds is likely to have resulted in the increased costs of homing due to longer flight times following release: unfamiliarity with the landscape likely led to the greater distances travelled and less efficient routes taken. Birds that demonstrated a lack of neophobia were not the dominant individuals inside the loft, and thus would have less access to resources such as food and potentially mates. However, a lack of neophobia makes the subordinate position possible, because subordinate birds that incur high travel costs would become calorie restricted and lose condition.

Ethics. All procedures described were conducted in accordance with appropriate national regulations and institutional ethical permissions.

Data accessibility. Electronic supplementary data and materials are available with the paper.

Authors' contributions. S.J.P. designed the study with input from J.C., E.L.S. and D.B. R.L.R. collected all laboratory-based personality data. The experiments were based on an initial idea conceived by J.C. S.J.P. performed all fieldwork and flight experiments, and C.R.W. and S.J.P. analysed the data. S.J.P. wrote the manuscript and all authors contributed to revisions.

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