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# **Boldness traits, not dominance, predicts exploratory flight range and homing behaviour in homing pigeons**

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Group living has been proposed to yield benefits which 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 (a) greater initial exploration of the local area around the home loft during spontaneous exploration flights (SEF), (b) faster and more efficient homing flights when released from further afield, and (c), 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 which 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 which 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.

## 1. Introduction

Group living has been proposed to yield benefits which 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 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 which 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.

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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

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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 such 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, is 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?

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An ideal model system for studying such questions about natural exploration and personality traits are 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  
110 from the Earth’s magnetic field, 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 optimisation [29, 30]. Leadership in pigeon flocks during homing exercises is driven by individual preferred speeds, with individuals flying faster when  
115 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  
120 and rank within a hierarchy, and how these traits influence how these traits influence an individual’s route learning and propensity to explore. Naïve 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  
125 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 (a) 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, (b) a higher position within the ground-based dominance hierarchy due to the combination of personality traits and perceived knowledge accrued from exploratory flights, and (c) 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

### 135 (a) *Birds & 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 3 months old, had lived together since hatching, and had never flown outside of the loft. Nine birds were used for experimental trials. The exact 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 a 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 (3 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 minutes 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. 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 x 60 cm wide). After the initial move, the solo bird



was left for 5 minutes in the carrier to recover and settle from being caught. The floor of the laboratory was divided into 3 x 1 metre zones radiating from the entrance to the pigeon carrier (Fig. 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; (a) time to first emergence, (b) time to enter each zone for the first time, and (c) total time spent in each zone overall. Trials ran for 15 minutes, and commenced after the 5-minute 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 minutes of observations. Each pigeon was tested 3 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, to remove the novelty of the environment, and focus the novelty on the foreign object; the same box and the floor set out in different zones; and took place 6 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 or 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) conspecifics. As with the laboratory exploration trials, birds were left for 5 minutes to settle following capture. After the 5-minute recovery period, the door to the carrier was opened, and the 15-minute 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, 3 trials of each novel object type (woodpigeon and jackdaw) were undertaken, and the order of these trials was randomised. 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 which 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' back to accustom them to carrying the additional mass. GPS data were downloaded using QTravel (QStarz; version 1.48(T)).

Firstly, 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  
230 released after the preceding bird had returned to the loft. Key parameters measured were (a) distance travelled, (b) furthest point reached from loft, and (c) 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.

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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 increasingly greater distances from the loft (supplementary table 1) 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  
240 minutes between individual releases. The first site was just *c.* 500 metres from the home loft, and the sixth release six 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 additional parameter measured in addition to those recorded for SEF was route efficiency (measured as the beeline route between home and release divided by  
245 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 metres 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

250 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  
255 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  
260 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 v0.9.1 of R version 3.3.2 [37, 38]. The significance of repeatability was assessed  
using likelihood ratio tests and the 95% confidence interval of repeatability was estimated  
using 10000 parametric bootstraps.

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### 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).  
270 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 supplementary table 1).

275 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 (supplementary table 3). In contrast, novel object score for woodpigeon and jackdaw were positively correlated ( $y = 1.597x - 0.44$ ,  $r^2 = 0.54$ ,  $F = 8.12$ ,  $P = 0.02$ ), with individuals 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 (supplementary table 3).

The mean furthest point (metres) reached during SEF ( $N = 3$ ) was significantly repeatable ( $R = 0.86 \pm 0.09$  [SE], 95% CI: 0.60 – 0.94,  $P < 0.001$ ), and was used as a measure of degree of exploration behaviour prior to homing flights (supplementary table 2). 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, supplementary table 2), farthest point reached was considerably further than the immediate surroundings.

Novel object score was positively correlated with mean further 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 4). Conversely, however, there was no association between latency to approach novel objects and the furthest point reached during SEF ( $y = 111.79x + 245.96$ ,  $r^2 = 0.56$ ,  $F = 8.94$ ,  $P =$

300 0.02, figure 4), 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 realising no other pigeons were present. There was no  
305 relationship between dominance rank and furthest point reached (supplementary table 1).  
Laboratory-based exploration score was also positively correlated with mean furthest point  
reached during SEF (figure 4), 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  
310 parameters over successive exploratory flights ( $N = 3$ ), with birds not generally increasing  
their furthest point reached over sequential successive flights.

Route efficiency was significantly repeatable ( $R = 0.86 \pm 0.09$  [SE], 95% CI: 0.60 – 0.94,  $P <$   
0.001), varied greatly among individuals (supplementary table 4), and as would be predicted,  
315 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 5),  
demonstrating that birds that had explored more during SEF from home were able to home  
320 more efficiently when released from novel sites. Similarly, mean route efficiency  
(supplementary table 4) was positively correlated with laboratory exploration score ( $y =$   
 $42.45x + 5.81$ ,  $r^2 = 0.53$ ,  $F = 7.96$ ,  $P = 0.03$ ) (figure 5), novel object score (table 1) ( $y =$   
 $75.68x + -3.944$ ,  $r^2 = 0.81$ ,  $F = 30.60$ ,  $P < 0.001$ ) (figure 5) 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

325 greater than zero for total distance travelled ( $R = 0.63 \pm 0.18$  [SE], 95% CI: 0.13 – 0.85,  $P <$   
0.001, supplementary figure 4), but low and with a bootstrapped 95% CI that abutted zero for  
total time out of loft ( $R = 0.32 \pm 0.20$  [SE], 95% CI: 0 – 0.68,  $P = 0.001$ ).

#### 4. Discussion

330 Individual birds who 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  
335 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  
340 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 which 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  
345 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

350 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*  
355 *tristis*) [43]). Until the initial release for 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  
360 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*

365 During SEF, very young pigeons are thought to utilise 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 of the local area [46, 47]. In the present study, the non-  
370 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 (figure 2-4). 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 (table 4).



375 Pigeons' short-range navigation, in the immediate home loft area or close to it, is thought to  
rely 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  
380 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  
385 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  
390 information to outside areas with which they have direct experience.

When released from further away, the pigeons who had explored more returned home more  
quickly, and by a more efficient route. This suggests they were better at 'pilotage'  
(navigation by familiar landmarks alone) or at using a map-and-compass strategy [44, 49-53].  
395 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

400 study, all birds came home eventually, but at least some birds, when released from the  
furthest point (Site 6, figure 3 and 4), 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 those previous studies [39, 48].

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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  
410 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  
415 this is the case, flights which are highly convoluted and extremely inefficient (e.g. bird 2,  
figures 3 and 4) 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 they made it home eventually demonstrates the  
420 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, due to the long periods of time that the birds spent perched (figures 3 and 4) as  
opposed to in active flight would suggest this is an unlikely explanation.

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*(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 behavior 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 which 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 which 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.

**Author contributions.** S.J.P. designed the study with input from J.C., E.L.C. 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.

**Competing interests.** No competing interests to declare.

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## References

1. Alexander RD. 1974 The evolution of social behaviour. *Annual Rev. Ecol. Syst.* **5**, 325–383.
2. Stacey PB. 1986 Group size and foraging efficiency in yellow baboons. *Behav. Ecol. Sociobiol.* **18**, 175–187.
3. Elgar MA. 1989 Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol. Rev.* **64**, 13–33.
4. Pays O, Beauchamp G, Carter AJ, Goldizen AW. 2013 Foraging in groups allows collective predator detection in a mammal species without alarm calls. *Behav Ecol.* **24**, 1229–1236.
5. Bill RG, Hernkind WF. 1976 Drag reduction by formation movement spiny lobsters. *Science* **193**, 1146–1148.
6. Liao JC, Beal DN, Lauder GV, Triantafyllou MS. 2003 Fish exploiting vortices decrease muscle activity. *Science* **301**, 1566–1569.
7. Portugal SJ, Hubel TY, Fritz J, Heese S, Trobe D, Voelkl B, Hailes S, Wilson AM, Usherwood JR 2014 Upwash exploitation and downwash avoidance by flap phasing in ibis formation flight. *Nature* **505**, 399–402.
8. Brown JS. 1988 Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.* **22**, 37–47.
9. Pitcher TJ, Magurran AE, Winfield IJ. 1982 Fish in larger shoals find food faster. *Behav. Ecol. Sociobiol.* **10**, 149–151.
10. Krause J, Ruxton GD. 2002 *Living in groups*. Oxford University Press. UK.
11. Chase ID, Tovey C, Spangler-Martin D, Manfredonia M. 2002 Individual differences versus social dynamics in the formation of animal dominance hierarchies. *PNAS* **99**, 5744–5749.
12. Cote SD. 2000 Dominance hierarchies in female mountain goats: stability, aggressiveness and determinants of rank. *Behaviour* **137**, 1541–1566.
13. Sloman KA, Armstrong JD. 2002 Physiological effects of dominance hierarchies: laboratory artefacts or natural phenomena? *J. Fish Biol.* **61**, 1–23.
14. Funghi C, Leitao AV, Ferriera AC, Mota PG, Cardoso GC. 2015 Social dominance in a gregarious bird is related to body size but not to standard personality assays. *Ethology* **121**, 84–93.

15. Colleter M, Brown C. 2011 Personality traits predict hierarchy rank in male rainbowfish social groups. *Anim. Behav.* **81**, 1231–1237.
- 510 16. Wilson DS, Clark AB, Coleman K, Dearstyne T. 1994 Shyness and boldness in humans and other animals. *Trends Ecol. Evol.* **9**, 442–446.
17. Stamps J, Groothuis TGG. 2010 The development of animal personality. Relevance, concepts and perspectives. *Biol. Rev.* **85**, 301–325.
18. Dingemanse NJ, de Goede P. 2004 The relation between dominance and exploratory behaviour is context-dependent in wild great tits. *Behav Ecol.* **6**, 1023–1030.
- 515 19. Johnstone RA, Manica A. 2011 Evolution of personality differences in leadership. *PNAS* **108**, 8373–8378.
20. Kurvers RHJM, Eijkelenkamp B, van Oers K, van Lith B, Wieren SEV, Ydenberg RC, Prins HHT. 2009 Personality differences explain leadership in barnacle geese. *Anim. Behav.* **78**, 447–453.
- 520 21. Nakayama S, Harcourt JL, Johnstone RA, Manica A. 2012 Initiative, personality and leadership in pairs of foraging fish. *PLoS One.* **7**, e36606.
22. Jolles JW, Fleetwood-Wilson A, Nakayama S, Stumpe MC, Johnstone RA, Manica A. 2015 The role of social attraction and its link with boldness in the collective movements of three-spined sticklebacks. *Anim. Behav.* **99**, 147–153.
- 525 23. Jolles J., Taylor BA, Manica A. 2016 *Anim. Behav.* Recent social conditions affect boldness repeatability in individual sticklebacks. **112**, 139–145.
24. Guilford T, Gagliardo A, Chappell J, Bonadonna F, Burt de Perera T, Holland R. 1998 Homing pigeons use olfactory cues for navigation in England. *J. Exp. Biol.* **201**, 895–900.
- 530 25. Gagliardo A, Ioale P, Filannino C, Wikelski M. 2011 Homing pigeons only navigate in air with intact environmental odours: a test of the olfactory activation hypothesis with GPS data loggers. *PLoS One.* **6**, e22385.
26. Wallraff HG, Chappell J, Guilford T. 1999 The roles of the sun and the landscape in pigeon homing. *J. Exp. Biol.* **202**, 2121–2126.
- 535 27. Biro D, Meade J, Guilford T. 2006 Route recapitulation and route loyalty in homing pigeons: pilotage from 25 km? *J. Nav.* **59**, 43–53.
28. Pettit B, Akos Z, Vicsek T, Biro D. 2016 Speed determines leadership and leadership determines learning during pigeon flocking. *Curr. Biol.* **25**, 3132–3137.

- 540 29. Pettit B, Flack A, Freeman R, Guilford T, Biro D. 2012 Not just passengers: pigeons can learn homing routes while flying with a more experienced conspecific. *Proc. Roy. Soc. B.* 20122160.
30. Watts I, Nagy M, Burt de Perera T, Biro D. 2016 Misinformed leaders lose influence over pigeon flocks. *Biol. Lett.* **9**, 20160544.
- 545 31. Nagy M, Vaserhelyi G, Pettit B, Roberts-Mariani I, Vicsek T, Biro D. 2013 Context dependent hierarchies in pigeons. *PNAS.* **110**, 13049–13054.
32. Portugal SJ, Sivess L, Martin GR, Butler PJ, White CR. 2017 Perch height predicts dominance rank in birds. *Ibis.*
33. David HA. 1987 Ranking from unbalanced paired-comparison data. *Biometrika* **74**,  
550 432–436.
34. David HA. 1988 The method of paired comparisons. London, Charles Griffin.
35. Gammell MP, De Vries H, Jennings DJ, Carlin CM, Hayden TJ. 2003 David's score: a more appropriate dominance index ranking method than Clutton-Brock et al.'s index. *Anim. Behav.* **66**, 601–605.
- 555 36. Dziejewcynski TL, Campbell BA, Kane JL 2016 Dose-dependent fluoxetine effects on boldness in male Siamese fighting fish. *J. Exp. Biol.* **219**, 797–804.
37. R Core Team. 2016 R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. R.
38. Schielzeth H, Stoffel M, Nakagawa S. 2017 rptR: Repeatability Estimation for  
560 Gaussian and Non-Gaussian Data. <https://CRAN.R-project.org/package=rptR>.
39. Schiffner I, Pavkovic T, Siegmund B, Wiltschko R. 2011 Strategies of young pigeons during 'map' learning. *J. Nav.* **64**, 431–448.
40. Galef BG, Laland KN. 2005 Social learning in animals: empirical studies and theoretical models. *Bioscience* **55**, 489–499.
- 565 41. Mettke-Hofmann C, Winkler H, Leisler B. 2002 The significance of ecological factors for exploration and neophobia in parrots. *Ethology* **108**, 249–272.
42. Fraser DF, Gilliam JF. 1987 Feeding under predation hazard: response of the guppy and Hart's rivulus from sites with contrasting predation hazard. *Behav. Ecol. Sociobiol.* **21**, 203–209.
- 570 43. Sol D, Griffin AS, Bartomeus I, Boyce H. 2011 Exploring or avoiding novel food resources? The novelty conflict in an invasive bird. *PLoS One* **6**, e19535.
44. Wiltschko R, Wiltschko W. 1985 Pigeon homing: change in navigational strategy during ontogeny. *Anim. Behav.* **33**, 583–590.

- 575 45. Biro D, Freeman R, Meade J, Roberts S, Guilford T. 2007 Pigeons combine compass and landmark guidance in familiar route navigation. *Proc. Natl. Acad. Sci. USA* **104**, 7471–7476.
46. Braithwaite VA. 1993 When does previewing the landscape affect pigeon homing? *Ethology*. **95**, 141–151.
- 580 47. Guilford T, Biro D. 2014 Route following and the pigeon’s familiar area map. *J. Exp. Biol.* **217**, 169–179.
48. Schiffner I, Wiltschko R. 2013 Development of the navigational system in homing pigeons: increase in complexity of the navigational map. *J. Exp. Biol.* **216**, 2675–2681
49. Wiltschko R. 1983 The ontogeny of orientation in young pigeons. *Comp. Biochem. Physiol.* **76a**, 701–708.
- 585 50. Wiltschko R, Wiltschko W. 1978 Evidence for the use of magnetic outward journey in homing pigeons. *Naturwissenschaften*. **65**, 112–113.
51. Wiltschko R, Wiltschko W. 1990 The process of learning sun compass orientation in young homing pigeons. *Naturwissenschaften*. **67**, 512–514.
- 590 52. Wiltschko R, Schiffner I, Fuhrmann P, Wiltschko W. 2010 The role of magnetite-based receptors in the beak in pigeon homing. *Curr. Biol.* **20**, 1534–1538.
53. Schiffner I, Wiltschko R 2014 The influence of social parameters on the homing behaviour of pigeons. *PLoS One* **9**, e112439.
- 595 54. Guilford T, Freeman R, Boyle D, Kirk H, Phillips R, Perrins C. 2011 A dispersive migration in the Atlantic puffin and its implications for migratory navigation. *PLoS One*. **6**, e21336.
55. Boon AK, Reale D, Boutin S. 2008 Personality, habitat use, and their consequences for survival in north American red squirrels. *Oikos* **117**, 1321–1328.
56. Wilson ADM, Godin JJ, Ward AJW. 2010 Boldness and reproductive fitness correlates in the Eastern mosquito fish. *Ethology*. **116**, 96–104.
- 600 57. Van Oers K, Drent PJ, Dingemanse NJ, Kempenaers B. 2008 Personality is associated with extra-pair copulation in great tits, *Parus major*. *Anim. Behav.* **76**, 555–563.
58. Reale D, Martin J, Coltman DW, Poissant J, Festa-Bienchet M. 2009 Male personality, life-history strategies and reproductive success in a promiscuous mammal. *J. Evol. Biol.* **22**, 1599–1607.
- 605 59. Santos



60. Biro PA, Stamps JA. 2010 Do consistent individual differences in metabolic rate promote consistent individual differences in behaviour? *Trends Ecol. Evol.* **25**, 653–659.
61. Careau V, Thomas D, Humphries MM, Reale D. 2008 Energy metabolism and animal personality. *Oikos* **117**, 641–653.
62. Portugal SJ, Green JA, Halsey LG, Arnold W, Careau V, Dann P, Frappell PB, Gremillet D, Handrich Y, Martin GR, Ruf T, Guillemette M, Butler PJ. 2016 Associations between resting, activity, and daily metabolic rate in free-living endotherms: no universal rule in birds and mammals. *Physiol. Biochem. Zool.* **89**, 251–261.
63. Usherwood JR, Stavrou M, Lowe JC, Roskilly K, Wilson AM. 2011 Flying in a flock comes at a cost in pigeons. *Nature* **474**, 494–497.
64. Pennycuik CJ. 1968. Power requirements for horizontal flight in the pigeon *Columba livia*. *J. Exp. Biol.* **49**, 527–555.
65. Mehlhorn J, Rehkaemper G. 2016 The influence of social parameters on the homing behaviour of pigeons. *PLoS One* **11**, e0166572.
66. Greggor AL, Jolles JW, Thornton A, Clayton NS. 2016 Seasonal changes in neophobia and its consistency in rooks: the effect of novelty type and dominance position. *Anim. Behav.* **121**, 11–20.
67. Biro D, Sasaji T, Portugal SJ. (2016) Bring a time-depth perspective to collective animal behaviour. *Trends Ecol. Evol.* **7**, 550–562.
68. Voelkl B, Portugal SJ, Unsold M, Usherwood JR, Wilson AM, Fritz J. 2015 Matching times of leading and following suggest cooperation through direct reciprocity during V-formation flight of Northern bald ibis. *PNAS (Proceedings of the National Academy of Sciences of the United States)*. **112**, 2115–2120.

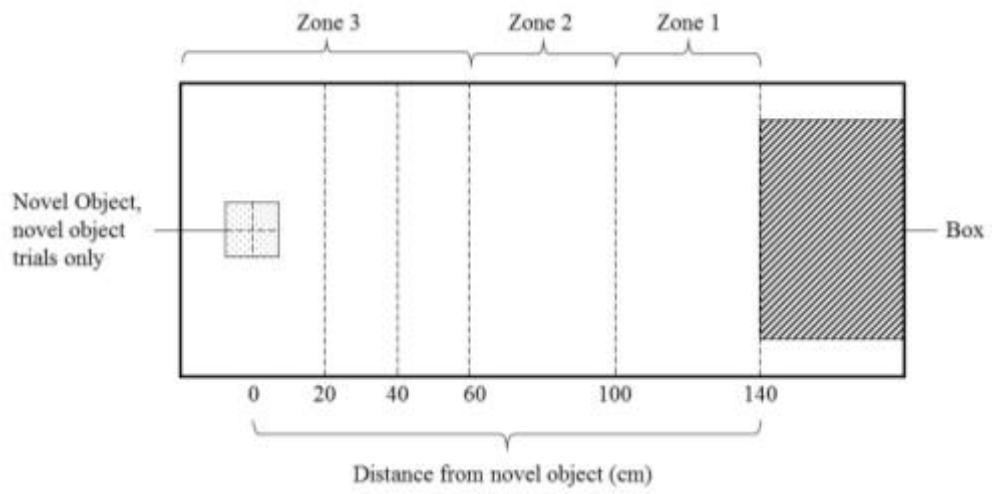
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**Table 1.**

Personality testing and dominance in 9 homing pigeons. Rank refers to the individuals' position within the dominance hierarchy as determined by David's Score (see main text). 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 (see 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).

<b>Pigeon ID</b>	<b>Body mass (g)</b>	<b>Tarsus length (mm)</b>	<b>Rank</b>	<b>Novel object (P) (score)</b>	<b>Novel object (P) (latency)</b>	<b>Novel object (J) (score)</b>	<b>Novel object (J) (latency)</b>	<b>Exploration (score)</b>
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

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

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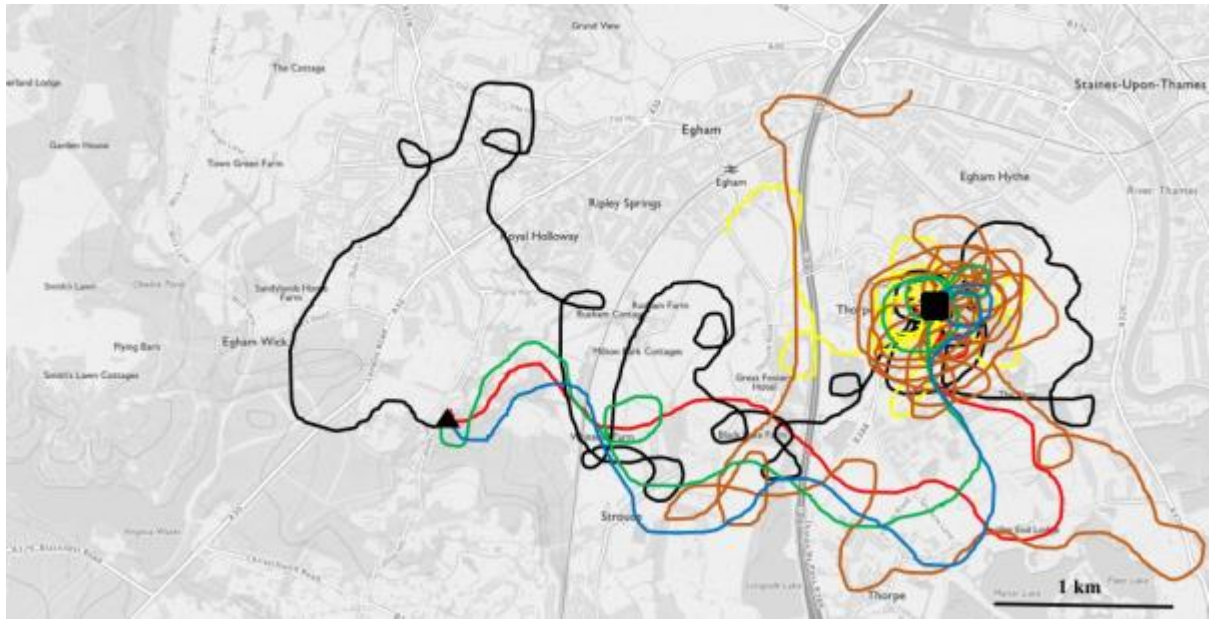


675 **Figure 2.** Initial homing flight from release site 2 (see table 2). Six pigeon GPS traces are  
 shown: pigeons 1 (green), 2 (black), 4 (yellow), 6 (red), 7 (blue) and 9 (brown) (see table 3).  
 The black triangle denotes the home loft, and the release site is represented by a black square.  
 Route efficiencies are detailed in table 4. Bird 4 did not return home within the battery-life of  
 the logger (*c.* 6 hours), and returned approximately 7.5 hours following release. Some initial  
 680 circling has been removed for presentation purposes. Background images taken and owned  
 by UK Ordnance Survey™.

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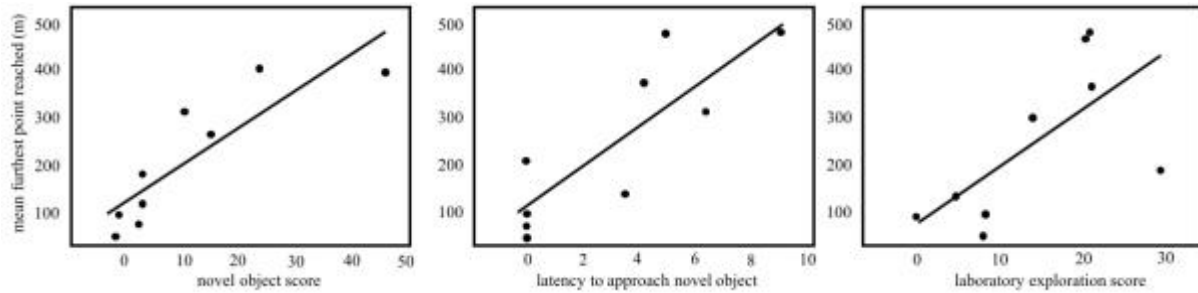
**Figure 3.** Initial homing flight from release site 6 (see table 2). Six pigeon GPS traces are shown: pigeons 1 (green), 2 (black), 4 (yellow), 6 (red), 7 (blue) and 9 (brown) (see table 3). The black triangle denotes the home loft, and the release site is represented by a black square. Route efficiencies are detailed in table 4. Birds 4 and 9 did not return home within the battery-life of the logger (*c.* 6 hours), 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™.

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**Figure 4.** Laboratory-based personality tests in 9 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, see table 1) versus mean (n = 3, full details in table 3) furthest point reaches (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)  $r^2 = 0.66$ ,  $F = 16.65$ ,  $P = 0.004$ , (b)  $r^2 = 0.72$ ,  $F = 21.15$ ,  $P = 0.002$ , (middle)  $r^2 = 0.50$ ,  $F = 8.94$ ,  $P = 0.02$ , and (right)  $r^2 = 0.39$ ,  $F = 6.06$ ,  $P = 0.043$  (see main text for regression equations).

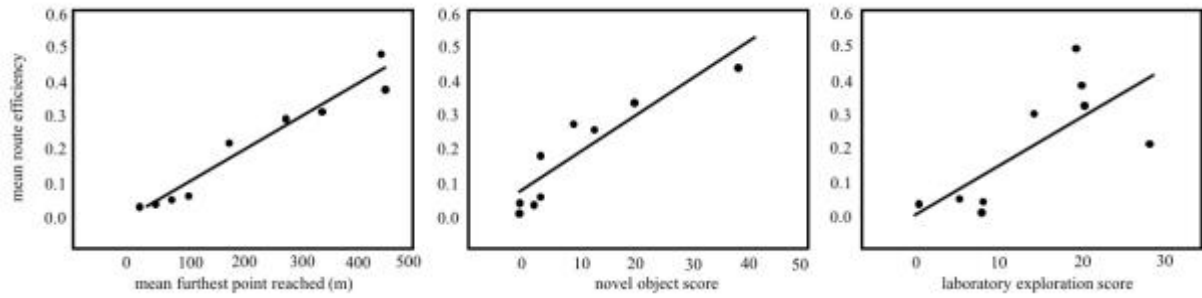
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**Figure 5.** (left) Mean furthest point reached (metres) during free-choice natural exploration flights versus mean route efficiency in 9 homing pigeons. Mean route efficiency (see supplementary table 4 for S.E.) versus (middle) novel object score (measured as time spent in respective zone close to novel object, see figure 1 and table 1), and (right) exploration score (see main text). 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 main text for regression equations).