

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

