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Short communication

Perch height predicts dominance rank in birds

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Dominant individuals within animal groups will frequently place themselves in the most beneficial position for maximal protection against predation. Higher perches are generally associated with reduced predation risk in birds, so we predicted that dominant birds will preferentially place themselves on higher perches. We tested this by determining the dominance hierarchy in two populations of captive birds (Homing Pigeons *Columba livia* and Great Cormorants *Phalacrocorax carbo*), and relating rank within the dominance hierarchy to observed perch height preferences. We found that perch choice was significantly repeatable in pigeons, and that more dominant individuals of both species selected higher perches. As well as facilitating early detection of and escape from potential predators, higher perches are also likely to facilitate the display of aggression to other group members.

Keywords: aggression, *Columba livia*, Cormorants, *Phalacrocorax carbo sinesis*, Pigeons, social structure.

It has long been established that living in groups confers benefits on each of the members by enhancing fitness above the level that would be accomplished through living solitarily (Alexander 1974). Such benefits can include enhanced vigilance and predator detection (Bill & Hernkind 1976, Stacey 1986, Elgar 1989, Pays *et al.* 2013), potential energetic saving through positive aero- or hydro-dynamic interactions (Liao *et al.* 2003, Portugal *et al.* 2014, Voelkl *et al.* 2015) and increased foraging efficiency (Pitcher *et al.* 1982, Brown 1988, Krause & Ruxton 2002). However, within single species groups, individual differences in physiology, morphology and personality can lead to conflicts and an outcome of these can be the emergence of dominance hierarchies (Chase *et al.* 2002). 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 (Cote 2000). These reductions result from individuals within the group having evaluated their chances of winning or losing such conflicts with particular individuals (Sloman & Armstrong 2002). 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 (Chase *et al.* 2002). Dominance hierarchies may be arranged in a linear fashion in which higher-ranked individuals dominate all individuals of lower rank (Cote 2000, Chase *et al.* 2002, Sloman & Armstrong 2002). Such a structure can result in the formation of stable group structures, but these can result in lower-ranked individuals having consistently reduced access to important resources such as food, mates, and nest and roost sites. Dominance hierarchies have often been linked to traits such as body mass and body size (e.g. tarsus length; French 2005, but see also Sarova *et al.* 2013), often with the larger individuals being top of the hierarchy (French 2005). One area that has received limited attention is how dominance manifests itself in the choice of individual positions within communal bird roosts. Variations in vulnerability to predation and in microclimate within a roost could result in the potential benefits of group roosting being unevenly distributed, and therefore higher ranking individuals may occupy favoured roost positions.

Using captive groups of Homing Pigeons *Columba livia* and Great Cormorants *Phalacrocorax carbo*, we tested the prediction that dominant individuals will preferentially select perches that place them physically above subordinates. It has previously been shown that in communal roosts of Rooks *Corvus frugilegus*, dominant individuals place themselves higher in roosting trees (Swingland 1977), but the generality of this finding has not been established. Great Cormorants are known to have preferred perches, returning to the same perch repeatedly, although the relationship between perch preference and rank within the dominance hierarchy is unknown (Reymondi & Zuchuat 1995).

METHODS

A group of 19 Homing Pigeons were housed at Royal Holloway (Egham, UK). All birds were 2 years old and

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had lived together since hatching. Birds were kept in a pigeon loft (dimensions 3.7 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, 1.30, 1.60 m), plus two additional single perches (1.30 m). Nine Great Cormorants (hereafter Cormorants) were collected under permit (English Nature) from nests at Rutland Water Nature Reserve (Oakham, UK) and housed in a 390-m^3 outdoor aviary at the University of Birmingham. Cormorants were identified to subspecies on the basis of gular pouch angle measurements (Newson *et al.* 2004), and comprised six *P. c. carbo*, one *P. c. sinensis* and two individuals with intermediate biometrics that may have been hybrids. The aviary had a ceiling height of 3 m and included 19 perches at heights ranging from 30 cm to 1.8 m; birds were also able to rest on the floor. The birds lived together from hatching and were between 12 and 16 months of age at the time of the study. Further details about husbandry can be found in full in White *et al.* (2007, 2008).

Determination of dominance

Dominance hierarchies in the Pigeons were studied between November 2015 and March 2016. Food was removed at 17:00 h on the day before each recording session. The following morning, all the pigeons were individually identified via a back-mounted sticker, and put into a pigeon carrier within their home loft, and 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 competing for access to the food. The first 30 min of agonistic interactions between all individuals following release from the carrier was analysed. Interactions recorded were: pecking, chasing, beak grabbing, neck grabbing and wing slapping (Supporting Information Video S1). The total number of interactions between individuals was recorded in a matrix, as initiators of aggressive acts (winners) or receivers of aggressive acts (losers) from each interaction. All aggressive interactions were recorded on the floor around the feeder. Preferred perch height and repeatability of perch choice for each individual Pigeon was determined 22 times by visual inspection of bird rings with a torch, 4 h after dusk, to ensure birds were fully roosted. Rings were inspected to determine perch fidelity and roosting perch height. Repeatability of perch selection was assessed using the 'ICCtest' function of the 'ICC' package v2.3.0 (Wolak *et al.* 2012) of R v2.2.2 (R Core Team, 2015, Vienna, Austria) to calculate an intra-class correlation coefficient from the variance components of a one-way ANOVA (Lessells & Boag 1987). The perch that each pigeon most commonly selected was then scored on an ordinal scale (1 = high, 2 = medium, 3 = low, 4 = ground), and a linear model was used to test for a relationship between perch height and David's score (see below).

For the Cormorants, birds were observed on 19 occasions during daylight during winter 2004–2005. Cormorants were hand-fed and so interacted with the feeder as much as with each other, hence agonistic interactions were observed outside feeding times. Agonistic interactions were defined as instances in which a bird chased or displaced another. Cormorants were also ranked on the basis of perch height selection. The height of a bird relative to its companions within 2 m in any direction was noted following feeding at other times throughout the day; birds were scored for relative height (i.e. scored as perching higher than or lower than neighbouring birds within 2 m) only when they were not engaged in agonistic interactions, and a distance of 2 m was selected because it was considered the approximate maximum distance over which pairs of birds might interact without moving. Due to differences in data recording, it was not possible to determine repeatability of perch selection in Cormorants because birds were scored only for their relative perch height compared with other birds within 2 m; the actual perch that they selected was not noted.

Agonistic interaction matrices for the Pigeons and Cormorants were used to produce a dominance hierarchy based on David's score (David 1987, 1988, Gammell *et al.* 2003). David's score is a measure of an individual's success in agonistic interactions, taking into account the relative strength of the other individuals with which an individual interacts. Large positive values of David's score identify individuals that are successful against many individuals, including against individuals that are themselves relatively successful. Large negative values identify individuals that are unsuccessful against many individuals, including against other individuals that are themselves usually unsuccessful.

Relative perch height data were used to construct a relative perch height selection matrix for each species, where the higher bird was considered the 'winner' of the interaction and the lower bird the 'loser'. David's scores were used to construct a second dominance hierarchy based on the perch height matrix. For Pigeons, David's scores based on the perch height matrix were not normally distributed (Shapiro–Wilk $W = 0.87$, $P = 0.01$), so Spearman's ρ was used to assess the relationship between David's scores calculated based on agonistic interactions and perch height selection.

Pearson's r was used for Cormorants. Trendlines were calculated using linear models for display. For both species, Pearson's r was used to assess the correlation between David's scores and body mass.

RESULTS

The repeatability of perch height selection was significantly greater than zero for Pigeons (Fig. 1a, intra-class correlation coefficient = 0.95; 95% confidence interval: 0.92–0.98), and Pigeons that selected high perches had significantly higher David's scores (i.e. were more aggressive) than Pigeons that selected low perches (Fig. 1b and 1c; $t_{17} = 3.19$, $P = 0.005$). Examination of the social network (Fig. 1b) shows a core of dominant, high-perching individuals with multiple reciprocated agonistic interactions, and a number of less well-connected subordinate low-perching individuals that are mostly the recipients of antagonistic interactions. Thus, interactions among dominant individuals are common and often bidirectional, whereas interactions between dominant and subordinate individuals are less common and are typically unidirectional.

For both Pigeons and Cormorants, there was a positive correlation between David's scores determined using agonistic interactions and perch height selection, indicating that dominant birds preferentially selected higher perches (Pigeons: Fig. 1d, Spearman's $\rho = 0.63$, $S = 421$, $P = 0.0004$; Cormorants: Fig. 1e, Pearson's $r = 0.69$, $t_7 = 2.52$, $P = 0.04$). For Pigeons, there was a significant correlation between body mass and David's score determined using agonistic interactions (Fig. 2a, $r = 0.73$, $t_{17} = 4.41$, $P = 0.004$), but not between body mass and David's score determined using perch height selection (Fig. 2b, $r = 0.44$, $t_{17} = 2.01$, $P = 0.06$). Similarly, for Cormorants there was a significant correlation between body mass and David's score determined using agonistic interactions (Fig. 2c, $r = 0.86$, $t_{17} = 4.57$, $P = 0.003$), but not between body mass and David's score determined using perch height selection (Fig. 2d, $r = 0.58$, $t_{17} = 1.89$, $P = 0.10$).

DISCUSSION

For both the Pigeons and Cormorants, there was a significant positive relationship between David's score and perch height, with birds that exhibited more aggressive behaviours favouring higher perches (Fig. 1). For both species, heavier birds had higher David's scores compared with lighter ones (Fig. 2), although the correlation was significant only for David's score determined by agonistic interactions ($P < 0.05$, Fig. 2a and 2c) and not for David's score determined by perch height selection ($P \leq 0.10$, Fig. 2b and 2d). Our results, therefore, suggest that dominant birds select higher perches than do subordinate birds, and that being heavier is associated with dominance.

The advantage of occupying a higher perch is likely to result from the birds' perceived risk of predation, as in natural environments being lower to the ground is likely to expose the bird to danger (Blumstein *et al.* 2004). For many passerines, for example, predation risk varies within a tree and is higher for the birds that use the outer parts of branches in the lower canopy (Ekman 1986, Suhonen 1993a,b) and the uppermost parts of young trees (Krams 2001). Moreover, a comprehensive study of flight intiation distance in response to disturbance found that 70% of the species studied flushed at greater distances when perched below 3 m (Blumstein *et al.* 2004). Although the wild counterparts of homing pigeons, Rock Doves, roost on cliff ledges as opposed to tree branches, it is likely that perceived risk is still not evenly distributed throughout a group when roosting.

For pigeons, a higher perch height on a ledge may confer benefits for escape speed during a predation event, or possible earlier detection of a predator (Newberry *et al.* 2001). When threatened by a bird of prey such as Peregrine Falcons *Falco peregrinus*, wild-type Rock Doves typically take flight as opposed to remaining on the cliff face (Cramp *et al.* 1994). A higher perch height would potentially allow a more rapid flight descent speed from the roost site, providing valuable escape time and a greater initial acceleration (Pennycuick 1989, Norberg 1990), reducing the chances of being predated. Similarly, higher perches may reduce energy expenditure and increase speed during take-off in general (Pennycuick 1989, Norberg 1990, Kullberg *et al.* 1998) and allow the dominant birds to take positions at the front of the flock, a position that has been shown to be more energetically profitable than being at the back (Usherwood *et al.* 2011). Although the perceived risk of predation is greater in the captive Pigeons than in wild birds, daily flights for exercise regularly brought the Pigeons into contact with local breeding raptors and it is likely, therefore, that the Pigeons perceived themselves as being under threat from potential predators.

Pigeons exhibited a high level of perch fidelity, with most birds returning to exactly the same perch every evening; perch fidelity has also been identified previously in Cormorants (Reymondi & Zuchuat 1995). Dominance hierarchies function to reduce direct conflict between members of a single-species group (Brown 1963, Smith 1976). It is likely that with the Pigeons, having a perch that each bird returns to for roosting acts to reduce conflict and limit direct aggressive interactions (Brown 1963, Smith 1976). The more dominant individuals demonstrated a higher degree of perch fidelity, along with choosing higher perches, than those birds ranked lower in the hierarchy (Fig. 1a), suggesting that

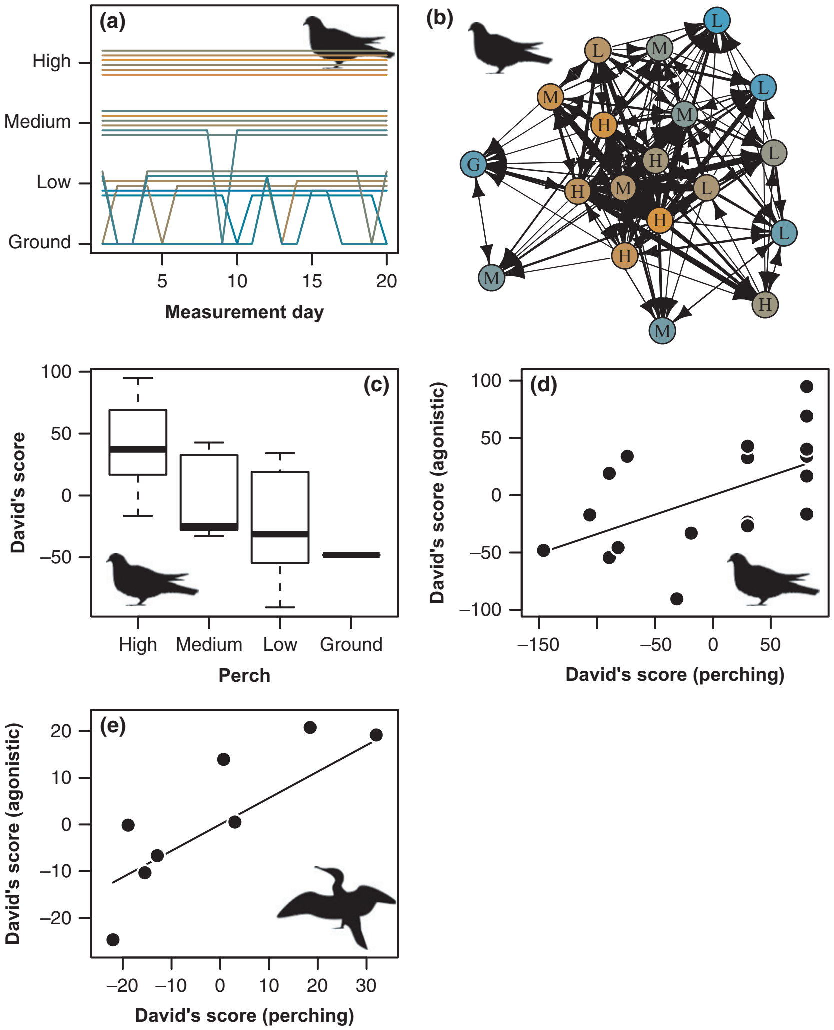

Figure 1. (a) Perch fidelity in 19 Homing Pigeons. Each line represents one individual, coloured by social status, from dominant (red) to subordinate (blue). The repeatability of perch height selection was significantly greater than zero (intraclass correlation coefficient = 0.95; 95% confidence interval: 0.92–0.98). (b) Social network for the 19 captive Homing Pigeons. Nodes coloured by social status, from dominant (red) to subordinate (blue). Arrows represent agonistic interactions between two individuals with lines proportional to number of interactions. Node codes refer to median perch height: H (high), M (medium), L (low) and G (ground). (c) The relationship between median perch height and David's score for the 19 Pigeons. Pigeons that selected high perches had significantly higher David's scores than Pigeons that selected low perches ($t_{17} = 3.19$, $P = 0.005$). (d,e) Correlations between David's score estimated from agonistic interactions and David's score estimated from perching behaviour, for Pigeons (d, $r = 0.55$, $t_{17} = 7.70$, $P = 0.02$) and Cormorants (e, $r = 0.69$, $t_7 = 2.52$, $P = 0.04$, $n = 9$).

either lower ranked individuals are fairly equal with respect to position within the hierarchy, or the greater choice of perch heights below the highest perches provides more opportunity for variation. It is possible that such a strict dominance hierarchy and associated perch fidelity is more prevalent in captive scenarios, where perch choices are limited, and a population is relatively closed and static in comparison with free-ranging individuals in a wild setting.

Higher perches have been linked to more successful prey capture (Greig-Smith 1983), and an increased scan zone for food, predator detection and incoming conspecifics to the roost (Fitzpatrick 1980). The link to conspecifics could be an explanation for the observed dominance–height pattern observed in the Cormorants, the structure of which is potentially less related to potential predation pressure than for the Homing Pigeons. More successful foragers have been observed

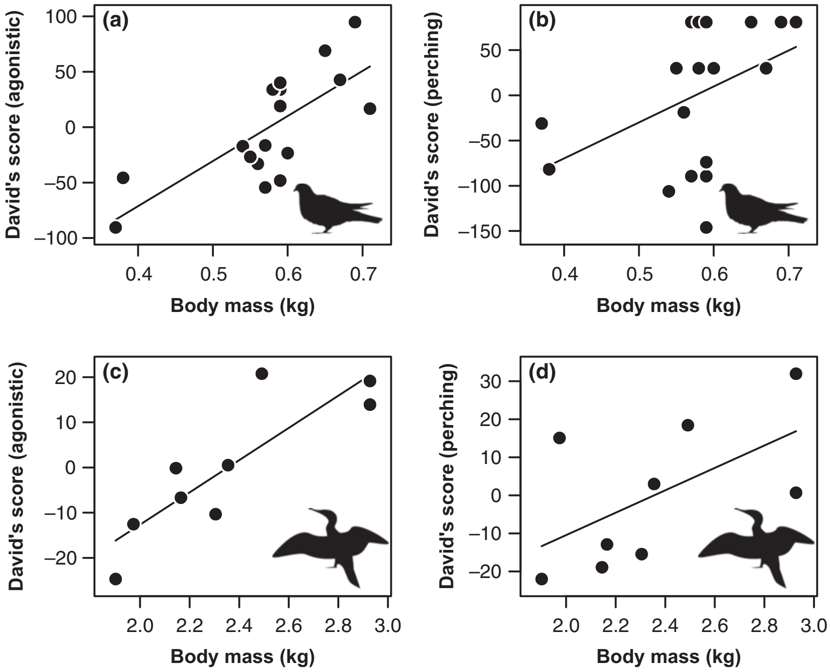

Figure 2. The relationship between dominance and body mass for (a,b) Pigeons and (c,d) Cormorants, with dominance assessed using David's score calculated from agonistic interactions (a,c) and perching preferences (b,d). The correlations between David's score and body mass are significant ($P < 0.05$) when David's score is assessed using agonistic interactions but not perching.

taking higher perches in avian groupings (Weatherhead, 1983), with higher perches generally perceived to be safer due to greater detection distance of predators and easier escape during a predation event. Subordinates tolerate this scenario whereby they are roosting in more vulnerable positions, as it provides them with an opportunity to follow these more successful foragers to superior feeding locations the following morning (Still *et al.* 1986). Moreover, higher perches in Cormorants may facilitate aggressive displays, allowing dominant birds to initiate antagonistic interactions with subordinates with only their beaks being vulnerable to return attack, whereas those subordinate birds perched below are more at risk of injury from dominant birds, having more of their bodies potentially exposed. Lastly, a greater height may provide thermoregulatory benefits for the dominant Cormorants or, more specifically, allow for more rapid drying of feathers. Wing-spreading is a common feature of Cormorants, and the duration of wing-spreading behaviour is influenced by the time spent in water, as Cormorant plumage is partially wettable (White *et al.* 2008). Higher perches may offer superior unobstructed heat and wind compared with lower perch heights, thus allowing dominant birds to dry their plumage quicker, reducing thermoregulatory costs and decreasing the time between potential aquatic foraging bouts.

The results from the current study, coupled with that of Swingland (1977), establish that more dominant individuals perch higher than subordinates in three species of birds from different avian orders. That this is the case in birds roosting on ledges (Pigeons) and trees (Cormorants, Rooks) suggests that an association between social dominance and perch selection may be a general relationship in birds, and the exact function of this phenomenon needs investigation.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Video S1. Neck grabbing and chasing.
Video S2. Wing slapping.