PERCH HEIGHT PREDICTS DOMINANCE RANK IN BIRDS

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Dominant individuals within animal groups will frequently place themselves in the

20 most beneficial position for maximal protection against predation, and for foraging

benefits. Higher perches are generally associated with reduced predation risk in birds,

so we hypothesized that dominant birds will preferentially place themselves on higher

perches, with subordinates typically perching at lower heights. We tested this

hypothesis 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. Higher

perches are also likely to facilitate the display of aggression to other group members,

30 while facilitating early detection and escape from potential predators. It is likely that

this perch fidelity and height choice may be exacerbated in captive scenarios due to a

closed population and limited area.

INTRODUCTION

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 as solitary individuals (Alexander 1974). Such benefits can include enhanced

vigilance and predator detection (Bill & Hernkind 1976, Elgar 1989, Pays *et al*. 2013,

Stacey 1986), potential energetic saving through positive aero- or hydro- dynamic

40 interactions (Liao *et al*. 2003, Portugal *et al*. 2014, Voelkl *et al*. 2015) and increased

foraging efficiency (Brown 1998, Pitcher *et al*. 2002, 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 50 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 (Chase *et al*. 2002 , Cote 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 including food, mates, and nest and roost sites. Dominance hierarchies have often been linked to traits such as body mass 60 and body size (e.g. tarsus length) (French 2005, but see also Sarova *et al*. 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 depredation and in microclimate within a roost could result in the potential benefits of group roosting to be unevenly distributed, and therefore, higher ranking individuals may occupy favoured roost positions.

Using captive groups of Homing Pigeons and Great Cormorants, we tested the hypothesis that dominant individuals will preferentially select perches that place them

physically above subordinates. It has previously been shown that in communal roosts

70   of Rooks (*Corvus frugilegus*), dominant individuals place themselves higher in

roosting trees (Swingland 1977), but the generality of this has not been established.

Great Cormorants are known to have preferred perches, returning to the same perch

repeatedly, though the relationship between perch preference and rank within the

dominance hierarchy is unknown (Reymondi & Zuchuat 1995).

METHODS

Birds

A group of 19 Homing Pigeons (*Columba livia*) (hereonin referred to as pigeons) were

housed at Royal Holloway (Egham, UK). All birds were two years old and had lived

80   together since hatching. Birds were kept in a pigeon loft (dimensions 12ft (long), 8ft

(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). Nine

Great Cormorants (*Phalacrocorax carbo*) (hereonin referred to as 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 meausrements (Newson *et al*. 2004), and were a mixture of six *P. c. carbo*, one

P. c. sinensis, and two individuals with intermediate biometrics that may represent

90   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) and White *et al*. (2008).

Determination of dominance

Dominance hierarchies in the pigeons were studied between November (2015) and March (2016). Food was removed at 17:00 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 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 feeder, thus 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. Interactions recorded were: pecking, chasing, beak grabbing, neck grabbing, and wing slapping (see Supplementary Video). 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. 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 hours after dusk, to ensure birds were fully roosted. Rings were inspected to determine (a) perch fidelity and (b) 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 (Lessels & Boag 1987). The perch that each pigeon most commonly selected was then scored on an ordinal scale (1 = highest, 2 = medium, 3 = low, 4 = ground), and a linear model was used to test for a relationship between perch height and David's score.

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 each other, and so agonistic interactions were observed outside of feeding times. Agonistic interactions were defined as instances where 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 neighboring 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. Unfortunately, due to differences in data recording, it is not possible to determine repeatability of perch selection in cormorants, because birds were scored only for their relative perch height compared to 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, David 1988, Gammell *et al*. 2003). David's score is a measure of 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 on the other hand, 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 was considered 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 pigeons and cormorants, 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 (Figure 1A, intraclass 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 (Figures 1B and 1C, $t_{17} = 3.19$, $P = 0.005$). Examination of the social network (Figure 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 agnostic interactions. Thus, interactions

among dominant individuals are common and often bidirectional, whereas interactions between dominant and subordinate individuals are less common and

170 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: Figure 1D, Spearman's $\rho = 0.63$, $S = 421$, $P = 0.0004$; cormorants: Figure 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 (Figure 2A, $r = 0.73$, $t_{17} = 4.41$, $P = 0.004$) but not between David's score determined using perch height selection (Figure 2B, $r = 0.44$, $t_{17} = 2.01$, $P = 0.06$). Similarly, for cormorants there

180 was a significant correlation between body mass and David's score determined using agonistic interactions (Figure 2C, $r = 0.86$, $t_{17} = 4.57$, $P = 0.003$) but not between David's score determined using perch height selection (Figure 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 (Figure 1). For both species, heavier birds had higher David's scores than lighter ones (Figure 2), though the correlation was

190 significant only for David's score determined by agonistic interactions ($P < 0.05$, Figures 2A and 2C) and not for David's score determined by perch height selection (P

≤ 0.10, Figures 2B and 2D). We therefore conclude that dominant birds select higher perches than 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 be more exposed to danger (Blumstein *et al*. 2004). It is likely that such variation in predation risk is a factor for all animal congregations (e.g. Bumann *et al*. 1997). Some previous field studies focusing on passerines have revealed that 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, Suhonen 1993b) 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 metres (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. Such structure in roost sites in particular suggests that dominant individuals are dictating the spatial arrangement of all individuals within the group (Mezquida *et al*. 2005), and it was noted that dominant pigeons would actively attack subordinates that attempted to land on higher perches (S. Portugal pers obs).

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, Simmons and Perrins, 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 upon. 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 in the captive pigeons is likely to be less of that in comparison to wild birds, daily flights for exercise regularly brought the pigeons into contact with local breeding raptors such as Sparrowhawks (*Accipiter nisus*), Peregrine Falcons, Common Buzzards (*Buteo buteo*), Common Kestrels (*Falco tinnunculus*), Red Kites (*Milvus milvus*) and Eurasian Hobbies (*Falco subbuteo*). It is likely, therefore, that the pigeons were under the perception as being under threat from potential predators.

Pigeons exhibited a high level of perch fidelity, with most birds returning to the same exact perch every evening, and perch fidelity has 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 (Figure 1A), suggesting that either lower ranked individuals are fairly equal with respect to position within the hierarchy, or the greater choice of perch heights below

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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 to free-ranging individuals in a wild setting.

The results from the current study, coupled with that of Swingland (1977) now establish that more dominant individuals perch higher than subordinates in three species of birds from different avian orders. Given that this is the case in birds
250 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 now the exact function of this phenomenon needs investigation.

Ethics

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

References

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Alexander R.D. 1974 The evolution of social behaviour. *Annual Rev. Ecol. Syst.* **5**, 325–383.

Bill, R.G. & Hernkind, W.F. 1976 Drag reduction by formation movement spiny lobsters. *Science* **193**, 1146−1148.

Blumstein, D.T., Fernandez-Juricic, E., LeDee, O., Larsen, E., Rodriguez-Prieto, I. & Zugmeyer, C. 2004 Avian risk assessment: effects of perching height and detectability. *Ethol.* **110**, 273–285.

Brown, J.L. 1963 Aggressiveness, dominance and social organizations in the Steller Jay. *Condor* **65**, 460–484.

Brown, J.S. 1988 Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.* **22**, 37–47.

280

Bumann, D., Krause, J. & Rubenstein, D. 1997 Mortality risk of spatial postions in animal groups: the danger of being in the front. *Behav.* **134**, 1063–1076.

Chase, I.D., Tovey, C, Spangler-Martin, D. & Manfredonia, M. 2002 Individual differences versus social dynamics in the formation of animal dominance hierarchies. *PNAS* **99**, 5744–5749.

Cramp, S., Simmons, K.E. & Perrins, C. 1977-1994 Handbook of the Birds of Europe, the Middle East and North Africa – the Birds of the Western Palearctic. Oxford, Oxford University Press. UK.

Cote, S.D. 2000 Dominance hierarchies in female mountain goats: stability, aggressiveness and determinants of rank. *Behaviour* **137**, 1541–1566.

David, HA. 1987 Ranking from unbalanced paired-comparison data. *Biometrika* **74**, 432–436.

David, H.A. 1988 The method of paired comparisons. London, Charles Griffin.

290

Ekman, J. 1986 Tree use and predator vulnerability of wintering passerines. *Ornis Scand.* **17**, 261–267

Elgar, MA. 1989 Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol. Rev.* **64**, 13–33.

French, A.R. 2005 Importance of body size in determining dominance hierarchies among diverse tropical frugivores. *Biotropica* **37**, 96–101.

Gammell, M.P., De Vries, H., Jennings, D.J., Carlin, C.M. & Hayden, T.J. 2003 David's score: a more appropriate dominance index ranking method than Clutton-Brock et al.'s index. *Anim. Behav.* **66**, 601–605.

Krams, I. 2001 Perch selection by singing chaffinches: a better view of surroundings and the risk of predation. *Behav. Ecol.* **12**, 295–300.

300

Krause, J. & Ruxton, G.D. 2002 Living in groups. Oxford University Press. UK.

Kullberg, C., Jakobsson, S. & Fransson, T. 1998 Predator-induced take-off strategy in great tits (*Parus major*). *Proc. Roy. Soc. B* **265**, 1659–1664.

Lessells, C.M. & P.T. Boag. 1987 Unrepeatable repeatabilities: A common mistake. *Auk* **104**, 116–121.

Liao, J.C., Beal, D.N., Lauder, G.V. & Triantafyllou, M.S. 2003 Fish exploiting vortices decrease muscle activity. *Science* **301**, 1566–1569.

Mezquida, E.T., Villaran, A. & Pascual-Parra, J. 2005 Microhabitat use and social structure in Linnet *Carduelis cannabina* and Corn Bunting *Miliaria calandra* at a winter roost in central Spain. *Bird Study* **52**, 323–329.

Newberry, R.C., Estevez, I. & Keeling, L.J. 2001 Group size and perching behavior in young domestic fowl. *App. Anim. Behav. Sci.* **73**, 117–129.

Newson, S.E.B., Hughes, I.C., Russell, G.R. & Sellers, R.M. 2004 Sub-specific differentiation and distribution of Great Cormorants *Phalacrocorax carbo* in Europe. *Ardea* **92**, 3–10.

Norberg, U.M. 1990 Vertebrate flight. Spring-Verlag.

Pays, O., Beauchamp, G., Carter, A.J. & Goldizen, A.W. 2013 Foraging in groups allows collective predator detection in a mammal species without alarm calls *Behav Ecol*. **24**, 1229–1236.

Pennycuick, C.J. 1989 Bird flight performance. Oxford, Oxford University Press. UK.

Pitcher, T.J., Magurran, A.E. & Winfield, I.J. 1982 Fish in larger shoals find food faster. *Behav. Ecol. Sociobiol*. **10**, 149–151.

Portugal, S.J., Hubel, T.Y., Fritz, J., Heese, S., Trobe, D., Voelkl, B., Hailes, S., Wilson, A.M. & Usherwood, J.R. 2014 Upwash exploitation and downwash avoidance by flap phasing in ibis formation flight. *Nature* **505**, 399−402.

Reymondi, A. & Zuchuat, O. 1995 Perch fidelity of cormorants *Phalacrocorax carbo* outside the breeding season. *Ardea* **83,** 281–284.

Sarova, R., Spinka, M., Stehulova, I., Ceacero F., Simeckova, M., Kotrba & R. 2013 Pay respect to the elders: age more than body mass, determines dominance in female beef cattle. *Anim. Behav*. **86**, 1315–1323.

Sloman, K.A. & Armstrong, J.D. 2002 Physiological effects of dominance hierarchies: laboratory artefacts or natural phenomena? *J. Fish Biol*. **61**, 1–23.

Smith, S.M. 1976 Ecological aspects of dominance hierarchies in black-capped chickadees. *Auk* **93**, 95–107.

Stacey, P.B. 1986 Group size and foraging efficiency in yellow baboons. *Behav. Ecol. Sociobiol*. **18**, 175–187.

Suhonen, J. 1993a Predation risk influences the use of foraging sites by tits. *Ecology* **74**, 1197–1203.

Suhonen, J. 1993b Risk of predation and foraging sites of individuals in mixed-species tit flocks. *Anim. Behav*. **45**, 1193–1198.

Swingland, IR. 1977 The social and spatial organization of winter communal roosting in Rooks (*Corvus frugilegus*). *J. Zool*. **182**, 509–528.

Usherwood, J.R., Stavrou, M., Lowe, J.C., Roskilly, K. & Wilson, A.M. 2011 Flying in a flock comes at a cost in pigeons. *Nature* **474**, 494–497.

Voelkl, B., Portugal, S.J., Unsold, M., Usherwood, J.R., Wilson, A.M. & 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.

White, C.R., Day, N., Butler, P.J. & Martin, G.R. 2007 Vision and foraging in cormorants: more like herons than hawks. *PLoS One* **2**, e639.

White, C.R., Martin, G.R. & Butler, P.J. 2008 Wing-spreading, wing-drying and food-warming in great cormorants, *Phalacrocorax carbo*. *J. Avian Biol.* **39**, 576–578.

Wolak, M.E., Fairbairn, D.J. & Paulsen, Y.R. 2012 Guidelines for estimating repeatability. *Methods in Ecol. Evol.* **3**, 129–5137.
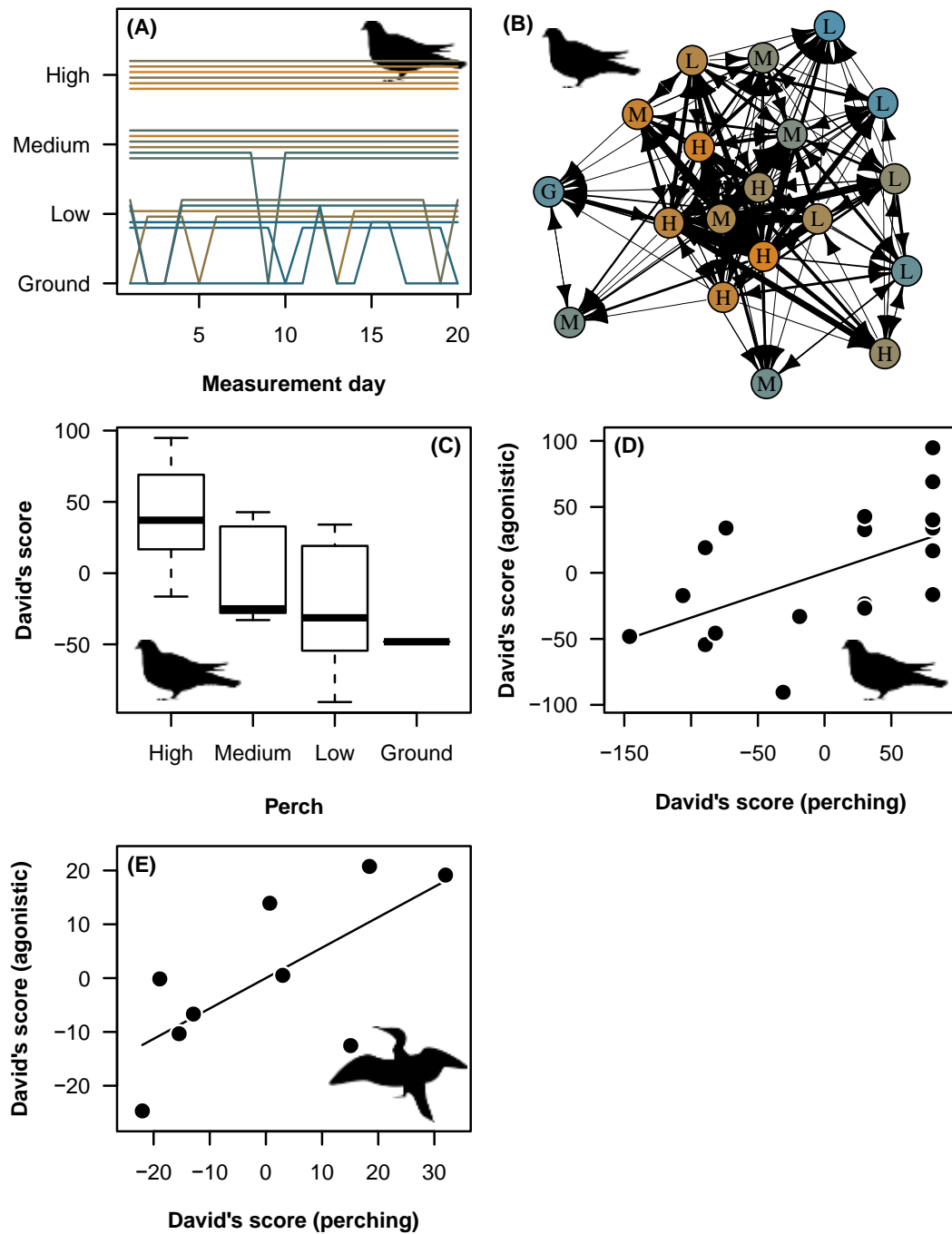
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Figure 1. (a) Perch fidelity in 19 homing pigeons. Each line represents one individual, coloured by social status, from dominant (red) to subordinate (blue). The repeatability of perch height selection was significantly greater than zero (intraclass 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 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).
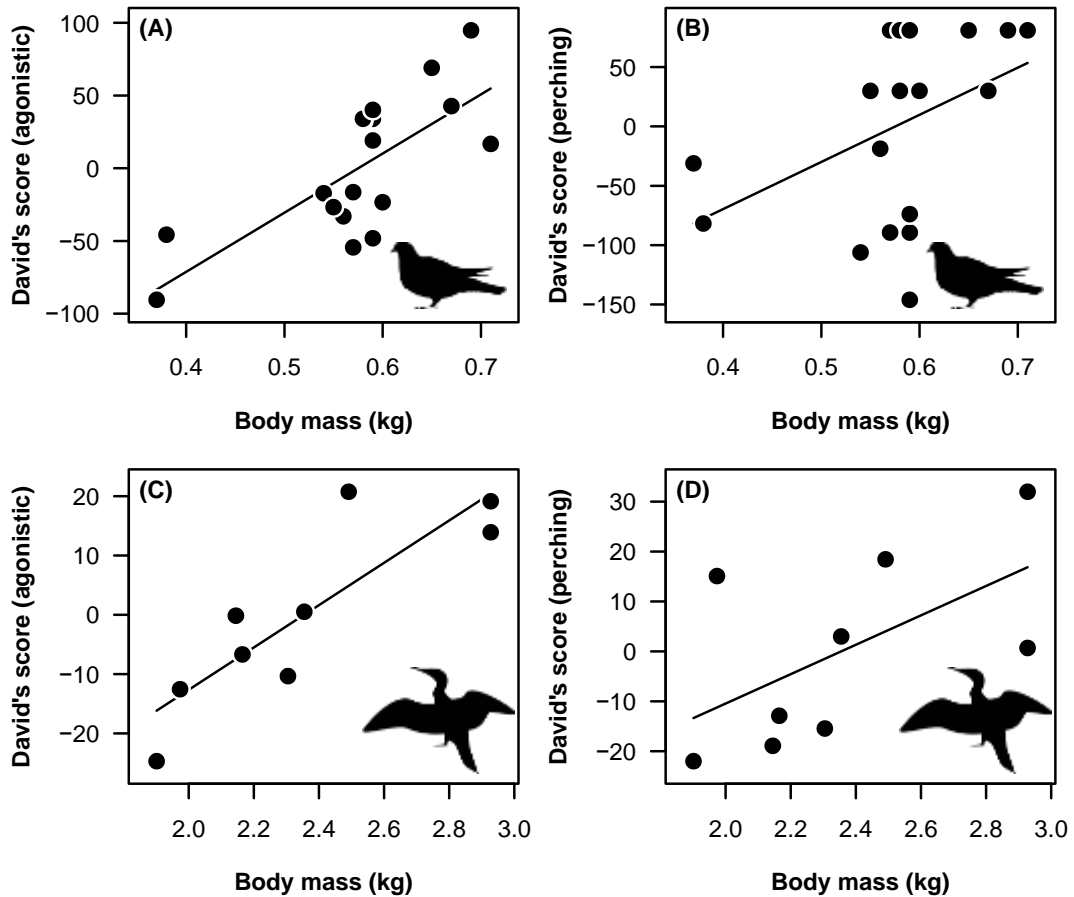
Figure 2. The relationship between dominance and body mass for (A, B) pigeons and (C, D) cormorants, with dominance assessed using David's score calculated from agonistic interactions (A, C) and perching preferences (B, D). The correlations between David's score and body mass are significant ($P < 0.05$) when David's score is assessed using agonistic interactions but not perching.