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When a Duck Initiates Movement, Do Others Follow? Testing Preference in Groups

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Abstract

Choice tests have been widely used to assess animal preferences. In the case of group-living species, these tests are commonly presented to animals in groups, because isolation can have strong effects on behaviour and motivation. However, assessing preference at the group level could be misleading if strong control of movement, through influential individuals, and group cohesion were present. The needs of majority of the population might not be properly represented by the test results. The current study investigated whether or not groups of ducks (four ducklings per group) have individuals that consistently initiate movement and considered the implications for group cohesion, synchronisation and a measure of preference during a choice test. In all groups included in the analyses, there were ducks that initiated more movements than the rest, and this trend was stronger when leading towards areas providing resources such as pools. Also, more ducks preferentially followed the first initiator (birds initiating most movements within a group) into the bathing area. Group cohesion was higher in groups that frequently had the same individual initiating movement. The number of followers following the ducks that initiated most movements was associated with the measure of preference (time spent at preferred area, as a proportion of total time spent at any area) but the number of movements initiated by these individuals was not. These results highlight the need to consider the effects of initiators and group-cohesive forces when conducting choice tests in groups of animals.

Keywords: choice test, cohesion, duck, leadership, movement initiators, social control

Introduction

Leadership has been referred to as the initiation of movements by one or more individuals who are then followed by other group members (Krause et al. 2000). One individual in a group may control when and where group movements occur. The controller of the movement may be the initiator, that is the one that moves first, or the leader, that is the one followed by the others, but may be neither (Broom 1981). When benefits arise from moving together, leader-follower patterns are likely to emerge (King 2010). However, the motivations of leaders and followers may differ because of their different needs (Conradt 1998). Furthermore, when individuals have reduced space availability, more allelomimetic behaviours develop with swifter social facilitation and higher cohesion (Camazine et al. 2001; Conradt & Roper 2003). Hence small groups of animals might behave in an extremely cohesive way, overlooking their own needs to favour social facilitation.

Social controllers of movement may present a problem for choice or preference tests performed in groups. Preference or choice tests are conducted to empirically evaluate preference or avoidance over two or more defined options. They have been used to make decisions about what animals should have access to in captive environments (Mason et al. 2001) and are used in behavioural and sensory ecology to understand how animals make decisions which have fitness consequences. They have also been used to understand behaviour by examining how groups of animals distribute themselves between two or more options (e.g. Zirbes et al. 2010). However, in despotic groups where one individual may be responsible for determining the majority of movements, preference or choice measures of the group could be reflecting the preferences or choices of the despot.

The processes of leading or controlling movement have been little documented in birds. Some studies in zebra finches have revealed that consistent controllers of movement are found in foraging pairs but that control was adjustable when new foraging pairs were formed (Beuchamp 2000). Referring to barnacle geese, Kurvers et al. (2009) described strong correlations between leadership and individual personality and how an individual's movements within a group were affected by the personality of other group members. It has been also reported that geese exhibit stable differences in behavioural traits (Pfeffer et al. 2002) and that closely-bonded individuals cluster during group movements (Ramseyer et al. 2009). In captive dabbling ducks, linear hierarchies have been described (Poisbleau et al. 2005) where dominance allowed for feeding- site monopolisation when resources were limited.

In recent years, researchers have agreed upon the fact that open water (water that allows at least head immersion) significantly improves the welfare of domestic ducks (Heyn et al. 2006; Waite et al. 2009; Jones & Dawkins 2010; O'Driscoll & Broom 2011), and choice tests have been conducted to assess the ducks' motivation for this type of resources (Cooper et al. 2002; Reiter 2003; Jones et al. 2009). Preference testing of isolated individuals could be stressful and misleading for

group-living species (Sherwin 2003). However, if preference is tested in groups of ducks and one individual has control over the group movements, the results would show the preferences of only one animal per group and would not be representative of the needs of all members of the flock.

When a choice test was performed to assess duck preferences for different types of pools (Liste et al. 2012), it was observed that groups with very strong preferences for one type of resource did not appear to visit the other option, suggesting highly cohesive groups. In this study, we investigated whether or not in small test-groups of ducklings, some individuals consistently initiate movements and are followed by the rest. This could also have implications for cohesion and synchronisation in the group. Moreover, we hypothesise that social control, leading and synchronisation could be resource-related, meaning that initiators or leaders might start a higher proportion of movements, attract more followers and facilitate the groups' clustering and cohesion when trying to access-specific resource areas (such as a bathing pool). Due to the observed results on the choice test mentioned previously (Liste et al. 2012), we expect to find identifiable initiators in most of the groups under study, and that these individuals will keep their roles steadily over time. It is also expected to observe ducklings moving in a more synchronised manner and following a more consistent initiator when moving towards the areas of the testing pens with a pool in them. The current paper uses previously recorded video images (Liste et al. 2012, but with a different research purpose) to reanalyse the animals' movements under a new perspective, considering factors such as group dynamics and cohesion that have been traditionally overlooked in choice test research.

Materials and Methods

The video images used in the current study are from a previous choice test, see Liste et al. (2012) for details, designed to compare the preference of Pekin ducks, *Anas platyrhynchos*, for different types of open water resources (pools). Ducklings belonged to a commercial enterprise (Cherry Valley Ltd. Lincolnshire, UK) and the study took place in one of their commercial farms, where the animals were brooded complying with RSPCA welfare standards for ducks (RSPCA 2011). At 21 d, the ducklings were moved to a test barn within the same farm. Ducklings of mixed sex were housed in groups of four, and 16 groups were tested in total accounting for 64 individuals included in the experiment. The test barn was divided into eight experimental pens and two replications were conducted, from May to August 2010, to complete the 16 experimental groups. Each of the four ducklings introduced to a testing pen was individually identified by marking the back with coloured spray. Pens consisted of virtually separated sectors with different resources on them: a straw-bedded zone (19.2 m²) where feeders were placed and animals could rest and eat, a raised drained platform with a perforated plastic floor (7.2 m²) where water-related resources (drinkers and pools) were placed, and a grooved concrete ramp (3.6 m²) connecting the two previous sections (for more details and a diagram of the test pens see Liste et al. 2012). The total floor area per pen was 30 m². Birds

were fed ad libitum, a standard commercial duck feed appropriate for their age. The bedding was topped up as needed and pools were emptied, cleaned and refilled once a week. At the end of the study, test ducklings were processed with the rest of the flock following commercial practices. The trial was approved by the ethical committee at the Veterinary School, University of Cambridge. As the study was purely observational and animals were not subjected to stressful manipulations other than those included in routine farm rearing, no other licences or permits were needed for the study.

The ducklings' behaviour was recorded using a CCTV system (WebCCTV NVR, from QuadroX, Herent, Belgium) and CCTV cameras (Sony CXD3142R, with 2.45 mm board lens, model BL2.45) between 29 and 48 d of age. Twenty-four hour video recordings were watched by a single observer on six specific days for the current analyses: days 29, 34, 36, 41, 43 and 48 post-hatch. Behaviour was continuously observed and movements between pen areas were recorded. For the current experiment, three pen areas were defined as: 'the bathing area' where pools were placed and ducks could engage in significant water-related activities such as drinking, dabbling and bathing at the pool, 'the feeding/resting area' straw-bedded area where feeders were placed and ducks could eat and rest, and 'the transition area' which included the pool platform decks, bell drinkers and grooved transition ramps. Within the bathing areas, two pools of different depths were available (one pool of 10 cm depth and a 20 or 30 cm depth option, depending on the choice being offered to the ducks). The time spent in each pool type was also recorded.

Statistical Analysis

In 12 of the original 16 groups, there were sufficient movements between areas (more than 90) to be included in the current analyses. The results from Dumont et al. (2005) suggest approx. 30 group movements are needed to detect individual differences in group movements (up to nine observation days were needed to detect differences with an average of three movements per day). We wished to detect differences in each of the three pen areas and so 90 was considered a sufficient number of movements. If any of the experimental groups had fewer than nine movements between pen areas within one observation day, these days were excluded from the analyses. Three of the 12 groups had 2 d of recordings excluded, one had 1 d of recordings excluded and the remaining eight groups had all six observation days included in the analyses. The total number of movements initiated per observation and group ranged from 114 to 550 (mean \pm standard deviation = 231 ± 80). When divided by the three pen areas, all areas were visited a mean of 58 times (± 32 , standard deviation). Ducks were considered to initiate a movement if they were the first in the group to move into an unoccupied pen area. The four ducks in each group were categorised according to the proportion of times they initiated movements. The individual initiating most movements across all 6 days of observation in a group was called Initiator 1; the one initiating the second highest number of movements was Initiator 2 and, similarly, Initiator 3 and Initiator 4. The proportion of movements by the Initiator 1 duck was compared with the 0.25

expected by chance using a one sample, one-sided t-test.

The proportion of movements initiated was analysed using general linear mixed models with restricted maximum likelihood (REML) through the lme function in the nlme package (Pinheiro et al. 2005). The proportion of movements made on each day of observation by each duck was transformed using the arcsine root transformation. The proportion of movements initiated was examined with initiator status, pen area and the interaction between these as fixed effects, observation day as a covariate and group was considered as a random effect. F values were used to test for fixed effects using the ANOVA.lme command. The random effects allowed for data from repeated sampling to be used without pseudoreplication effects.

For each movement initiated into an unoccupied area of the pen, the number of ducks that followed was recorded and then the mean number of followers for each initiated movement was calculated for each duck and pen area on each observation day. The mean number of followers was examined as a response variable with initiator status, pen area and the interaction between these as fixed effects and group was included as a random effect (using the lme and ANOVA.lme functions as above).

The time spent in the preferred pool, as a proportion of the total time spent in the bathing area for each group on each day, was used as a measure of strength of preference (as in Liste et al. 2012). The proportion of time spent in the preferred bathing area was also transformed using the arcsine root transformation. The proportion of time spent in the preferred bathing area was examined with the mean number of followers and the total proportion of movements initiated by Initiator 1 included as fixed effects, observation day as a covariate and group as a random effect (using the lme and ANOVA.lme functions as above).

Finally, cluster scores were calculated as the maximum number of ducks in one area divided by the total number of areas occupied (Collins et al. 2011). Cluster scores were calculated after each scored movement within the group. To exclude possibly that cluster scores were not independent of the number of movement transitions made, a general linear mixed model examined the mean cluster score per observation against the total transitions made in that observation as a fixed effect, with pen as a random effect (using the lme command and ANOVA.lme, as outlined above). The mean cluster score and proportion of all movements initiated by Initiator 1 were calculated per group and analysed with a Pearson's correlation. All analyses were conducted using R (R Development Core Team 2011) with F and p values presented for the models.

Results

All groups included in the analyses contained ducks that initiated significantly more movements than the 25% expected by chance ($t = 14.00$ $p < 0.001$). In nine of the

twelve groups, one individual (Initiator 1) consistently initiated most movements to unoccupied areas on all days of observation. In the three remaining groups, the same individual initiated most of the movements on at least 50% of observed days (Table 1).

An interaction effect between pen area and initiator status was found ($F_{6,424} = 2.50, p = 0.022$). There was a higher likelihood of Initiator 1 initiating movements into the bathing area than any other duck. When moving towards this pen area, Initiator 1 initiated a higher proportion of movements than Initiator 2, by an estimated mean of 0.05 ± 0.02 ($p = 0.04$), Initiator 3, estimated mean of 0.06 ± 0.02 ($p = 0.01$) and Initiator 4, estimated mean of 0.04 ± 0.02 ($p = 0.05$). The proportion of movements initiated was not statistically significant for initiator status for any other pen areas. No effects of observation day could be found.

An interaction between pen area and initiator status was found for the number of ducks following each initiator ($F_{6,423} = 4.67, p < 0.001$). More ducks preferentially followed Initiator 1 into the bathing area (Fig. 1b) than Initiator 2 by an estimated mean of 0.46 ± 0.21 ($p = 0.02$), Initiator 3 by 0.55 ± 0.21 ($p = 0.01$) and Initiator 4 by 0.65 ± 0.21 ($p = 0.01$). The number of ducks following each initiator was not statistically significant for any other pen areas. No effects of observation day could be found.

The measure of preference, proportion of time spend in the preferred water resource, was significantly associated with the number of followers, but not the proportion of movements initiated by Initiator 1. For each additional mean follower of Initiator 1, the proportion of time spent in preferred water resource was increased by an estimated 0.21 ± 0.04 ($F_{1,30} = 4.98, p = 0.03$).

The overall mean cluster score was 1.89 ± 0.45 which indicates that three ducks or more were often together in the same location. Cluster scores were independent of the total transitions made within an observation ($F_{1,40} = 0.00, p = 0.99$), but mean cluster scores were higher when the proportion of movements initiated by Initiator 1 was higher (Fig. 2, $r = 0.669, n = 12, p = 0.017$).

Discussion

Clear initiators were found in the current study, and it was apparent that they controlled movements as they were followed by group members, especially when going into the pools. This could indicate leadership, and not just activity synchronisation (Dumont et al. 2005), because of the consistency found in the initiators throughout the trial. The best explanation for consistency in animal order during spontaneous group movements is the existence of leadership (Lamprecht 1991; Sueur 2011). If we accept that ducks in this study have shown evidence of leadership, the nature of this leadership influenced measures of preference. The strength of preference for a water resource, as measured in a preference test using these same ducks (Liste et al. 2012), was affected by the strength of followership of

the leader (number of ducks that followed Initiator 1). But the number of movements initiated by the 'leader' duck (Initiator 1) did not affect the measure of preference. In this case, the leader's influence on group behaviour was indicated

Table 1: Number of days of observation in which each duck (categorised according to its Initiator status) initiated the most movements to unoccupied areas of the pen

	Pen 1	Pen 2	Pen 3	Pen 4	Pen 5	Pen 6	Pen 7	Pen 8	Pen 9	Pen 10	Pen 11	Pen 12
Initiator 1	100%	50%	100%	100%	100%	100%	60%	100%	50%	100%	100%	100%
Initiator 2	0%	25%	0%	0%	0%	0%	20%	0%	25%	0%	0%	0%
Initiator 3	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
Initiator 4	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%

Figure 1. (a) Proportion of movements initiated by each duck (regarded by its Initiator status) to each pen area across all observation days. (b) Mean number of individuals following each duck (regarded by its Initiator status) when moving into the different pen areas across all observation days.

Figure 2. Cohesiveness of groups according to movement initiation: Correlation between mean clustering scores (maximum number of ducks in one area divided by the total number of areas occupied) across all pens and observation days and mean proportion of movements initiated by Initiator 1. not only by the attempts to lead, through initiation of movement, but also by the success in leading the group, through initiated movements that were followed by other group members. There are several features of the current study which may have supported the formation of leaders. The consistency in initiation of movements is important because when groups are stable the probability for an exclusive individual leader is higher (Reinhardt 1983). In the current study, the initiator order was found to be consistent across time with a quick development of social organisation, by 29 d of age, which stayed unaltered for at least three more weeks. The ducks in this study

were all of the same age and type, so their needs should have been similar. A consensus cost can arise if individuals with needs which are in conflict with the group can be offset by the benefits of maintaining group cohesion (Conradt & Roper 2005). It is not clear whether individuals followed because their motivation was similar to that of the initiators, resulting in a low consensus cost, or had different motivations but were driven to follow the initiator to retain group cohesion, resulting in a higher consensus cost. Individual animals can have a bigger influence in movement decisions in small groups (as was the case in this study) rather than large groups (Dumont et al. 2005; Krüvers et al. 2011). It has been observed that geese do not push others or prompt others to move away when initiating movements (Ramseyer et al. 2009), and ducks in the present study behaved similarly. Ducks were confined in pens and study areas were small making it difficult for animal order to be altered once started.

Group cohesion is usually considered to depend both on the behaviour and identity of the initiator of a movement (Johnstone & Manica 2011) and on the behavioural state of the potential followers. In some species, witnessing the movement of a conspecific is sufficient to initiate movement in others (Pillot et al. 2010). Ducks in this study were choosy about who they followed, preferring to follow first initiators. In general, individuals are more likely to be initiators if they have particular morphological, physiological or behavioural traits that increase their propensity to act first or have a lower giving up propensity than their group-mates (Krause et al. 2000). The propensity to act may be dynamic and variable, and individuals with the greatest needs at any time could determine the group behaviour (Conradt et al. 2009; Rands 2011). Research into following decisions within a group has primarily focused on perceived knowledge (Reebs 2000) and the way knowledge might be shared (Sumpter et al. 2008). Understanding individual roles in following behaviour has perhaps been less well explored. Krüvers et al. (2009) found that the boldness of both leaders and followers in pairs of geese determined success in locating foraging patches. In a cohesive group, an initiated movement only becomes a consensus decision when other group members follow. Thus followers can be just as influential in determining group movement decisions as initiators (Stueckle & Zinner 2008). Such studies highlight the importance of considering individual roles in following as well as initiating movement.

In the current study, having a clear initiator, which could be indicative of strong controllers of group activities, meant the groups were more cohesive and clustered. Furthermore, in group choice tests, cohesive forces could prevent individuals from moving around freely and could limit the display of choice. From observations made during the previous choice test (Liste et al. 2012), it was clear that in the groups where ducks displayed strong preferences (more than 90% of the bathing time in the same pool) the animals moved less and had consistent initiators. Researchers conducting choice tests need to consider carefully the potential effects of factors affecting group behaviour on study design and interpretation of results. Whilst conducting choice tests in the absence of group members may be stressful, misleading and lacking in external validity, conducting preference testing in groups

may represent the decisions of the few rather than the many. This is most true for cohesive despotic groups where one individual controls most group movements, as suggested by the ducks in this study. In different species or group compositions cohesion might be lower, movements may be more equally distributed among group members or cohesion may be maintained through shared motivation (such as it has been found in small groups of laying hens, Asher et al. 2013). Preference testing performed on such groups would be more representative of the needs of the many than in despotic groups. When choice testing in despotic groups, it may be more appropriate to consider each 'choice' as reflective of the preferences of only the animal that initiated the movement.

It seems that domestication and factors associated with farming, such as very large flocks living together in unnatural environments and lack of phenotypical differentiation, have not eliminated leadership in ducks, especially when approaching specific resources such as bathing water. There are reported differences in behaviour between domestic and mallard ducks. A study comparing adult Aylesbury vs. mallard ducks found marked differences in the amount of time fighting and performing dominance behaviours (Desforges 1973). It was concluded that domestication had affected the social behaviours of ducks, but a great deal of variation was found due to individual differences, mainly regarding tolerance of subordinates. In general, fighting and dominance was reduced in domestic ducks, and they also rested closer and less scattered than mallards. However, space use and social organisation are dependent of the type of activity so bathing behaviour could differ from resting or fighting.

Additional experiments should be performed to uncover how the mechanisms underlying the observed patterns in movement initiation work. A wider study with a bigger sample size including different treatments would probably offer clearer information about the topic and the reasoning behind the movement decisions discussed above. Treatments such as different group sizes or different resources in the areas under study are some examples that could be further investigated.

In conclusion, the current analyses and discussions are just an example that could be applied to any choice test performed on group-living animals to help assessing the relevance of the test's results. Studies of captive populations, including farmed species, can provide great scope for investigating the role of certain individuals in group behaviour. Moreover, this type of research will not only provide insight into the evolution and maintenance of social behaviour, but also could inform management of social species at the farm level and be helpful to efforts to improve welfare.

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