



Mallards Feed Longer to Maintain Intake Rate under Competition on a Natural Food Distribution

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Abstract

Animals foraging in groups may benefit from a faster detection of food and predators, but competition by conspecifics may reduce intake rate. Competition may also alter the foraging behaviour of individuals, which can be influenced by dominance status and the way food is distributed over the environment. Many studies measuring the effects of competition and dominance status have been conducted on a uniform or highly clumped food distribution, while in reality prey distributions are often in-between these two extremes. The few studies that used a more natural food distribution only detected subtle effects of interference and dominance. We therefore conducted an experiment on a natural food distribution with focal mallards *Anas platyrhynchos* foraging alone and in a group of three, having a dominant, intermediate or subordinate dominance status. In this way, the foraging behaviour of the same individual in different treatments could be compared, and the effect of dominance was tested independently of individual identity. The experiment was balanced using a 4 × 4 Latin square design, with four focal and six non-focal birds. Individuals in a group achieved a similar intake rate (i.e. number of consumed seeds divided by trial length) as when foraging alone, because of an increase in the proportion of time feeding (albeit not significant for subordinate birds). Patch residence time and the number of different patches visited did not differ when birds were foraging alone or in a group. Besides some agonistic interactions, no differences in foraging behaviour between dominant, intermediate and subordinate birds were measured in group trials. Possibly group-foraging birds increased their feeding time because there was less need for vigilance or because they increased foraging intensity to compensate for competition. This study underlines that a higher competitor density does not necessarily lead to a lower intake rate, irrespective of dominance status.

Introduction

Foraging together with competitors may be beneficial or detrimental to the individuals involved. Group foraging generally increases safety, because potential predators are detected faster due to the many-eyes effect (Pulliam 1973; Clark & Mangel 1986), predation risk is diluted (Neill & Cullen

1974), and predators may be less effective as they get confused during an attack (Krakauer 1995). Group foraging may also have the additional benefit of faster location of food patches (Clark & Mangel 1984, 1986), in which resources can be shared, reducing the variance in food encounter rate (Giraldeau & Beauchamp 1999). With the use of public information, collected by observing the foraging

success of others, individuals can assess the quality of resource patches or locate the good-quality patches easier (Templeton & Giraldeau 1995).

Both the spatial position in a group and food availability can affect the foraging success of individuals in a group. Foraging at the edge of a group increases vigilance and lowers the foraging success of birds in contrast to individuals foraging at the centre of flocks (Beauchamp 2005; Fernández-Juricic & Beauchamp 2008). When food is limited, the number of foragers can depress an individual's feeding rate (Hake & Ekman 1988). When this is caused through the depletion of available prey, it is called exploitative or scramble competition (Krebs 1978). Caused through behavioural interactions, such as aggression, kleptoparasitism or by creating a barrier to a resource (Brockmann & Barnard 1979; Kotrschal et al. 1993; Shealer & Burger 1993), it is collectively termed interference or contest competition (Miller 1967). However, interference competition may also be very subtle without apparent interactions. For instance, the presence of foraging companions might induce self-imposed reductions in feeding rates, independently of resources or interactions with foragers (Gauvin & Giraldeau 2004). Dominance status of group foraging individuals plays an important role, affecting foraging behaviour and energy intake (Desrochers 1989; Henderson & Hart 1995; Smith et al. 2001). Dominant birds may monopolise the high-quality patches (Theimer 1987; Vahl et al. 2005a), forcing subordinates to positions where they experience a higher predation risk and lower food intake (Schneider 1984; Koivula et al. 1994).

The way food is dispersed in the environment may determine competition strength and interact with the effects of dominance status. In a homogeneous environment for example, where all patches have the same quality, foragers gain an equal intake rate and dominance status has little to no effect on the foraging success of individual flock members (Vahl et al. 2005a; Gyimesi et al. 2010). However, when food is highly clumped, interference competition reduces the intake rate of group-foraging birds (Gyimesi et al. 2010), and dominant birds are able to monopolise the high-quality patches, hereby reducing the foraging success of subordinate birds (Vahl et al. 2005a). In reality, the distribution of prey densities is commonly not uniform nor highly clustered but has a spatial structure in-between these extremes (Klaassen & Nolet 2008; Kraan et al. 2009).

Besides a highly clumped and uniform food distribution, Gyimesi et al. (2010) also studied interference competition and effects of dominance on a

natural food distribution. Birds in groups of two had a lower intake rate compared with single foragers, but among group-foraging birds, dominant birds did not gain a significantly higher intake rate than subordinates. Only subtle effects of interference and dominance have been detected on a natural food distribution compared with those on a highly clumped food distribution. So, before we can extrapolate these results to the field, more work on natural food distributions, for instance with larger group sizes and better control for individual identity, is needed. We therefore decided to conduct an experiment on a natural food distribution in which birds were foraging alone and in a group of three, experimentally manipulating their dominance status. Focal birds were tested in our experiment equally often as singles or in groups, as the dominant, intermediate or subordinate individual. This enabled us to compare the foraging behaviour of the same individuals in different treatments, estimate the variance of all treatment groups equally well and test for the effect of dominance independently of individual identity.

The experiment was conducted with mallards *Anas platyrhynchos* in which the effects of competitor density and dominance status on the behaviour of focal individuals were measured on a natural food distribution (hereafter called moderately clumped). To ensure that food depletion did not affect intake rate in the trials, the duration of both single and group trials was kept short. It was expected that the interactions while competing for the high density patches would lead to a loss of foraging time and consequently a lower intake rate while foraging in a group than when foraging alone. Furthermore, in search for high density patches, group foragers were expected to visit more patches but on average spend less time per patch (i.e. a lower patch residence time), compared with single foragers. We also expected that after controlling for individual identity, dominant individuals would occupy the high density patches and hereby realise a higher intake rate than lower-ranked individuals. Owing to the monopolisation of the high density patches, dominant individuals would visit fewer patches, have a longer patch residence time and therefore forage longer than subordinates.

Methods

Subjects and Housing

We used female mallards (>1 yr), as the focus was competition for food and not for mates. Previous

experiments with mallards in a similar setting have shown that they are easy to handle and perform well in foraging trials (Klaassen et al. 2007; Gyimesi et al. 2010). All birds were captive bred: 11 birds originated from a waterfowl breeder (P. Kooy & Sons, 't Zand, The Netherlands) and two birds were bred at the Netherlands Institute of Ecology. All birds had been kept at our waterfowl facility at the NIOO-KNAW in Nieuwersluis for at least a year prior to the experiment. The birds were individually marked with colour rings to allow visual recognition, and the primary feathers of one wing were clipped to prevent the birds from flying. The mallards were jointly housed in an outdoor aviary (10 × 5 × 2 m height), with access to a freshwater pond and shelter in the form of tall vegetation surrounding the aviary. Food consisted of a mixture of commercial food pellets and seed-based mixed grains, which was provided in two food dispensers. Drinking water was always available. Experimental trials were carried out in an indoor waterfowl experimental facility, containing a water-filled basin (2 × 2 m). All trials took place in spring (Apr.–May 2008). During the training period and experiment, the birds were set on a strict feeding regime, in which they only received a fixed amount of food (400 g) in the afternoon in the outdoor aviary. After the study, the birds were set on an *ad libitum* feeding regime in the aviary. The experiment received ethical approval by the KNAW Animal Experiment Commission (DEC protocol CL0801).

Pre-Experimental Treatment

The first 17 d, we determined the dominance hierarchy of the birds by 0.5-h observations in the outdoor aviary, both in the morning and during feeding in the afternoon when the birds were allowed to feed *ad libitum* from the food dispensers. Each agonistic interaction ($n = 746$) between the individuals was scored in a dominance matrix, which is the most efficient way to determine the dominance status of individuals (de Vries et al. 1993; Poisbleau et al. 2006). Winners were those individuals that either chased their opponent away or that held ground after being attacked (Vahl et al. 2005a). A linear dominance hierarchy for mallards was found, in accordance with results of other studies (Poisbleau et al. 2005, 2006). By making a graphical representation, we could select those individuals that were consistently dominant, intermediate or subordinate (Fig. 1). In total, six non-focal birds were selected, namely three birds from the highest and three from

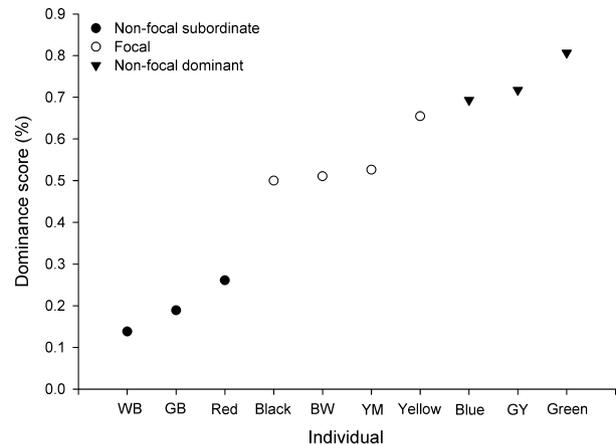


Fig. 1: Dominance score (%) of each individual participating in the experiment, calculated as the number of interactions won divided by the total number of interactions of a given individual bird.

the lowest-ranking individuals, assigned as dominant non-focals and subordinate non-focals, respectively. Of the intermediate-ranking group, four birds were selected and assigned as focal individuals. The remaining three individuals served as a back-up for the birds participating in the experiment (but eventually did not have to be used) and remained in the outdoor aviary to maintain a stable dominance hierarchy.

After determining the dominance hierarchy, the birds were familiarised with the experimental environment, procedures and experimentators. In 13 pilot days, each bird participated only once a day, either alone in a single trial or together with two competitors in group trials.

Food Distribution

Mallards are sensitive to the spatial pattern of the food distribution and the food density thereof and use pre-harvest information (i.e. prior knowledge of the food distribution acquired during earlier visits) in their assessment of the content of patches (Klaassen et al. 2007). Pondweed tuber densities (g/m^2) and spatial variation in density, measured in 2001 in the Lauwersmeer area (Nolet et al. 2006), were used as a template as mallards are known to forage on pondweed tubers (Anderson & Low 1976; Combs & Fredrickson 1996). Four wheat grain densities, of 5, 10, 20 and 40 seeds per tray (11, 23, 46 and 91 g/m^2 , respectively), were offered in 64 plastic trays (15 × 15 × 8 cm each), representing patches (Fig. 2). Of the 64 trays, six trays were filled with five seeds, 15 with 10 seeds, 35 with 20 seeds, and

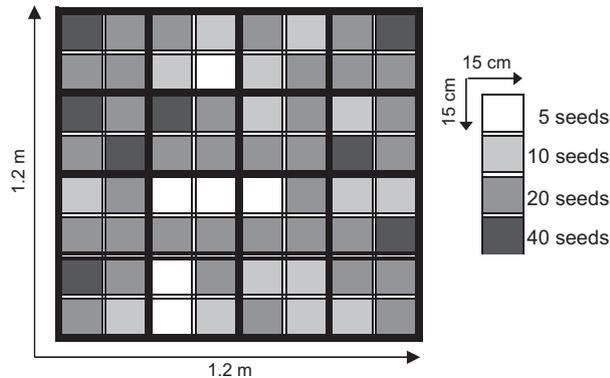


Fig. 2: Moderately clumped food distribution used in the experiment.

eight with 40 seeds (1200 seeds; 61.7 ± 3.5 g) and covered with sand to avoid the visual detection of seeds. The trays were placed next to each other at the bottom of the water-filled basin, forming a total of 1.2×1.2 -m foraging area. The water level above these trays was kept at 32 cm above the sediment, enabling the mallards to reach the food by up-ending (i.e. feeding with the posterior part of the body pointing upward and the anterior part of the body submerged; Cramp & Simmons 1977). Seed density did not vary within and between trials, but to prevent the birds from knowing the exact position of the rich corner of the food distribution, the original set-up was rotated daily in a random order of 90° , 180° or 270° . In this way, the absolute positions of the food patches changed each day, while the same food distribution was used.

Experimental Design and Procedure

The design used for the experiment was a 4×4 Latin square. The effect of four treatments was studied using four focal individuals, with each treatment and focal bird occurring once a day (to correct for day effects and to assure equal motivation), resulting in four consecutive experimental days. The four treatments consisted of a focal bird (1) foraging solitarily, or foraging in a group of three being either; (2) dominant; (3) intermediate; or (4) subordinate. A focal individual was assigned as being dominant, intermediate or subordinate, depending on the dominance status of accompanying non-focal birds: together with two subordinate non-focal birds, the focal was dominant; together with both a dominant and subordinate non-focal bird, the focal bird had an intermediate dominance status, and together with two dominant non-focal birds, the focal was subordinate. Non-focal individuals were also scheduled to

take part in trials once a day to assure the same motivational status. The same 4×4 Latin square design was replicated immediately after finishing the first series, using the same focal and non-focal individuals. This resulted in 31 trials in total (for unknown reasons, one focal bird did not participate during one trial).

All experimental trials were carried out between 0700 and 1600 h. Birds participating in trials were caught in animal transport cages with the help of a sluice system in the outdoor aviary and transported to the experimental room. Before the start of each trial, the birds were weighed in the transport cages to monitor their condition. Observations were carried out from an adjacent room through a one-way window. Trial time was kept short to minimise effects of depletion; both single and group trials lasted 60 s, starting when the first individual started to forage. The foraging behaviour of the mallards was recorded with a digital video camera (Panasonic NV-GS15; 0.8 Megapixels), positioned approximately 2.5 m above the basin.

Data Analysis

After each trial, the content of all trays was sieved over a 2-mm sieve, and the number of seeds was counted to determine the consumed number of seeds per tray. The sieving error, estimated as the number of seeds miscounted from trays where the birds had not fed, was marginal (average 0.2%, $n = 23$ trays).

The recorded trials were analysed with Observer 5.0 (Noldus Information Technology, Wageningen, The Netherlands) at one-fifth of the normal speed. For each focal individual, the proportion of time feeding (i.e. head under water) per trial, feeding time per tray per visit (patch residence time) and the number of different trays visited per trial were registered. A focal bird was considered to visit a patch when the head was under water and clearly visibly in the tray. To assess the intake rate (seeds/s) over the trial per focal bird, the number of consumed seeds was divided by the total trial length (i.e. the time spent feeding, plus swimming and food processing time with the head above water). For each trial, the mean patch residence time was calculated.

When a non-focal bird had foraged from the same tray before or after a focal bird fed at that tray, this had to be taken into account in the assessment of the number of consumed seeds. We determined the instantaneous intake rate (seeds/s feeding) for each focal bird, by including only those trays where only

the focal had foraged from during the experiment. Per dominance trial (i.e. dominant, intermediate and subordinate), an average instantaneous intake rate was calculated for each of the four seed densities. This instantaneous intake rate multiplied by the time the focal bird had foraged from that tray gave the number of consumed seeds. The instantaneous intake rate was based on the seed density left in the tray, so when a non-focal bird was the first to feed from a tray, the number of seeds consumed by the non-focal was calculated and subtracted from the original seed density. The instantaneous intake rate of the non-focal birds was based on the data of all focal birds together, separately per dominance status and seed density.

Generalised linear models (GLMs) were performed with trial type (i.e. single, group subordinate, group intermediate and group dominant) as the main factor of interest, and focal bird, replicate (i.e. first or second series) and day as random factors. Tukey *post hoc* tests were used to identify differences in behaviour between birds foraging alone and in a group having a dominant, intermediate or subordinate status, as well as differences between group-foraging birds with a different dominance status. All analyses were two tailed. Model assumptions were checked. All data were normally distributed, which was confirmed by Kolmogorov–Smirnov tests. The variances in each experimental condition were similar, which was tested with a Levene's test. Observations were independent, and sample sizes fairly balanced. All statistical analyses were conducted using SPSS 17.0 (SPSS Inc., Chicago, IL, USA).

Results

Generalised linear model results are given in Table 1. Intake rate did not differ between focal birds foraging alone or in a group, with either having a subordinate, intermediate or dominant status (see also

Fig. 3a). However, the proportion of feeding per trial time differed among treatments. Contrary to our expectation, birds foraging in a group being either intermediate ($p = 0.040$) or dominant ($p = 0.038$) were feeding a larger proportion of the trial time than when foraging alone (Fig. 3b), while subordinate birds foraging in a group were feeding a similar proportion of the trial time as when foraging alone ($p = 0.203$). Feeding time did not vary among group-foraging birds with a different dominance status: subordinate birds were feeding a similar proportion of the time as intermediate ($p = 0.828$) and dominant birds ($p = 0.778$), and intermediate birds were feeding a similar proportion of the time as dominant birds ($p = 0.999$). Also not in line with our expectations, patch residence time did not differ when foraging alone or in a group, having either a subordinate, intermediate or dominant status (Fig. 3c), and the number of different trays visited by focal mallards did not differ among treatments (Fig. 3d). No effect of depletion was measured in single and group trials (Table 2).

In five of 23 group trials, agonistic interactions were observed with the focal bird being the attacker or being attacked: three subordinate trials (subordinate focal attacked by dominant non-focal), one intermediate trial (intermediate focal attacked by dominant non-focal) and one dominant trial (dominant focal attacked subordinate non-focal). All the observed agonistic interactions were in the expected direction, with higher-ranked individuals attacking lower-ranked ones.

Discussion

Group-foraging birds managed to achieve a similar intake rate as when foraging alone, which could be explained by the longer feeding time, i.e. intermediate and dominant birds were feeding a larger proportion of the trial time than solitary foragers. Other

Table 1: Results of the mixed model with trial type (i.e. single, group subordinate, group intermediate and group dominant) as fixed factor, and focal bird, replicate and day as random factors

	df	Intake rate (seeds/s)		Time feeding (%)		Patch residence time (s)		Visited trays	
		F	p	F	p	F	p	F	p
Intercept	1	45.976	0.021	271.766	0.000	86.547	0.005	357.573	0.011
Trial type	3	1.129	0.361	3.425	0.037	2.145	0.126	1.992	0.148
Focal bird	3	3.700	0.029	23.458	0.000	12.217	0.000	3.447	0.036
Replicate	1	7.788	0.011	3.542	0.074	0.000	0.995	0.046	0.833
Day	3	2.047	0.140	0.373	0.774	1.144	0.356	1.050	0.392

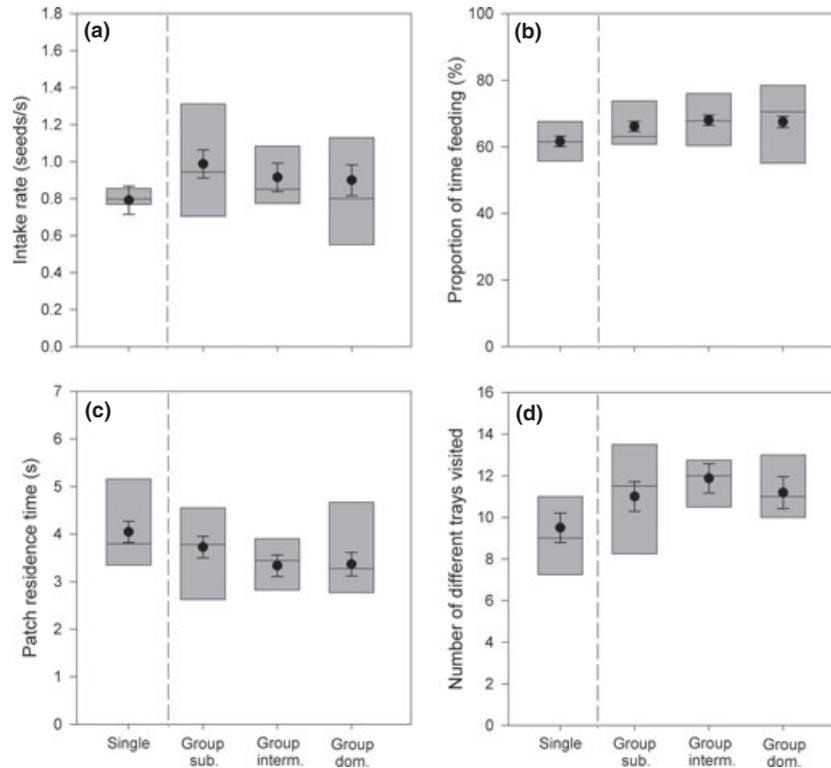


Fig. 3: Focal mallards foraging alone or with two competitors, with the focal having a subordinate, intermediate or dominant status. (a) Intake rate, (b) proportion of time feeding per trial, (c) patch residence time and (d) number of different trays visited. Box plots give medians and 25%- and 75% quartiles. Error bars give $\bar{x} \pm SE$, after correcting for individual differences, replicate and day.

Table 2: Percentage of seeds left in the trays at the end of single and group trials, with group trials divided in subordinate, intermediate and dominant regarding the dominance status of the focal mallard. The number of seeds left in the trays after foraging is given between brackets. Each trial started with a total number of 1200 seeds

	Series 1				Series 2			
	Day 1	Day 2	Day 3	Day 4	Day 1	Day 2	Day 3	Day 4
Single	98 (1170)	96 (1149)	96 (1154)	96 (1150)	96 (1152)	95 (1138)	96 (1147)	96 (1152)
Group subordinate	88 (1058)	88 (1061)	89 (1068)	91 (1090)	89 (1070)	81 (972)	88 (1056)	81 (977)
Group intermediate	88 (1054)	88 (1053)	91 (1089)	85 (1025)	84 (1008)	90 (1084)	88 (1053)	88 (1061)
Group dominant	89 (1063)	91 (1096)	86 (1036)	87 (1045)	91 (1091)	83 (990)	89 (1063)	85 (1023)

differences between solitary and group foragers were not significant, so neither the number of patches visited nor the patch residence time differed between group and solitarily foraging birds. When comparing our results with the study of Gyimesi et al. (2010) where group density was lower (two instead of three individuals), group foragers apparently did not suffer more from interference competition in terms of a reduction in intake rate in our experiment. Instead, it seems that birds foraging in a group of three are able to compensate for the decrease in intake rate caused by competition by foraging longer.

It is very difficult to assess the causes responsible for individuals to feed longer when foraging in a group. One reason how birds in a group can forage

longer, thereby increasing their foraging rate, might be a reduction in vigilance for predators (Cresswell 1997; Beauchamp 1998). Group-foraging redshanks *Tringa totanus*, for example, are able to maintain their intake under competition by foraging a greater proportion of their time because of a decrease in individual vigilance (Sansom et al. 2008). Also laboratory experiments have shown that even in well-trained birds, a reduction in vigilance was observed with an increase in group size (Beauchamp & Livoireil 1997; Gauvin & Giraldeau 2004; Vahl et al. 2005b). Besides vigilance for predators, birds may also be vigilant to observe the behaviour and decisions of group members to assess the quality of resource patches (i.e. public information; Valone

1989). Vigilance is generally scored when a bird raises its head from the head-down foraging position to at least a horizontal position ('head-up vigilance'; Metcalfe 1984), but this is a difficult measure to score as mallards normally have their head in a horizontal position, for instance when swimming or after foraging up-ending, and these behaviours cannot be attributed solely to vigilant behaviour. Hence, we cannot exclude that a reduction in vigilant behaviour also contributed to the increase in the proportion of time feeding in our group-foraging mallards.

Another reason for birds to change their behaviour when foraging in a larger group might be increased competition for resources (Clark & Mangel 1986; Beauchamp 2003). For instance, in nutmeg mannikins *Lonchura punctulata*, the increase in feeding rate with group size was attributed to increased competitive pressure (Rieucan & Giraldeau 2009). Similar results were found in the diving behaviour of tufted ducks *Aythya fuligula*, suggesting that birds in a larger group were foraging more intensively than when foraging alone (Halsey et al. 2006). This explanation might well be applicable in our study, namely that group-foraging birds with an intermediate or dominant status were able to increase the proportion of time feeding by foraging more intensively. We did not detect a significant increase in the number of visited trays or a decrease in patch residence time in group-foraging birds as was expected. However, a clear trend is visible, which could imply that birds in a group, especially birds with an intermediate or dominant status, are foraging slightly more intensively than when foraging alone. Though, it seems that intensive foraging may also come with a cost: the number of unsuccessful pecks in our study was higher in group trials (12 of 23) than in single trials (1 of 8). This could explain that despite the fact that group-foraging birds were feeding a larger proportion of the time, they did not achieve a higher intake rate than when foraging alone. Competitive pressure could also explain why solitary mallards did not feed longer to increase their intake rate: perhaps solitary mallards learned that in single trials, there was no competition for food, and therefore their work load was lower compared with group foragers. While interference competition is expected to have a negative effect on intake rate of group-foraging mallards, increased foraging intensity may mask these effects. Interestingly, intermediate and dominant group-foraging birds increased foraging intensity, possibly to limit the effects of exploitative competition (although this probably would only take effect

on a longer run than our experimental trials). It would be interesting to include exploitative competition explicitly in future experiments by allowing trials to be longer.

One of the limitations of this study could be the small sample size of four focal individuals (note that 13 individuals were needed in total because non-focals were included in the experiment). Nevertheless, with this number, we could perfectly balance our experiment (a 4×4 Latin square design) with four individuals participating in the experiment as singles, dominants, intermediates and subordinates, and with all four treatments carried out on a single day (to correct for day effects) with each mallard participating only once a day (to assure equal motivation), which allowed us to correct for differences among individuals. A larger sample size, while sticking to this balanced design, would have implied an 8×8 Latin square design, resulting in eight treatment trials per day, and an increase from 13 to 26 birds. This was practically unfeasible because the four trials per day already covered a large part of the day (0700–1600 h). In addition, it is important to point out that each individual should be equally motivated to participate in each trial. With eight trials per day, this is difficult to achieve because the individuals participating in the last trials would be starving much longer than individuals participating in the first trials.

To conduct this experiment in a proper way, trial time had to be reasonably long to measure effects of interference competition and dominance, but, on the other hand, had to be kept short to minimise depletion to ensure that measured effects were attributed to interference instead of exploitative competition. Trial time had to be similar for single and group trials to compare differences in foraging behaviour of focal birds. Based on these criteria, trial time was set at 60 s for single and group trials. Results show that depletion effects were successfully avoided during the experiment, and differences in foraging behaviour could be assigned to interference competition. In group trials, we did not measure differences in foraging behaviour between dominant, intermediate and subordinate birds, even though we observed some agonistic interactions between individuals. One explanation could be the short trial time, which inhibits dominant birds to effectively use their status to achieve a higher intake rate than lower-ranked individuals on a moderately clumped food distribution. However, in the study of Gyimesi et al. (2010), where trial time was set at 120 s, dominant birds were visiting fewer patches and were feeding longer

per patch, but this did not result in a higher intake rate. Thus, even when trial time was twice as long, no effect of dominance status on intake rate was measured. To prevent the birds from learning this short trial time, we varied the trial time during the training period between 30 and 180 s. A second possibility for the lack of dominance effects detected in this study could be the fact that mallards were feeding by up-ending, which could make it more difficult to observe competitors and for dominants to find the high density patches on a moderately clumped food distribution. However, in this study, we observed dominant birds attacking subordinates despite the up-ending. The potential benefit dominant birds achieved by these interactions could be the increase in the proportion of time feeding compared with foraging alone, while this difference was not measured in subordinates.

In conclusion, our findings demonstrate that on a moderately clumped food distribution, individuals foraging in a group, except for subordinate birds, achieve a similar intake rate as when foraging alone because of an increase in the proportion of time feeding. When foraging in a group, dominant birds achieve a similar intake rate as lower-ranked individuals.

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