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Benefits of foraging in small groups: An experimental study on public information use in red knots *Calidris canutus*

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ABSTRACT

Social foraging is common and may provide benefits of safety and public information. Public information permits faster and more accurate estimates of patch resource densities, thus allowing more effective foraging. In this paper we report on two experiments with red knots *Calidris canutus*, socially foraging shorebirds that eat bivalves on intertidal mudflats. The first experiment was designed to show that red knots are capable of using public information, and whether dominance status or sex affected its use. We showed that knots can detect the foraging success of conspecifics and choose a patch accordingly. Neither dominance status nor sex influenced public information use. In the second experiment, by manipulating group size, we investigated whether public information use affected food-patch discovery rates and patch residence times. We showed that the time needed before locating a food patch decreased in proportion to group size. Also, an individual's number of patch visits before locating the food declined with group size, and, to our surprise, their average patch residence time did as well. Moreover, knots differed in their search strategy in that some birds consistently exploited the searching efforts of others. We conclude that socially foraging knots have the potential to greatly increase their food-finding rate by using public information.

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1. Introduction

Foraging in groups, i.e. 'social foraging', is a common phenomenon (Beauchamp, 2014; Clark and Mangel, 1986; Danchin et al., 2008; Krause and Ruxton, 2002; Stephens et al., 2007; Sumpter, 2010). The main cost of social foraging is competition for resources (Goss-Custard, 1980; Tregenza, 1995). The benefits of social foraging include increased safety from predation (Pulliam, 1973), increased time that could be spent foraging rather than on anti-predation vigilance (Lima, 1995), and the accessibility of public information on the availability and quality of food patches (Clark and Mangel, 1984; Dall et al., 2005; Danchin et al., 2004; Giraldeau and Dubois, 2008; Valone, 2007). There is a growing body of literature on public information use in a range of different species (see Blanchet et al., 2010; Rieucau and Giraldeau, 2011; Valone, 2007). Public information was originally narrowly defined as 'information on the quality of a food patch' (Valone, 1989). Following Wagner and Danchin (2010), we adopt the broad and intuitive definition of public information as 'any potential information that is accessible to others' (i.e. any information that is not private).

Public information can indicate the location of food (local enhancement, Pöysä, 1992; Thorpe, 1956), as well as the quality (e.g., food density) of a food patch (Valone, 1989). Many different species use local enhancement to select where to eat (Galef and Giraldeau, 2001). It is especially beneficial when food is clumped and patches are large enough not to be monopolised (Beauchamp, 1998); if patches are small, dominant foragers can exploit food discoveries of subordinates (Vahl and Kingma, 2007). Several studies have shown that the time needed to discover food patches decreases with group size (Beauchamp, 1998, 2014; Pitcher et al., 1982). The slope of this relationship on a double log scale allows quantification of the effect of increased group size on food patch discovery rate (comparable to the 'additivity coefficient', Ranta et al., 1993). A slope of −1 indicates that the time needed to find a food patch declines proportionally to group size (full additivity). A slope between −1 and 0 indicates diminishing returns in patch-finding rate as group size increases, e.g., as group size increases

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foragers spend more time keeping track of the foraging success of others at the expense of finding food themselves.

Information gained from nearby foraging conspecifics can help individuals make more accurate and faster estimates of patch resource density (Clark and Mangel, 1984, 1986; Valone, 1989), i.e. allowing foragers to maximise energy gain by wasting less time in unprofitable patches (Charnov, 1976; Coolen et al., 2005; Smith et al., 1999; Templeton and Giraldeau, 1996; Valone and Templeton, 2002; van Gils et al., 2003). Foragers can optimise their patch residence times by means of Bayesian updating (McNamara et al., 2006; Valone, 2006). Central to Bayesian updating is that foragers optimise their patch departure decision by combining prior information on resource density with sampling information on a patch (Green, 1980; Iwasa et al., 1981; McNamara and Houston, 1980; McNamara, 1982; McNamara et al., 2006; Oaten, 1977). By using public information, personal sampling information can be complemented to then allow faster and more accurate estimates of patch resource density (Clark and Mangel, 1984, 1986; Valone, 1989). Although Bayesian updating was at the core of studying public information (Valone, 1989), few studies have combined the two approaches (e.g., Templeton and Giraldeau, 1995; Valone and Giraldeau, 1993).

Red knots *Calidris canutus* are shorebirds that forage on patchily distributed bivalves that live burrowed in the soft sediments of intertidal mudflats (Kraan et al., 2009a,b; Piersma et al., 1993; van Gils et al., 2005; Zwarts and Blomert, 1992) (reviewed in Piersma, 2012). In search of their hidden prey, knots sample the mudflat by probing the sediment (Piersma et al., 1998). When a prey is detected, it is briefly handled and subtly moved into the mouth without any obvious swallowing motion (see Online Supplementary video). Previously, van Gils et al. (2003) experimentally showed that individual knots are capable of Bayesian updating to maximise the net energy gain while exploiting patches. Red knots regularly forage in groups of 4,000–15,000 individuals (Piersma et al., 1993). Due to the large spatial extent of food patches (Kraan et al., 2009b), knots can avoid costs of interference competition in the field (Bijleveld et al., 2012; Vahl et al., 2005; van Gils and Piersma, 2004). In combination with the cryptic nature of their buried prey, this makes red knots likely candidates for using public information to increase their foraging success (Bijleveld et al., 2010).

In this paper we report on two complementary experiments. The first experiment was designed to show that foraging red knots are capable of detecting food discoveries of group mates and use this public information to locate hidden food patches. The second experiment was designed to quantify the benefits of group size per se (i.e. public information) on patch discovery rates and patch residence times. In the first experiment we challenged knots to choose between two foraging patches in a dichotomous preference test. Both patches had two foraging knots (demonstrator birds), but only one patch contained burrowed (hidden) prey items. As dominant foragers are predicted to take advantage of public information more than subordinate foragers (Barta and Giraldeau, 1998), dominance was incorporated as an explanatory variable.

In the second experiment we offered 48 patches of which only one contained hidden prey. We manipulated the level of public information by varying group size between 1 and 4. We recorded cumulative searching time and number of patches visited before finding the food patch, and calculated patch residence times. Assuming that knots search randomly between patches, we hypothesise that the number of patch visits declines proportionally to group size. Patch residence time should not be affected by group size as it depends on patch sample information (e.g., Valone, 1989) that was not publicly available (each patch would accommodate one bird only). As cumulative searching time equals the number of patch visits times the average patch residence time, we hypothesise that cumulative searching times should also decrease proportionally to group size.

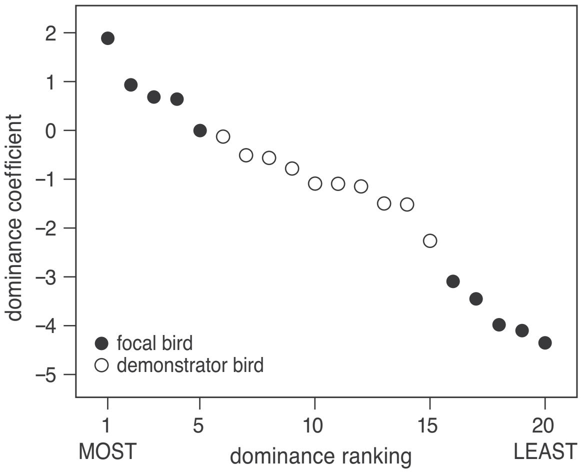

Fig. 1. Social status of the birds in experiment 1 ranked by dominance coefficients. The five most and five least dominant birds were selected as focal birds, and the 10 intermediately dominant birds were selected as demonstrator birds.

2. Materials and methods

2.1. Experiment 1: do knots use public information?

On 28 September 2008, 20 adult red knots *Calidris canutus islandica* were caught with mist nets near the islet of Griend, The Netherlands (53°15′ N, 5°15′ E), and brought back to the NIOZ Royal Netherlands Institute for Sea Research, Texel, The Netherlands. The birds were housed in aviaries that were 4.5 m long, 1.5 m wide and 2.5 m high and lined with white Trespa (Trespa International BV, Weert, The Netherlands). The aviaries were equipped with running salt water along a coated concrete surface, fresh water for drinking and bathing, and a stretch of sand covered in 5 cm water to resemble the knots' natural mudflat habitat. The birds were maintained on a diet of blue mussels *Mytilus edulis*.

In order to estimate relative dominance of all birds, we recorded the number of pair-wise aggressive interactions between foraging individuals, i.e. threatening, charging (moving towards conspecifics), and receding. We also scored the winners and losers of each interaction ($n = 831$). Individuals that retreated from an aggressive interaction were taken as losers. We observed these aggressive interactions in two 15 min sessions each day for 10 days prior to the experiment. On the basis of these interactions, and assuming transitivity (i.e. if bird A is dominant over B and B is dominant over C, then A is dominant over C), we calculated dominance coefficients with a logistic regression (for details on the dominance hierarchy analyses see Bijleveld et al., 2012; van der Meer, 1992). We divided the knots into three dominance groups: five subordinates, ten intermediates and five dominants. The most and least dominant birds were 'focal birds', while the intermediate group would act as 'demonstrator birds' during the trials (Fig. 1).

The setup for this experiment was comparable to previous experiments on social information use (e.g., Coolen et al., 2005). We divided the indoor experimental arena (7 m × 7 m × 3.5 m) in two equal halves separated by a polyester sheet (Fig. 2A). In each of the two halves we placed one patch of 1 m^2 and 20 cm deep filled with wet sand. In the middle of the arena we cut a hole in the polyester sheet to fit a cubical cage (1 m^3) made of wired mesh (1 cm^2). On the two sides of the cage – facing both patches – vertical sliding doors were fitted that could be remotely opened simultaneously, thus providing access to the patches from the central cage. The water in the arena was kept at such a level that only the patches and cage were above water. Horizontal sliding doors on both sides connected the experimental arena to the aviaries.

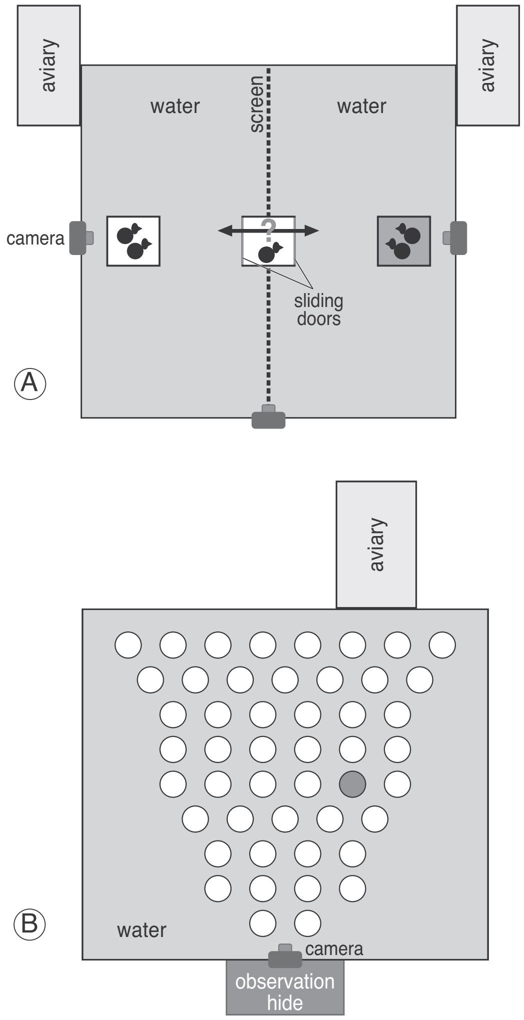

Fig. 2. Setup for experiments 1 and 2. Panel A gives the setup for experiment 1 in which we tested the ability of red knots to detect and exploit the foraging success of other knots. The shaded patch indicates the randomly assigned food patch. In panel B we provide the setup for experiment 2 in which we investigated the effect of group size on red knot food-finding rate. The shaded patch indicates the single food patch that was randomly assigned to one of the 48 patches before each trial.

Before each trial we introduced two demonstrator birds into each of both aviaries adjacent to the experimental arena to rest for a minimum of 5 min. The demonstrator birds were randomly selected from the intermediately dominant group of birds. Preferably, demonstrator birds were not used on the food patch in two consecutive trials; in 16 trials this could not be prevented given the trial schedule, but the intake rates of these birds did not differ from demonstrator birds that were not used in consecutive trials (0.002 SE 0.030, $F_{1,118} = 0.003$, $P = 0.96$).

We buried 120 blue mussels with a length of 8 (±0.5) mm at a depth of approximately 2 cm in one randomly selected patch and smoothed the patch-surface afterwards. In order to avoid leaving visible cues to the location of food burial, we applied similar treatment to the opposite patch but without actually burying prey. We then placed the focal bird in the central cage to rest for a minimum of 2 min, after which the demonstrator birds were allowed to enter the experimental arena. Two demonstrator birds would start foraging on the empty patch and two demonstrator birds would start foraging on the food patch. Birds were not able to switch between patches because of the polyester sheet. Before opening the central cage's sliding doors allowing the focal bird access to the patches, the focal bird was able to observe the demonstrator birds for 2 min. The birds were not fed outside these trials (they obtained all the food during the trials in the experimental period lasting 10 days) and were, therefore, motivated to choose the patch with food. Once the focal bird left the central cage the doors closed and the focal bird was allowed to forage for 3 min on the patch it had chosen. Depending on the choice it made, this foraging bout was successful or unsuccessful. An edited video recording of a trial can be found in the Online Supplementary Material.

Supplementary video related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.beproc.2014.09.003.

All trials were recorded on video with three cameras (one for each patch and one for the central cage). The videos were analysed with The Observer software (v4.0 Noldus Information Technology). For the minute preceding the opening of the sliding doors, we scored the time that focal birds spent on the food-patch side, or the empty-patch side of the central cage. Additionally, we counted the number of mussels eaten by the demonstrator birds before the sliding doors were opened. In these 2 min, each demonstrator bird ingested an average of 13.1 mussels (4.6 SD) on the food patch. In six trials, the demonstrator birds were able to find a stray mussel in the empty patch as well. The number of intakes on the 'empty' patch, however, was always much less than the number of intakes on the food patch. The birds, thus, never received false information and we included these trials in the analyses.

Between 19 and 28 November 2008, each focal bird was trialled 12 times making a total of 120 trials. For practical reasons we split the 120 trials into 12 blocks of 10 trials. Each block included each focal bird once, and in half of these blocks the food patch was on the left, and in the other half the food patch was in the right of the experimental arena. The order of blocks was determined by pairwise (food patch on the left or right side of the arena) random selection (Milinski, 1997). To get acquainted with the experimental setup, there was a 4 week training period before the experiment. Nevertheless, sometimes the focal birds were scared of the central cage's doors opening. This especially happened when a bird was walking back and forth against one of the sliding doors at the time they were opened. The opening of the door then startled the birds which thus left the cage on the opposite side. We scored this behaviour, defined by whether focal birds jumped or ran away to the other side of the cage at the moment the sliding doors opened, from video recordings – blind to the location of the food patch – and included this as explanatory variable ('opposite') in the analyses.

2.2. *Experiment 2: are food patches found faster in groups?*

In this experiment we used four adult red knots (also of the *islandica* subspecies) that were caught on 19 February 1999 near the island of Texel, The Netherlands (53°09′ N, 4°54′ E). The birds were housed in a similar fashion as explained above, and between 3 and 14 June 1999 we studied their patch finding rate as a function of group size in an experimental design comparable to that used by Pitcher et al. (1982). In an outdoor experimental arena (7 m × 7 m × 3 m), we placed 48 buckets (0.3 m in diameter) filled with wet sand in knee-deep water at a distance of approximately 0.7 m from each other such that the birds needed to make little flights in order to move between patches (similar to van Gils et al., 2003). Patches were aligned such that a single camera covered all patches (Fig. 2B). Out of the 48 patches, only one contained buried prey items (approximately 240 blue mussels of a medium size class around 10 mm); the other 47 patches were empty.

Before each trial, we placed the birds that were scheduled for that specific trial in the aviary next to the arena (the other birds were kept in a box in the meantime). The opening of the door to the arena defined the start of the trial, upon which the focal birds would start searching through the patches. A trial ended when all birds had found the patch containing food.

In total, we carried out 96 trials with 24 trials per group size. In order to balance the number of trials between birds, each bird participated in 60 trials; respectively 6, 12, 18 and 24 trials for group sizes 1–4. This experimental design yielded a sample size of 240 estimates on behavioural variables for the statistical analyses. All trials were recorded on video and later analysed with The Observer software (v 4.0 Noldus Information Technology), allowing accurate estimation of time budgets. Our ethogram included ‘searching for food’, ‘flying’, and ‘other’. We also scored the patch on which the bird was located at any given time.

2.3. *Statistical analyses*

We analysed all data in R v3.0.1 (R Core Team, 2013). In order to control for repeated measures on focal birds, we initially analysed experiment 1 in a linear mixed-effects model with focal bird identity as a random effect. However, the estimated variance of focal bird was approximately zero (0.06, 95% CI (0; 0.50)), which simplified these analyses to a linear model. We thus analysed whether focal birds chose the food patch in a generalised linear model with binomial error structure. As explanatory variables we included ‘dominance’ (a factor indicating if the focal bird was dominant or subordinate), ‘sex’, and ‘opposite’ (see Section 2.1). In order to circumvent the experimental artefact that focal birds were sometimes startled by the opening of the sliding doors, we additionally calculated the ratio of time that focal birds spent on the food-patch side of the central cage to that on the empty-patch side. We analysed the logit of this ratio in a linear model with only an intercept.

We analysed the data from experiment 2 in general linear models with Gaussian error structure and cumulative searching times, the number of patch visits, or patch residence times (i.e. cumulative searching time per patch) as response variables. In order to control for pseudo-replication, we averaged the response variables per trial. To normalise model residuals and to account for the non-linear relationship between response variables and group size (continuous variable from 1 to 4), we $\log_{10}$ transformed these variables. We also investigated whether birds searched randomly between the 48 patches in experiment 2. If birds would search randomly, the number of unique patch visits is given by $48 \times \left(1 - \left(\frac{47}{48}\right)^n\right)$, where n is the total number of patch visits including the revisits. In order to investigate individual differences in between-patch searching behaviour we additionally analysed a focal bird’s contribution (%) to the total number of unique patches visited per trial. We averaged these data per focal bird and group size, and after $\log_{10}$ transforming these variables we analysed them in a linear model with Gaussian error structure, and focal bird identity, group size and their interaction as explanatory variables.

3. Results

3.1. *Do knots use public information?*

Without seeing the food directly and based on the demonstrator birds’ behaviour, red knots were able to select the food patch in 74.6% of the trials (95% CI (62.5; 83.8%)). There was no effect of a focal bird’s dominance or sex (Table 1A and Fig. 3), but focal birds had a 36.0 percentage points lower chance of selecting the food patch when they were startled by the opening sliding doors (‘opposite’) compared to when they were not (Table 1A). In the minute preceding the opening of the sliding doors, focal birds spent 67.1% of their time (95% CI (56.6; 76.1%)) on the food-patch side of the central cage as opposed to the empty-patch side (Table 1B), suggesting that our results are robust to the experimental artefact that focal birds were sometimes startled by the opening of the sliding doors.

Table 1
Results from the statistical analyses of experiment 1: do knots use public information? In (A) the focal bird’s choice of the food patch was the response variable, and as explanatory variables we included opposite (see Section 2.1), a focal bird’s sex, and its dominance status. The intercept represents dominant females that were not startled by the opening of the sliding doors (‘opposite’, see Section 2.1). In (B) we show the results of a linear model with the ratio of time that focal birds spent on the food-patch side of the central cage to the empty-patch side. Note that the estimates are on a logit scale.

Response variables	Predictor variables	Estimates	SE	*P*
(A) Food-patch choice	Intercept	1.18	0.39	<0.01
	Opposite	−1.57	0.40	<0.01
	Male	−0.16	0.50	0.74
	Subordinate focal	−0.12	0.40	0.77
(B) Time spent near food patch	Intercept	0.71	0.23	<0.01

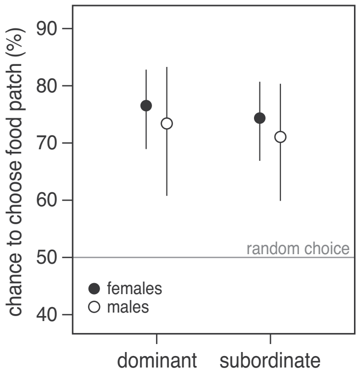

Fig. 3. Patch choice in experiment 1: do knots use public information? The proportion of trials that focal birds selected the food patch, based on the demonstrator birds’ behaviour, was 75%, and independent of sex and social dominance.

3.2. *Are food patches found faster in groups?*

The between-patch searching behaviour of focal birds was approximately random, but slightly more efficient than that (Fig. 4). An empty patch was usually given up within a second of probing and once the first bird had encountered the food patch, the others would rapidly join. As a result the cumulative searching times until the food patch was discovered decreased with group

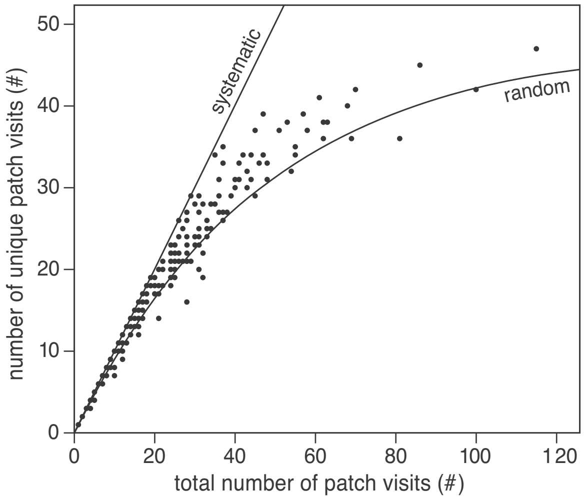

Fig. 4. Red knot searching behaviour in experiment 2. We investigated whether birds searched randomly between the 48 patches in experiment 2. The lines represent the expectations for random searching behaviour, and for reference, also that for systematically searching foragers for which each patch visited is a new patch ($y = x$). Each dot represents mean values per trial and per bird.

Table 2
Results from the statistical analyses of experiments 2: are food patches found faster in groups? We analysed the (A) cumulative searching times (s) and (B) number of patches visited (#) before finding the food patch, as well as (C) patch residence times (s). These behaviours, as well as group size were $\log_{10}$ transformed.

Response variables	Predictor variables	Estimates	SE	*P*
(A) Cumulative searching times	Intercept Group size	1.10 −0.70	0.12 0.30	<0.01 0.02
(B) Number of patches visited	Intercept Group size	1.22 −0.41	0.08 0.20	<0.01 0.04
(C) Patch residence times	Intercept Group size	0.12 −0.29	0.05 0.13	0.03 0.02

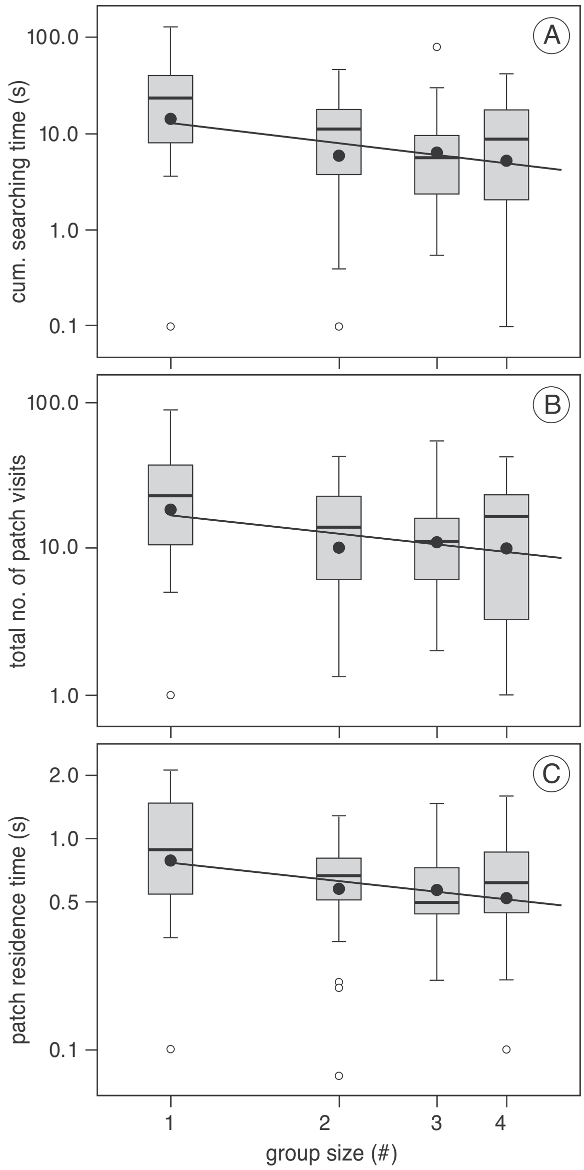

Fig. 5. The effects of group size on different foraging behaviours in experiment 2: are food patches found faster in groups? For each bird, until it had found its first food item, we recorded the cumulative searching times (A), the number of patches visited (B), and the patch residence times (C) and analysed these variables as a function of group size. Each data point represents the mean per trial.

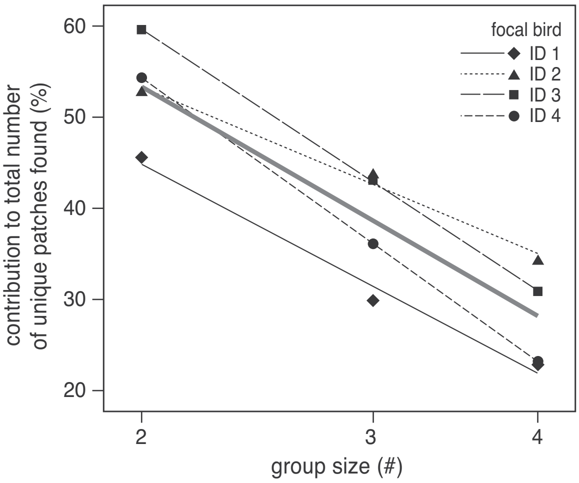

Fig. 6. Between-individual differences in patch searching behaviour in experiment 2. We analysed an individual's average contribution to the number of unique patches searched until the food patch was found. The solid line indicates full proportionality to group size with a slope of −1 on a double logarithmic scale, and the other lines represent the statistical fit for each focal bird. Some focal birds (ID 2 and 3) consistently search more unique patches than others (ID 1 and 4). In the context of producer–scrounger tactics, the former can be seen as producers and the latter as scroungers.

size (Table 2A and Fig. 5A). On a log–log scale, the slope of this regression did not differ from −1 (−0.70, 95% CI (−1.29; −0.11), $t_{(94)} = -1.02$, $P = 0.31$), implying that the food finding rate was proportional to group size. The $\log_{10}$ transformed duration (s) of an individual's searching bouts increased with group size (0.65 SE 0.21, $P < 0.01$) indicating that birds searched more intermittently when alone. The number of patches visited per bird decreased with group size (Table 2B and Fig. 5B), but the slope of this relationship did differ significantly from −1 (−0.41, 95% CI (−0.80; −0.02), $t_{(94)} = -2.97$, $P < 0.01$). We did not predict an effect, but patch residence times also decreased with group size (Table 2C and Fig. 5C). A bird's contribution to the number of unique patches found declined with group size ($F_{1,4} = 837$, $P < 0.01$, Fig. 6), and differed significantly between focal birds both in intercept ($F_{3,4} = 59.4$, $P < 0.01$, Fig. 6) and in slope ($F_{3,4} = 11.1$, $P = 0.02$, Fig. 6).

4. Discussion

We showed that red knots detect successful foraging of conspecifics and are capable of exploiting this public information to select their food patches. Consequently, socially foraging red knots can benefit from public information by a reduction of the time needed to locate food patches compared to when feeding alone. Moreover, knots differed in their search strategy in that two individuals consistently exploited the searching effort of the other two (Fig. 6).

Social foragers can benefit from public information, but as group sizes increase these benefits are gradually offset by increased competition for resources (Beauchamp, 2014; Ranta et al., 1993). For instance, the food finding rate of greenfinches *Carduelis chloris* increased less than proportionally with group size, indicating diminishing returns of social foraging benefits (Hake and Ekman, 1988). When food patches contain enough food and/or are large enough, detrimental effects of interference competition will be low and social foraging can be beneficial for an individual's long-term intake rate (Danchin et al., 2008). In our experimental setup (i.e. with respect to patch sizes, food distribution, and group sizes) red knots could profit maximally from public information as evidenced by the decrease in cumulative searching times proportional to group size. The mechanism behind this proportional decrease was, however, different than we imagined beforehand. We hypothesised that this proportional decline in cumulative searching times would be caused by a proportional decline in the number of patch visits, and that patch residence times would be unaffected by group size. However, both the number of patch visits as well as patch residence times decreased less than proportionally with group size, and their combined effects resulted in a decrease in searching times proportional to group size.

The literature on public information use is growing rapidly and many species have been shown to use public information (Brown and Laland, 2003; Coolen et al., 2005; Danchin et al., 1998; Kurvers et al., 2010b; Ranta et al., 1993; Shrader et al., 2007; Smith et al., 1999; Sontag et al., 2006; Templeton and Giraldeau, 1995; van Bergen et al., 2004). On the other hand, there are also several experimental studies in which the use of public information could not be confirmed (see Valone, 2007). Whether individuals will use public information is influenced by an individual's capability to detect relevant cues, the reliability and costs of acquiring public information (Giraldeau et al., 2002; Valone and Giraldeau, 1993; Valone, 2007), and the reliability of personal information (Nordell and Valone, 1998). For instance, foraging nine-spined sticklebacks *Pungitius pungitius* relied on public information when personal information was unreliable (van Bergen et al., 2004). Due to the random assignment of the food patch in experiment 1, the personal information that birds collected in previous trials was unreliable as indicator of the food-patch location in the current trial. Therefore, birds should maximally rely on public information.

The use of public information will also depend on the types of cues that are available. An experimental study with budgerigars *Melopsittacus undulates* did not reveal public information use (Valone and Giraldeau, 1993). Perhaps handling times were too short (<1 s) to accurately acquire public information (Valone and Templeton, 2002). Yet, red knots have handling times <1 s (Bijleveld et al., 2012), and nevertheless they seem capable of using public information. Possibly, red knots did not only use handling times as a cue for patch quality, but also other behaviours that correlate with foraging success. Together with an increase in the time spent handling prey, knots on the food patch in experiment 1 also searched more and moved around less than on the empty patch. Such behaviours could provide longer lasting and more accurate cues on patch quality. Similarly, in experiment 2 longer patch residence times could have provided information on the presence of food (van Gils et al., 2003).

Social foragers can search for food themselves (producers) or search for the food discovered by others (scroungers) (e.g., Beauchamp, 2014). As dominant foragers can displace subordinate foragers from food patches, dominant birds might be more likely to use public information in selecting foraging patches (Barta and Giraldeau, 1998). Several studies confirm these predictions (Lendvai et al., 2006; Liker and Barta, 2002). For instance, in order to increase their foraging success, dominant black-tailed godwits *Limosa limosa islandica* displaced nearby group members that had higher intake rates (Sirot et al., 2012). In our study, there was no difference between dominant and subordinate focal birds in the use of public information. Compared to the costs of aggression, perhaps dominant red knots cannot benefit from aggressively displacing group members. In the field, red knots forage on bivalves that are patchily distributed over what otherwise may appear like homogenous landscapes (Kraan et al., 2009a). Red knots can use public information to locate such hidden food patches, yet these patches are probably large enough to avoid the costs of social foraging (Bijleveld et al., 2012). This large scale will particularly reduce possible benefits of monopolising food patches by dominant birds (Beauchamp, 1998; Vahl and Kingma, 2007).

Another benefit of social foraging is social facilitation (Zajonc, 1965). Social facilitation occurs when the mere presence of other animals affects an individual's behaviour (Hoppitt and Laland, 2013). In the case of foragers, an increase in the intensity of searching behaviour could stimulate this behaviour in other group members. For instance, capuchin monkeys *Cebus paella* were more motivated and successful foragers when they could see a foraging conspecific compared to when they were alone (Dindo et al., 2009). A possible benefit of social facilitation is that, as competition increases with group size, it allows foragers to scramble for the limited resources (Parker, 2000; Shaw et al., 1995). Studies on social facilitation are under-represented in the literature (Dindo et al., 2009), possibly because it has been considered a process that must be ruled out when studying social learning (Hoppitt and Laland, 2013). Social facilitation itself is an interesting mechanism that is capable of facilitating social learning (Galef, 1993) and increasing a social forager's (short-term) intake rate (Shrader et al., 2007).

Contrary to our prediction, we found that patch residence times decreased with group size. Why we found this decrease is subject to further study, but for now we can provide four non-mutually exclusive hypotheses. First, the decline in patch residence times with group size could reflect an increase in the intensity of searching behaviour (social facilitation) due to an increase in scramble competition (Parker, 2000; Shaw et al., 1995).

Second, the decrease in patch residence times could be caused by a propensity to stay together. Individuals that are left behind may be at greater risk of predation, and need to join the group to obtain the safety-benefits of social foraging (e.g., van den Hout et al., 2008). Separated individuals can more rapidly join the group by decreasing their patch residence times (Shrader et al., 2007; Vásquez and Kacelnik, 2000). That knots foraged on patches close to each other is illustrated by the fact that the number of patch visits until the food was found declined less than proportionally to group size, i.e. as group size increased birds increasingly overlapped in the patches they searched.

Third, individuals in groups are able to allocate more time to foraging instead of, for example, anti-predation vigilance (Beauchamp, 2014; Caraco, 1979). Lone foragers are more often vigilant than foragers in groups, and their foraging bouts are more often interrupted by vigilance behaviour (Beauchamp, 2014). Due to these interruptions, the searching efficiency (instantaneous area of discovery) of lone foragers could be reduced compared to individuals in groups (Dukas and Kamil, 2001). As a consequence lone foragers need to search longer than when in a group to obtain similar patch sample information, i.e. have longer patch residence times. Indeed, we found that knots foraging alone had shorter searching bouts compared to when foraging in groups.

Fourth, as group size increased individuals were more often chased from their patch. Birds 'scrounged' on the information produced by others through joining them on their patch. Because the patches could accommodate one bird only, the producers would then fly off to another patch and continue searching. This behaviour increased with group size and as a consequence, patch residence times could have declined as group sizes increased.

The use of producer or scrounger tactics can differ consistently between individuals. In barnacle geese *Branta leucopsis*, for instance, producer–scrounger tactics are associated with personality variation (Kurvers et al., 2010a), and certain individuals will more readily use public information than others (Kurvers et al., 2010b). Interestingly, we also found such differences in foraging tactics between focal birds. The contribution to new patch discoveries varied consistently between focal birds meaning that certain knots scrounge on the foraging information produced by others and that public information use depends on personality (Fig. 6). Another study showed that certain knots are consistently more explorative with shorter patch residence times than others that were more sedentary (Bijleveld et al., 2014). Perhaps, these sedentary birds scrounge on the information provided by exploratory birds, but how personality relates to producer–scrounger tactics and public information use remains to be investigated.

5. Conclusion

In this study we have shown that red knots are capable of detecting and using public information to increase their food-finding rate, and that knots show consistent individual differences (personalities) in public information use, i.e. producer–scrounger tactics. Dominant knots were not able to exploit public information more than subordinate birds, perhaps because in nature dominant birds cannot monopolise food due to the large patch sizes of their invertebrate prey on extensive intertidal mudflats.

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