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

3

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15 Running title: Benefits of foraging in small groups

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17

18 **Abstract**

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

34

35 **Key-words:** animal personality; consistent individual differences; inadvertent social
36 information; local enhancement; producer-scrounger games; social foraging

37

38 **1. Introduction**

39 Foraging in groups, i.e. ‘social foraging’, is a common phenomenon (Beauchamp 2014; Clark
40 and Mangel 1986; Danchin et al. 2008; Krause and Ruxton 2002; Stephens et al. 2007;
41 Sumpter 2010). The main cost of social foraging is competition for resources (Goss-Custard
42 1980; Tregenza 1995). The benefits of social foraging include increased safety from predation
43 (Pulliam 1973), increased time that could be spent foraging rather than on anti-predation
44 vigilance (Lima 1995), and the accessibility of public information on the availability and
45 quality of food patches (Clark and Mangel 1984; Dall et al. 2005; Danchin et al. 2004;
46 Giraldeau and Dubois 2008; Valone 2007). There is a growing body of literature on public
47 information use in a range of different species (see Blanchet et al. 2010; Rieucou and
48 Giraldeau 2011; Valone 2007). Public information was originally narrowly defined as
49 ‘information on the quality of a food patch’ (Valone 1989). Following Wagner and Danchin
50 (2010), we adopt the broad and intuitive definition of public information as ‘any potential
51 information that is accessible to others’ (i.e. any information that is not private).

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

63 indicates diminishing returns in patch-finding rate as group size increases, e.g., as group size
64 increases foragers spend more time keeping track of the foraging success of others at the
65 expense of finding food themselves.

66 Information gained from nearby foraging conspecifics can help individuals make more
67 accurate and faster estimates of patch resource density (Clark and Mangel 1984, 1986; Valone
68 1989), i.e. allowing foragers to maximise energy gain by wasting less time in unprofitable
69 patches (Charnov 1976; Coolen et al. 2005; Smith et al. 1999; Templeton and Giraldeau 1996;
70 Valone and Templeton 2002; van Gils et al. 2003). Foragers can optimise their patch
71 residence times by means of Bayesian updating (McNamara et al. 2006; Valone 2006).
72 Central to Bayesian updating is that foragers optimise their patch departure decision by
73 combining prior information on resource density with sampling information on a patch (Green
74 1980; Iwasa et al. 1981; McNamara and Houston 1980; McNamara 1982; McNamara, Green,
75 and Olsson 2006; Oaten 1977). By using public information, personal sampling information
76 can be complemented to then allow faster and more accurate estimates of patch resource
77 density (Clark and Mangel 1984, 1986; Valone 1989). Although Bayesian updating was at the
78 core of studying public information (Valone 1989), few studies have combined the two
79 approaches (e.g., Templeton and Giraldeau 1995; Valone and Giraldeau 1993).

80 Red knots *Calidris canutus* are shorebirds that forage on patchily distributed bivalves
81 that live burrowed in the soft sediments of intertidal mudflats (Kraan et al. 2009a; Kraan et al.
82 2009b; Piersma et al. 1993; van Gils et al. 2005; Zwarts and Blomert 1992) (reviewed in
83 Piersma 2012). In search of their hidden prey, knots sample the mudflat by probing the
84 sediment (Piersma et al. 1998). When a prey is detected it is briefly handled and subtly moved
85 into the mouth without any obvious swallowing motion (see Online Supplementary video).
86 Previously, van Gils et al. (2003) experimentally showed that individual knots are capable of
87 Bayesian updating to maximise the net energy gain while exploiting patches. Red knots

88 regularly forage in groups of 4,000-15,000 individuals (Piersma et al. 1993). Due to the large
89 spatial extent of food patches (Kraan et al. 2009b), knots can avoid costs of interference
90 competition in the field (Bijleveld et al. 2012; Vahl et al. 2005; van Gils and Piersma 2004;
91 van Gils et al. (in press)). In combination with the cryptic nature of their buried prey, this
92 makes red knots likely candidates for using public information to increase their foraging
93 success (Bijleveld et al. 2010).

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

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

112 times the average patch residence time, we hypothesize that cumulative searching times
113 should also decrease proportionally to group size.

114

115 **2. Materials and methods**

116 2.1 EXPERIMENT 1: DO KNOTS USE PUBLIC INFORMATION?

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

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

137 The setup for this experiment was comparable to previous experiments on social
138 information use (e.g., Coolen et al. 2005). We divided the indoor experimental arena (7 m × 7
139 m × 3.5 m) in two equal halves separated by a polyester sheet (Fig. 2A). In each of the two
140 halves we placed one patch of 1 m² and 20 cm deep filled with wet sand. In the middle of the
141 arena we cut a hole in the polyester sheet to fit a cubical cage (1 m³) made of wired mesh (1
142 cm²). On two sides of the cage – facing both patches – vertical sliding doors were fitted that
143 could be remotely opened simultaneously, thus providing access to the patches from the
144 central cage. The water in the arena was kept at such a level that only the patches and cage
145 were above water. Horizontal sliding doors on both sides connected the experimental arena to
146 the aviaries.

147 Before each trial we introduced two demonstrator birds into each of both aviaries
148 adjacent to the experimental arena to rest for a minimum of 5 min. The demonstrator birds
149 were randomly selected from the intermediately dominant group of birds. Preferably,
150 demonstrator birds were not used on the food patch in two consecutive trials; in 16 trials this
151 could not be prevented given the trial schedule, but the intake rates of these birds did not
152 differ from demonstrator birds that were not used in consecutive trials (0.002 SE 0.030, $F_{1,118}$
153 = 0.003, $P = 0.96$).

154 We buried 120 blue mussels with a length of 8 (± 0.5) mm at a depth of approximately
155 2 cm in one randomly selected patch and smoothed the patch-surface afterwards. In order to
156 avoid leaving visible cues to the location of food burial, we applied similar treatment to the
157 opposite patch but without actually burying prey. We then placed the focal bird in the central
158 cage to rest for a minimum of two minutes, after which the demonstrator birds were allowed
159 to enter the experimental arena. Two demonstrator birds would start foraging on the empty
160 patch and two demonstrator birds would start foraging on the food patch. Birds were not able
161 to switch between patches because of the polyester sheet. Before opening the central cage's

162 sliding doors allowing the focal bird access to the patches, the focal bird was able to observe
163 the demonstrator birds for two minutes. The birds were not fed outside these trials (they
164 obtained all the food during the trials in the experimental period lasting 10 days) and were,
165 therefore, motivated to choose the patch with food. Once the focal bird left the central cage
166 the doors closed and the focal bird was allowed to forage for three minutes on the patch it had
167 chosen. Depending on the choice it made, this foraging bout was successful or unsuccessful.
168 An edited video recording of a trial can be found in the Online Supplementary Material.

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

179 Between 19 and 28 November 2008, each focal bird was trialled 12 times making a
180 total of 120 trials. For practical reasons we split the 120 trials into 12 blocks of 10 trials. Each
181 block included each focal bird once, and in half of these blocks the food patch was on the left,
182 and in the other half the food patch was in the right of the experimental arena. The order of
183 blocks was determined by pairwise (food patch on the left or right side of the arena) random
184 selection (Milinski 1997). To get acquainted with the experimental setup, there was a four
185 week training period before the experiment. Nevertheless, sometimes the focal birds were
186 scared of the central cage's doors opening. This especially happened when a bird was walking

187 back and forth against one of the sliding doors at the time they were opened. The opening of
188 the door then startled the birds which thus left the cage on the opposite side. We scored this
189 behaviour, defined by whether focal birds jumped or ran away to the other side of the cage at
190 the moment the sliding doors opened, from video recordings – blind to the location of the
191 food patch – and included this as explanatory variable (‘opposite’) in the analyses.

192

193 2.2 EXPERIMENT 2: ARE FOOD PATCHES FOUND FASTER IN GROUPS?

194 In this experiment we used 4 adult red knots (also of the *islandica* subspecies) that were
195 caught on 19 February 1999 near the island of Texel, The Netherlands (53°09' N, 4°54' E).
196 The birds were housed in a similar fashion as explained above, and between 3 and 14 June
197 1999 we studied their patch finding rate as a function of group size in an experimental design
198 comparable to that used by Pitcher et al. (1982). In an outdoor experimental arena (7 m × 7 m
199 × 3 m), we placed 48 buckets (0.3 m in diameter) filled with wet sand in knee-deep water at a
200 distance of approximately 0.7 m from each other such that the birds needed to make little
201 flights in order to move between patches (similar to van Gils et al. 2003). Patches were
202 aligned such that a single camera covered all patches (Fig. 2B). Out of the 48 patches, only
203 one contained buried prey items (approximately 240 blue mussels of a medium size class
204 around 10 mm); the other 47 patches were empty.

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

210 In total, we carried out 96 trials with 24 trials per group size. In order to balance the
211 number of trials between birds, each bird participated in 60 trials; respectively 6, 12, 18 and

212 24 trials for group sizes 1 to 4. This experimental design yielded a sample size of 240
213 estimates on behavioural variables for the statistical analyses. All trials were recorded on
214 video and later analysed with The Observer software (v 4.0 Noldus Information Technology),
215 allowing accurate estimation of time budgets. Our ethogram included ‘searching for food’,
216 ‘flying’, and ‘other’. We also scored the patch on which the bird was located at any given
217 time.

218

219 2.3 STATISTICAL ANALYSES

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

231 We analysed the data from experiment 2 in general linear models with Gaussian error
232 structure and cumulative searching times, the number of patch visits, or patch residence times
233 (i.e. cumulative searching time per patch) as response variables. In order to control for
234 pseudo-replication, we averaged the response variables per trial. To normalise model residuals
235 and to account for the non-linear relationship between response variables and group size
236 (continuous variable from 1 to 4), we \log_{10} transformed these variables. We also investigated

237 whether birds searched randomly between the 48 patches in experiment 2. If birds would
238 search randomly, the number of unique patch visits is given by $48 \times (1 - (\frac{47}{48})^n)$, where n is the
239 total number of patch visits including the revisits. In order to investigate individual
240 differences in between-patch searching behaviour we additionally analysed a focal bird's
241 contribution (%) to the total number of unique patches visited per trial. We averaged these
242 data per focal bird and group size, and after \log_{10} transforming these variables we analysed
243 them in a linear model with Gaussian error structure, and focal bird identity, group size and
244 their interaction as explanatory variables.

245

246 **3. Results**

247 3.1 DO KNOTS USE PUBLIC INFORMATION?

248 Without seeing the food directly and based on the demonstrator birds' behaviour, red knots
249 were able to select the food patch in 74.6% of the trials (95% CI (62.5; 83.8%)). There was
250 no effect of a focal bird's dominance or sex (Table 1A and Fig. 3), but focal birds had a 36.0
251 percentage points lower chance of selecting the food patch when they were startled by the
252 opening sliding doors ('opposite') compared to when they were not (Table 1A). In the minute
253 preceding the opening of the sliding doors, focal birds spent 67.1% of their time (95% CI
254 (56.6; 76.1%)) on the food-patch side of the central cage as opposed to the empty-patch side
255 (Table 1B), suggesting that our results are robust to the experimental artefact that focal birds
256 were sometimes startled by the opening of the sliding doors.

257

258 3.2 ARE FOOD PATCHES FOUND FASTER IN GROUPS?

259 The between-patch searching behaviour of focal birds was approximately random, but slightly
260 more efficient than that (Fig. 4). An empty patch was usually given up within a second of
261 probing and once the first bird had encountered the food patch, the others would rapidly join.

262 As a result the cumulative searching times until the food patch was discovered decreased with
263 group size (Table 2A and Fig. 5A). On a log-log scale, the slope of this regression did not
264 differ from -1 (-0.70, 95% CI (-1.29; -0.11), $t_{(94)} = -1.02$, $P = 0.31$), implying that the food
265 finding rate was proportional to group size. The \log_{10} transformed duration (s) of an
266 individual's searching bouts increased with group size (0.65 SE 0.21, $P < 0.01$) indicating that
267 birds searched more intermittently when alone. The number of patches visited per bird
268 decreased with group size (Table 2B and Fig. 5B), but the slope of this relationship did differ
269 significantly from -1 (-0.41, 95% CI (-0.80; -0.02), $t_{(94)} = -2.97$, $P < 0.01$). We did not predict
270 an effect, but patch residence times also decreased with group size (Table 2C and Fig. 5C). A
271 bird's contribution to the number of unique patches found declined with group size ($F_{1,4} =$
272 837, $P < 0.01$, Fig. 6), and differed significantly between focal birds both in intercept ($F_{3,4} =$
273 59.4, $P < 0.01$, Fig. 6) and in slope ($F_{3,4} = 11.1$, $P = 0.02$, Fig. 6).

274

275 **4. Discussion**

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

281 Social foragers can benefit from public information, but as group sizes increase these
282 benefits are gradually offset by increased competition for resources (Beauchamp 2014; Ranta,
283 Rita, and Lindström 1993). For instance, the food finding rate of greenfinches *Carduelis*
284 *chloris* increased less than proportionally with group size, indicating diminishing returns of
285 social foraging benefits (Hake and Ekman 1988). When food patches contain enough food
286 and/or are large enough, detrimental effects of interference competition will be low and social

287 foraging can be beneficial for an individual's long-term intake rates (Danchin, Giraldeau, and
288 Cézilly 2008). In our experimental setup (i.e. with respect to patch sizes, food distribution,
289 and group sizes) red knots could profit maximally from public information as evidenced by
290 the decrease in cumulative searching times proportional to group size. The mechanism behind
291 this proportional decrease was, however, different than we imagined beforehand. We
292 hypothesized that this proportional decline in cumulative searching times would be caused by
293 a proportional decline in the number of patch visits, and that patch residence times would be
294 unaffected by group size. However, both the number of patch visits as well as patch residence
295 times decreased less than proportionally with group size, and their combined effects resulted
296 in a decrease in searching times proportional to group size.

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

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

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

336 Folmer, and Piersma 2012). This large scale will particularly reduce possible benefits of
337 monopolising food patches by dominant birds (Beauchamp 1998; Vahl and Kingma 2007).

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

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

356 Second, the decrease in patch residence times could be caused by a propensity to stay
357 together. Individuals that are left behind may be at greater risk of predation, and need to join
358 the group to obtain the safety-benefits of social foraging (e.g., van den Hout et al. 2008).
359 Separated individuals can more rapidly join the group by decreasing their patch residence
360 times (Shrader et al. 2007; Vásquez and Kacelnik 2000). That knots foraged on patches close

361 to each other is illustrated by the fact that the number of patch visits until the food was found
362 declined less than proportionally to group size, i.e., as group size increased birds increasingly
363 overlapped in the patches they searched.

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

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

378 The use of producer or scrounger tactics can differ consistently between individuals. In
379 barnacle geese *Branta leucopsis*, for instance, producer-scrounger tactics are associated with
380 personality variation (Kурvers et al. 2010a), and certain individuals will more readily use
381 public information than others (Kурvers et al. 2010b). Interestingly, we also found such
382 differences in foraging tactics between focal birds. The contribution to new patch discoveries
383 varied consistently between focal birds meaning that certain knots scrounge on the foraging
384 information produced by others and that public information use depends on personality (Fig.
385 6). Another study showed that certain knots are consistently more explorative with shorter

386 patch residence times than others that were more sedentary (Bijleveld et al. 2014). Perhaps,
387 these sedentary birds scrounge on the information provided by exploratory birds, but how
388 personality relates to producer-scrounger tactics and public information use remains to be
389 investigated.

390

391 **5. Conclusion**

392 In this study we have shown that red knots are capable of detecting and using public
393 information to increase their food-finding rate, and that knots show consistent individual
394 differences (personalities) in public information use, i.e. producer-scrounger tactics.

395 Dominant knots were not able to exploit public information more than subordinate birds,
396 perhaps because in nature dominant birds cannot monopolise food due to the large patch sizes
397 of their invertebrate prey on extensive intertidal mudflats.

398

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414

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615

616

617 **Tables and figures**

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

	response variable	predictor variables	estimate	SE	<i>P</i>
(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

625

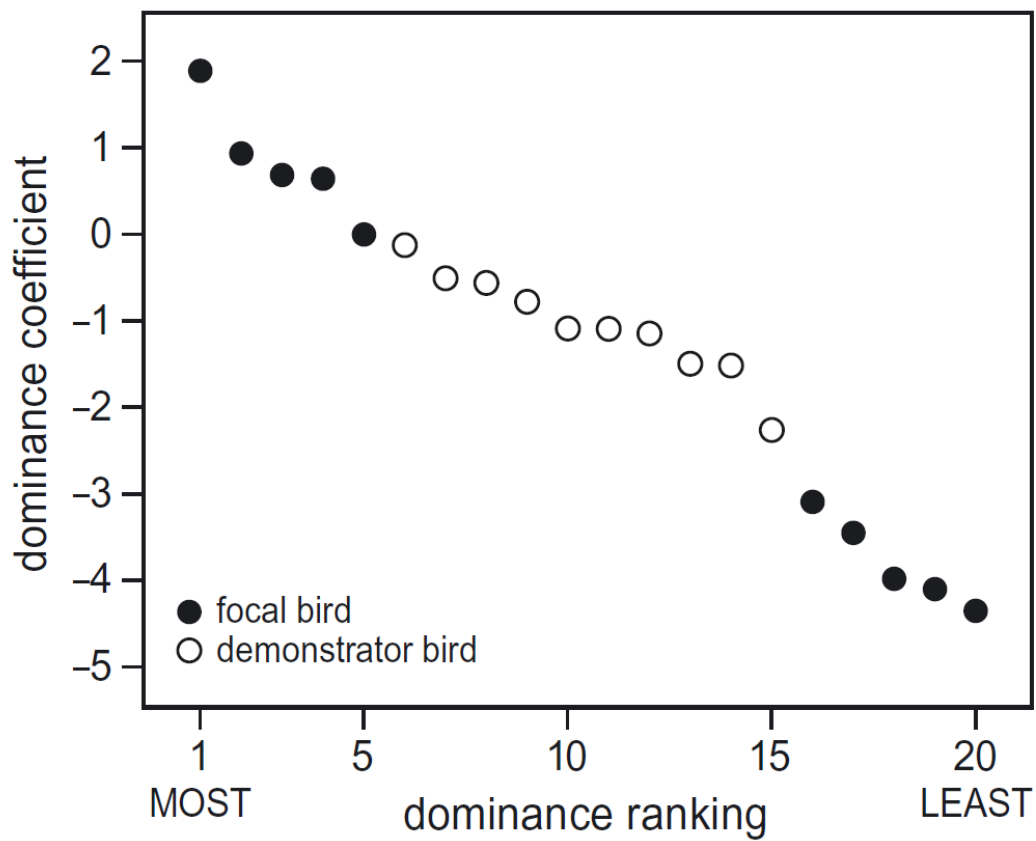
626 **Table 2** Results from the statistical analyses of experiments 2: are food patches found faster
 627 in groups? We analysed the (A) cumulative searching times (s) and (B) number of patches
 628 visited (#) before finding the food patch, as well as (C) patch residence times (s). These
 629 behaviours, as well as group size were log₁₀ transformed.

	response variable	predictor variables	estimate	SE	<i>P</i>
(A)	cumulative searching times	intercept	1.10	0.12	<0.01
		group size	-0.70	0.30	0.02
(B)	number of patches visited	intercept	1.22	0.08	<0.01
		group size	-0.41	0.20	0.04
(C)	patch residence times	intercept	0.12	0.05	0.03
		group size	-0.29	0.13	0.02

630

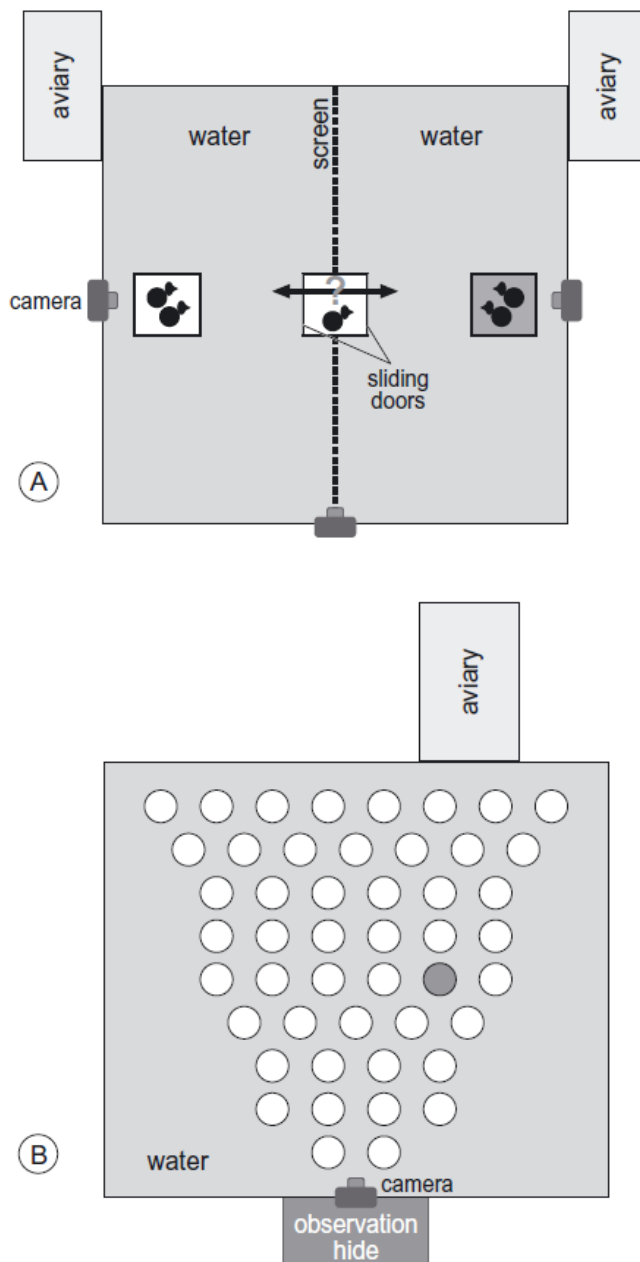
631 **Figures**

632 **Fig. 1** Social status of the birds in experiment 1 ranked by dominance coefficients. The 5 most
633 and 5 least dominant birds were selected as focal birds, and the 10 intermediately dominant
634 birds were selected as demonstrator birds.



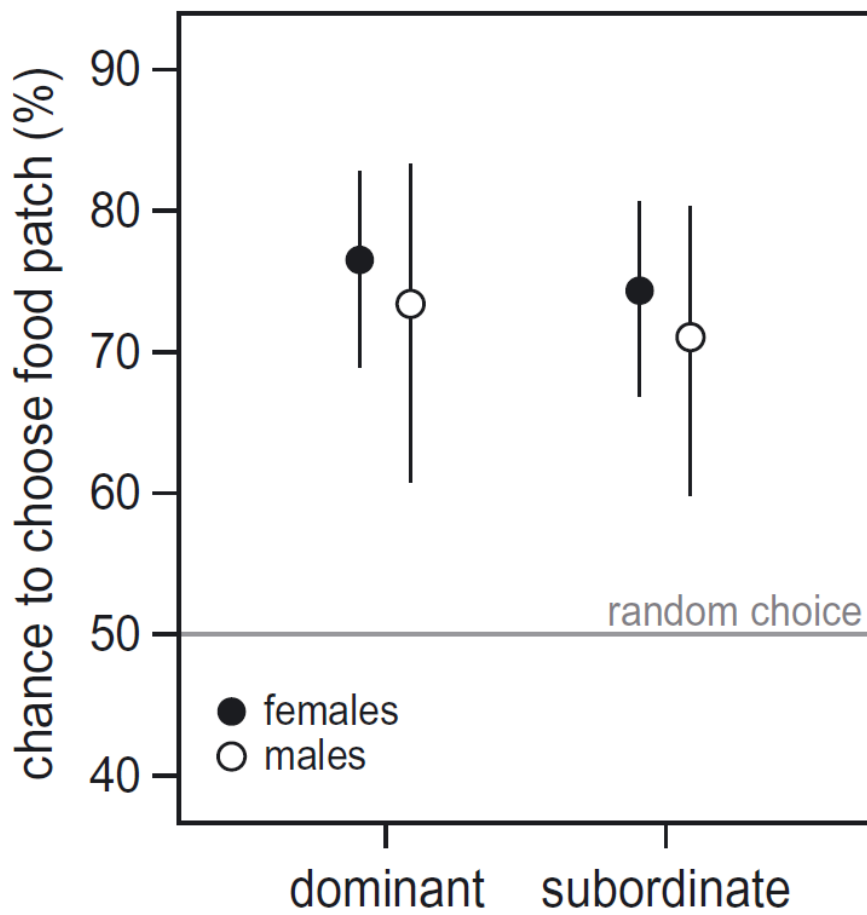
635

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



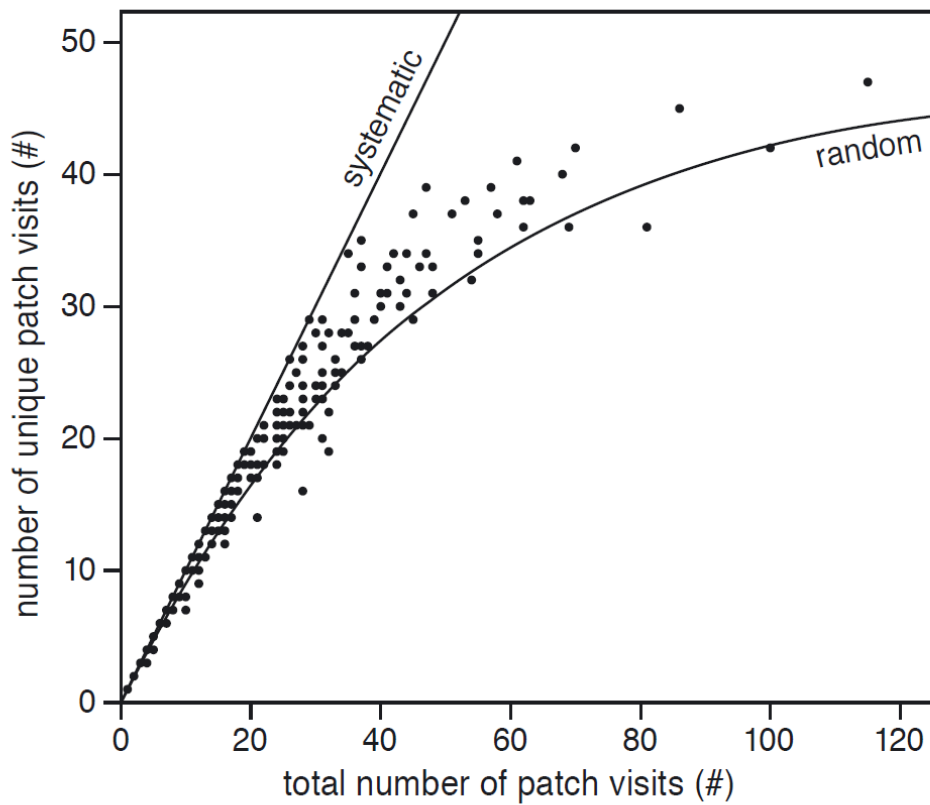
642

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



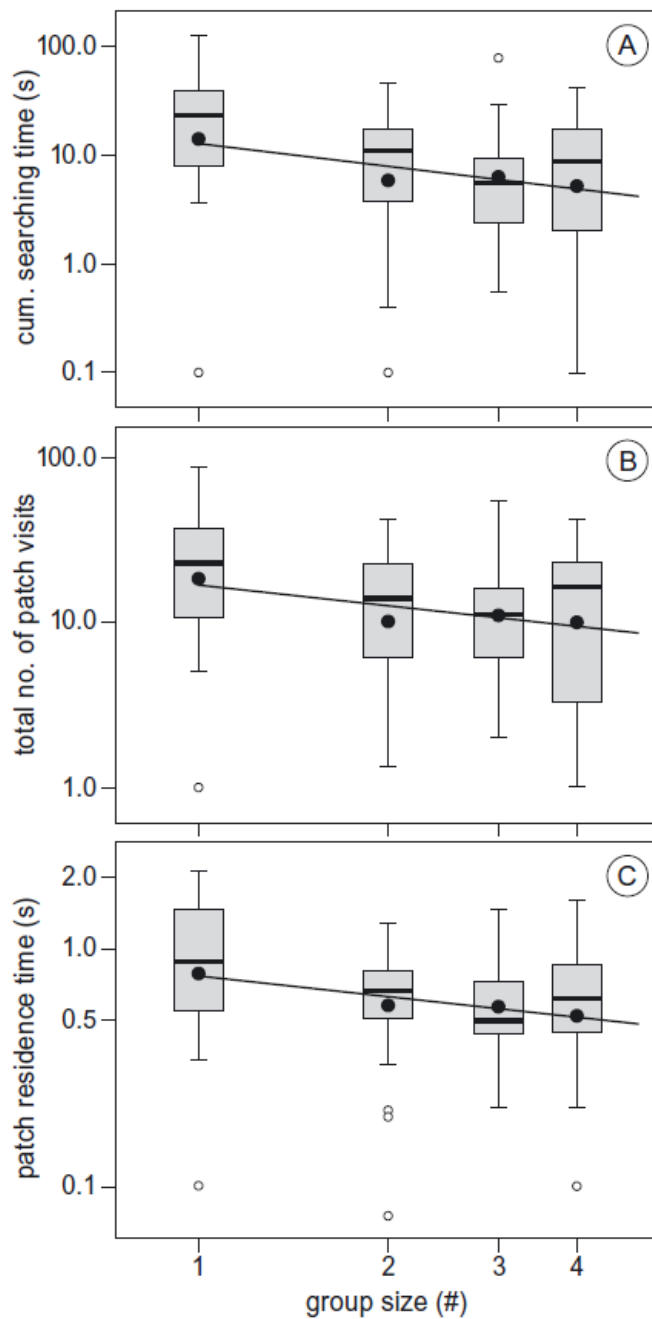
646

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



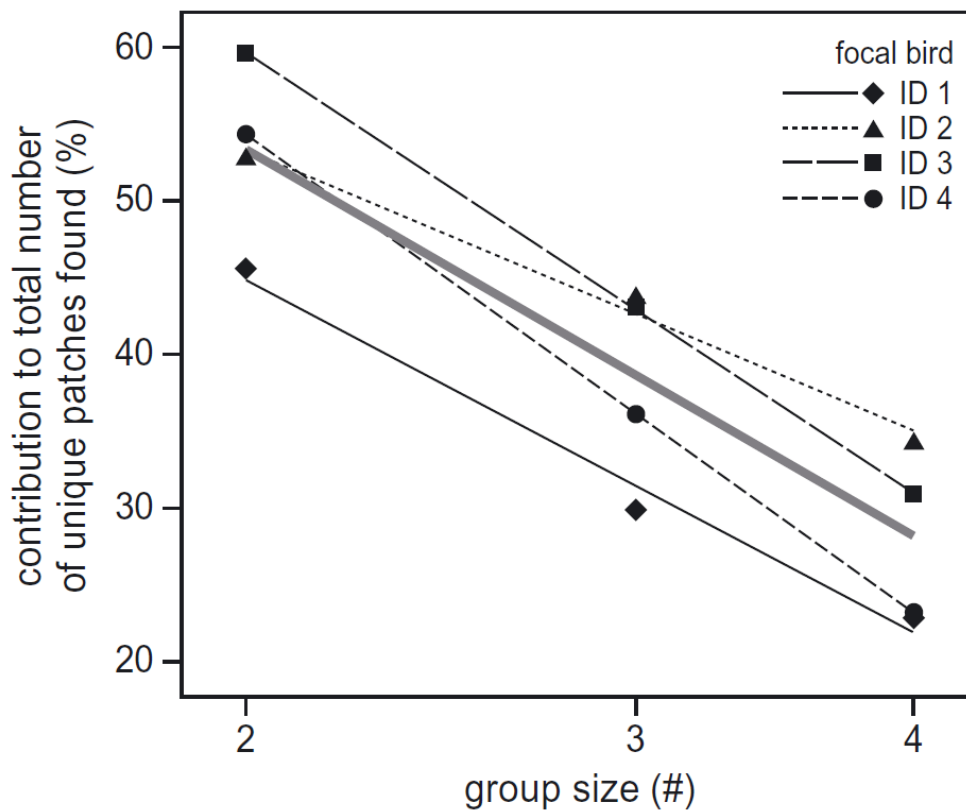
652

653 **Fig. 5** The effects of group size on different foraging behaviours in experiment 2: are food
654 patches found faster in groups? Until the first food item was found we recorded the
655 cumulative searching times (A), the number of patches visited (B), and the patch residence
656 times (C) as a function of group size. Each data point represents the mean per trial.



657

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



665