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Ignorant hooded crows follow knowledgeable roost-mates to food: support for the information centre hypothesis

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Communal roosting in birds may function to enhance foraging efficiency, as explained by the information centre hypothesis, which predicts that successful foragers return from the roost to the rewarding food patch and that birds ignorant of this food follow knowledgeable roost-mates. We tested these predictions by exposing 34 radio-tagged, free-ranging, flock-living hooded crows (*Corvus corone cornix*) to a novel experimental set-up mimicking a superfluous food patch with maximum temporal and spatial unpredictability. Each replicate lasted two days and was located on a new site. Data were collected during ten replicates over three years. First, a crow was more likely to visit the experimental food patch on the second day when it had been there on the first day. Second, when a crow had not been at this food patch on the first day, it was more likely to visit it on the second day if it had roosted together with a crow that had been there on the first day, but only if this knowledgeable roost-mate returned to the food patch on the second day. Our results support the information centre hypothesis and suggest that communal roosting might function to enhance foraging efficiency in hooded crows.

Keywords: communal roosting; field experiment; hooded crow; information centre hypothesis

1. INTRODUCTION

One important function of aggregation in birds is enhanced foraging success, for instance through public information about food location and quality provided by other group members (e.g. Greene 1987; Krebs & Davies 1993; Giraldeau 1997; but see Andersson *et al.* 1981). The evolution of the spectacular gathering of large numbers of individuals at nocturnal communal roosting sites in many populations of flock-living birds is not clearly understood, although increased foraging efficiency may have been a key factor, while decreased predation risk and thermal stress and increased encounter rates with potential mates and, thus, decreased costs of mate assessment may have been additional factors (Beauchamp 1999; Blanco & Tella 1999). A controversial explanation is that individuals join such assemblages in order to gain information from conspecifics about where food may be found (Ward & Zahavi 1973; Weatherhead 1983; Mock *et al.* 1988; Richner & Heeb 1996; Zahavi 1996). Among the conditions that must be met for roosts to serve as information centres, the two most crucial ones are that successful foragers must return from the roost to the rewarding food source and that birds ignorant of the location of this food must follow knowledgeable roost-mates (Mock *et al.* 1988).

Although many studies have investigated communal roosting (Beauchamp (1999) and references therein), few have reported data on the individual roosting strategies of free-ranging birds. Such data are an absolute requirement for providing insight into the functions of communal roosting (Beauchamp 1999) and can only be collected by use of radio telemetry. Moreover, two major prerequisites for proper testing of the hypothesis that roosts function as information centres, that is manipulation of the spatial and temporal occurrence of food and recognition of individual birds at this food and at communal roosts, have not been simultaneously fulfilled in any study except one (Marzluff *et al.* 1996). Therefore, with the possible exception of the latter study, no convincing evidence for the information centre hypothesis as an explanation for avian communal roosting has hitherto been demonstrated from data on wild birds (Mock *et al.* 1988, Beauchamp 1999).

For a forager, the value of information gained at a communal roost will increase with increasing spatial and temporal unpredictability of food patches and be largest when each food patch lasts just long enough to allow a bird that detects it to make one round trip to roost (Waltz 1982). Our test design therefore included creating a superfluous food patch that appeared unpredictably and lasted for only two days in each replicate and locating the foragers by radio telemetry. We used hooded crows because both territorial and non-territorial individuals exploit ephemeral food sources outside the breeding season and then often gather in flocks during the daytime and at communal roosts at night (Cramp & Perrins 1994).

2. MATERIAL AND METHODS

(a) *Study area and general methods*

The study was conducted in a small-scale, mixed farmland–forest landscape, with a declining farmland–forest ratio with increasing altitude (150–500 m above sea level), situated at *ca.* 60°50′ N, 11°10′ E in south-eastern Norway (see Hansen *et al.* (2000) for details). The crows studied did not have access to any rubbish tip or similar patch offering food with high spatial and temporal predictability. Therefore, a crow's feeding site often changed from day to day due to changes in the spatial distribution of food left available by the farming in the area. During 1993–1997, radio-tagged crows were recorded to gather

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at 56 communal roosting sites in the study area, including six large communal roosts and territorial crows also often roosted solitarily in their territory (C. A. Smedshaug, Ø. Bråthen, G. A. Sonerud, E. Arestøl, G. F. Karlsen and H. Hansen, unpublished data). Due to the small-scale distribution of habitat patches and the numerous potential roosting sites, no crow had to fly far from a feeding site in order to find a woodlot that was suitable for roosting.

The 34 crows used in the present study had been trapped and radio tagged in April and May 1993 (2 crows), 1995 (13 crows), 1996 (10 crows) and 1997 (9 crows) with permission from the Directorate for Nature Management and from the National Animal Research Authority in Norway, as described in more detail by Hansen *et al.* (2000). The radio transmitter (Biotrack, Wareham, UK) was mounted as a backpack with a harness made of tubular Teflon tape (Bally Ribbon Mills, Bally, PA, USA) locked with plier-flattened small cylinders of sterling silver. This package weighed *ca.* 18 g and made up less than 4.0% of the crow's body mass (C. A. Smedshaug, unpublished data). A crow's sex was determined from a combination of body mass and body measure (Slagsvold 1983), as well as from the occurrence of brood patch at trapping and behaviour during the breeding season. Its territorial status in the present study was determined separately from its breeding status for each year; a crow that had been nesting earlier in the same year was termed territorial, whereas a crow that had showed no sign of nesting that year was termed non-territorial. Out of the 34 crows, 29 were territorial throughout the study (18 males and 11 females), 1 was non-territorial in one year and territorial in the next two years (a female) and 4 were non-territorial throughout (3 males and 1 female).

(b) *Field experiment protocol*

Data were collected during ten replicates in November–December 1995 (three), 1996 (four) and 1997 (three) when the ground was snow covered and the ambient air temperature was less than 0 °C (one exception). At this time of the year, the probability that a crow roosted at the same site two nights in a row was only 0.38 and the probability that two crows roosted together was independent of whether they were observed together during the day (C. A. Smedshaug, Ø. Bråthen, G. A. Sonerud, E. Arestøl, G. F. Karlsen and H. Hansen, unpublished data). Each replicate was started in darkness by establishing a food patch (*ca.* 40 kg of frozen swine intestines) on farmland. Later during the same night each tagged crow was located at roost. The food patch was kept under continuous observation throughout the following day from a car at a distance of *ca.* 100 m by use of binoculars and radio-receiving equipment. When crows were observed at the patch, the radio frequencies of all tagged crows were scanned at least approximately every 15 min in order to reveal which crows were present. On the second night each tagged crow was again located at roost. The following day the patch was kept under observation in the same way as on the first day and the remaining food was collected in the evening, with the exception that, in 1997, the observations were terminated around midday. In 1996–1997 the observer of the patch on the second day was kept unaware of the spatial distribution of roosting crows on the second night.

If no radio-tagged crow appeared at the food patch during the first day, the replicate was aborted and the food removed on the second night (five cases). Food was never put out at the same site twice in order to ensure that it appeared temporally and spatially unpredictable.

(c) *Statistics*

One crow per replicate was used as a population unit in statistical tests. The intra-individual variance component estimate was larger than the interindividual one (estimated variance component model) (SAS 1995) (G. A. Sonerud, C. A. Smedshaug and Ø. Bråthen, unpublished data) for all behavioural variables analysed (presence or absence at food on the first day (i.e. potential leader or not) (see § 3), presence or absence of potential leaders among roost-mates on the second night for crows absent from food on the first day (i.e. potential follower or naive) (see § 3), distance from food to roosting site on the first and second nights, number of radio-tagged roost-mates on the first and second nights and presence or absence at food on the second day). Therefore, data from different individuals could be pooled without biasing the results or increasing the probability of making a type I error (Leger & Didrichsons 1994). The effects of single categorical variables on a crow's probability of visiting the food patch on the second day were tested by the likelihood-ratio test (SAS 1995), unless $n < 20$ when Fisher's exact test was used (SAS 1995). The independent effects of multiple variables and their interactions on a crow's probability of visiting the food patch on the second day were tested by the likelihood-ratio test (SAS 1995) in logistic regression models produced by backward elimination of variables (Agresti 1996; Hardy & Field 1998). These variables were a crow's sex, its territorial status, the distance from the food patch to where the crow roosted on the second night, the number of tagged roost-mates it had on the second night, whether the crow was a potential follower or naive (see § 3) and whether the observer of the patch on the second day knew the spatial distribution of roosting crows on the second night. Variables with unstable parameter estimates were excluded from the models. All statistical tests were two-tailed.

3. RESULTS

A radio-tagged crow was classified as having one of three roles in each replicate: (i) a potential leader visiting the patch on the first day, (ii) a potential follower absent from the patch on the first day, but roosting together with at least one potential leader on the second night, and (iii) naive, i.e. absent from the patch on the first day and not roosting together with any potential leader the following night. The 34 radio-tagged crows were in the study area during, on average, 5.0 ± 0.45 (mean ± s.e.) replicates (range 1–10), adding up to 170 cases. They were potential leaders in, on average, $16.2 \pm 3.4\%$ (range 0–60%) of the replicates they were involved in, potential followers in $12.2 \pm 3.3\%$ (range 0–75%) and naive in $71.6 \pm 4.2\%$ (range 25–100%). Eleven crows were naive in all replicates they were involved in, 15 were potential leaders at least once, 14 were potential followers at least once and six were both potential leaders in at least one replicate and potential followers in at least one other. The roles were thus not individually fixed. On average, the crows roosted 3.5 ± 0.19 km (range 0.3–9.8 km) ($n = 159$) and 3.7 ± 0.19 km (range 0.4–9.8 km) ($n = 154$) from the food patch on the first and second nights, respectively and were with 2.5 ± 0.28 (range 0–11) ($n = 159$) and 1.3 ± 0.14 (range 0–6) ($n = 154$) tagged conspecifics.

A crow was significantly more likely to visit the food patch on the second day when it was a potential leader compared to when it was a potential follower or naive

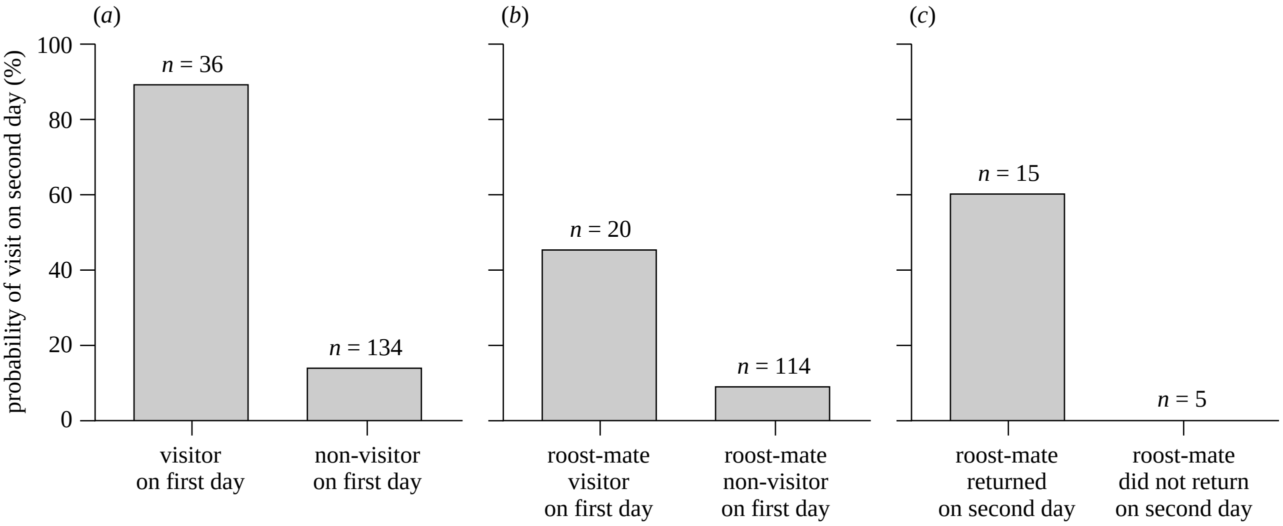

Figure 1. The probability that a radio-tagged hooded crow visited the experimental food patch on the second day of a replicate depending on (*a*) whether it had visited the patch on the first day or not, (*b*) whether, as a first-day non-visitor, it had roosted together with a first-day visitor or not and (*c*) whether, as a first-day non-visitor, it had roosted together with a first-day visitor which returned to the patch on the second day or with one that did not return.

(figure 1*a*) ($\chi^2 = 73.18$, $n = 170$, d.f. = 1 and $p < 0.0001$), when it was a potential follower compared to when it was naive (figure 1*b*) ($\chi^2 = 14.10$, $n = 134$, d.f. = 1 and $p = 0.0002$) and when at least one of the potential leaders among its roost-mates returned compared to when none of them returned (figure 1*c*) ($\chi^2 = 7.34$, $n = 20$, d.f. = 1 and $p = 0.007$). This suggests that knowledgeable crows returned from roost and that ignorant crows followed knowledgeable roost-mates to food. The two former comparisons yielded significant differences even when all cases when a crow roosted less than 2 km from the patch were excluded (87 versus 12% and 38 versus 9%) ($\chi^2 = 50.48$, $n = 136$, d.f. = 1 and $p < 0.0001$ and $\chi^2 = 6.83$, $n = 113$, d.f. = 1 and $p = 0.009$, respectively) while the latter did not due to small sample size (56 versus 0%) (Fisher's exact test, $n = 13$ and $p = 0.10$). This suggests that the observed behaviour was hardly an effect of the crows simply detecting the food patch directly from the roost.

In the cases when a crow was classified as a follower it roosted per definition with at least one tagged conspecific on the second night and, therefore, with significantly more tagged conspecifics than when it was classified as naive (2.7 ± 0.37 versus 0.73 ± 0.14) ($t = 5.74$, d.f. = 119 and $p < 0.0001$). Therefore, in order to eliminate the possibility that the probability of following was a function of number of roost-mates *per se* rather than of whether any roost-mate was a leader, we excluded all cases in which a crow did not roost with any tagged conspecific on the second night. Then, the number of tagged roost-mates when a crow was naive increased to 2.2 ± 0.26 ($n = 33$), which was not significantly different from that of a potential follower ($t = 1.17$, d.f. = 51 and $p = 0.25$). With this restriction, a crow was still significantly more likely to visit the food patch on the second day when it was a potential follower compared to when it was naive, both when no restriction was made on distance from roost to food (45 versus 10%) ($\chi^2 = 9.55$, $n = 68$, d.f. = 1 and $p = 0.002$) and when the cases when a crow roosted less than 2 km from the food patch were excluded (38 versus 11%) ($\chi^2 = 4.75$, $n = 59$, d.f. = 1 and $p = 0.029$).

When a crow was a potential leader, the final model of variables significantly affecting the probability that the crow visited the food patch on the second day included only the distance from its roost site to the patch on the second night and this probability decreased with increasing distance (logistic regression: full model deviance $D = 19.90$ and d.f. = 33, lack of fit $\chi^2 = 19.90$, d.f. = 18 and $p = 0.34$, significance of model $\chi^2 = 4.98$, d.f. = 1 and $p = 0.026$ and parameter estimates, slope −0.467 ± 0.225 and intercept 3.92 ± 1.26). Hence, when no potential leader returned, resulting in none of the potential followers visiting the patch either (figure 1*c*), the crows roosted significantly farther from the patch than when at least one potential leader returned (6.2 ± 1.2 versus 3.2 ± 0.65 km) ($t = 2.29$, d.f. = 18 and $p = 0.034$). In the latter cases, the final model of variables significantly affecting the probability that a potential follower visited the food patch on the second day included only the number of tagged roost-mates on the second night and this probability increased with increasing number of roost-mates (full model deviance $D = 15.16$ and d.f. = 14, lack of fit $\chi^2 = 3.03$, d.f. = 2 and $p = 0.22$, significance of model $\chi^2 = 5.03$, d.f. = 1 and $p = 0.025$ and parameter estimates, slope 0.814 ± 0.428 and intercept −1.82 ± 1.24). This suggests that, when being a potential follower, a crow found food by following roost-mates.

When a crow was naive, none of the measured variables could significantly explain the probability that it visited the food patch on the second day, which suggests that the crow found the food by chance. However, we cannot exclude the possibility that, when a crow was naive in our study design, it may have been a potential follower of an untagged potential leader which had spent the night at a different communal roost to any of the potential leaders among the tagged crows.

In eight of the nine cases of a follower visiting the patch, it arrived simultaneously with the associated leader, in six cases on the leader's first visit to the patch that day and in two cases simultaneously with a leader on its second visit that day. There was no indication that followers were excluded from feeding when arriving at the patch. In addition, there was no indication that potential leaders concealed their foraging success because, when a crow was a potential leader, it did not choose to roost with significantly fewer tagged conspecifics relative to the previous night, compared to when it was a potential follower or a naive (1.7 ± 0.58 versus 1.1 ± 0.28 fewer roost-mates) ($t = 0.96$, d.f. = 146 and $p = 0.34$).

4. DISCUSSION

The following seven components of the information centre hypothesis must be fulfilled in order to avoid rejection of the hypothesis (Mock *et al.* 1988).

(i) Knowledgeable birds return to rewarding patches.
(ii) Some birds discover rewarding patches which others are ignorant of.
(iii) Ignorant birds are able to identify knowledgeable birds.
(iv) Ignorant birds leave the roost together with knowledgeable birds.
(v) Ignorant birds follow knowledgeable birds as they return to rewarding patches.
(vi) Ignorant birds are allowed to feed when arriving at a rewarding patch.
(vii) The net benefit of being a follower exceeds that of searching for food.

Our results fulfil components (i), (ii), (v) and (vi) and, indirectly, components (iii) and (iv) as well, which may be waived (Mock *et al.* 1988). With regard to component (iii), a parsimonious explanation would be that an unsuccessful forager would gain by simply following other birds at random from the roost and, because previously unsuccessful birds would have a lower site fidelity than successful birds, departure destinations would be skewed towards more rewarding foraging patches than average (Waltz 1982). With regard to component (iv), our data showed that the follower arrived simultaneously with the associated leader at the patch on the second day in all cases except one.

A potential leader's probability of returning the next day was only affected by the distance from their roost to the food patch. This suggests that the benefit of the experimental food patch, corrected for the cost of commuting, was traded against the net benefit of searching for and exploiting other food sources or that a crow was more likely to discover other food sources on its way from the roost to the food patch with increasing travel distance. A potential follower's probability of visiting the food patch when at least one of its potential leaders returned was only affected by the number of roost-mates. This positive effect of roost-mates may simply be due to a crow having a higher probability of joining a leader with more roost-mates.

Why should a potential leader join a communal roost and, thus, risk revealing its knowledge? First, it may do so as a defence against sudden devaluation of its knowledge, caused, for instance, by heavy snowfall causing previously known food sources to become hidden and unavailable (Zahavi 1996). Such conditions would increase the value of any information the crow may obtain from conspecifics about the location of other potentially available food patches and the crow would be expected to put more effort into upgrading this information by joining conspecifics at communal roosts, as predicted by the information centre hypothesis (Zahavi 1971, 1996; Ward & Zahavi 1973). In fact, the radio-tagged crows in our study area moved longer from pre-roost to roost with increasing snowfall in the previous 24 h, indicating that they searched for a communal roost where their information of rewarding food sites was most likely to be upgraded (Hansen *et al.* 2000).

Second, a potential leader may join a communal roost as a means of status signalling through revealing information about the location of newly discovered food sites to ignorant non-kin conspecifics (Heinrich 1988) or as a means of recruiting ignorant conspecifics to benefit from group foraging on the food the next day (Richner & Heeb 1996; see also Mesterton-Gibbons & Dugatkin 1999). We have no direct data for rejecting any of these hypotheses. However, we found that, when being a potential leader, a crow did not roost with relatively more tagged conspecifics compared to when it was a potential follower or a naive. This suggests that it did not advertise its foraging success or at least did not succeed in attracting conspecifics. On the other hand, the crow did not choose to roost with relatively fewer tagged conspecifics either, compared to when it was a potential follower or a naive. This fits with the assumption that flock-living birds feeding on emphemeral food do not suffer from sharing with conspecifics because the food may be rapidly consumed by larger food competitors or covered by snow anyway (e.g. Marzluff *et al.* 1996; Buckley 1997).

Third, superior and dominant foragers may join a communal roost in order to lower their exposure to predators, while inferior birds may join these roosts in order to trade a more vulnerable position at the roost against knowledge of the whereabouts of food sites (Weatherhead 1983). We reject this hypothesis because it hinges on a permanent hierarchy in food finding, dominance and roost settlement, whereas we found that the roles of potential leaders and potential followers were not individually fixed. Similarly, individual ravens (*Corvus corax*) have been shown to perform both the leader and follower roles (Marzluff *et al.* 1996).

To the best of the authors' knowledge, our field test of the information centre hypothesis is the first to rely solely on radio-tagged, free-ranging birds exposed to food being manipulated in order to appear with maximum spatial and temporal unpredictability. The use of radio telemetry enabled us to reveal the role performed by each individual in each replicate. Although we have no data for evaluating the last of the seven components that must be fulfilled in order to avoid rejection of the hypothesis (Mock *et al.* 1988), i.e. whether the net benefit of being a follower exceeds that of searching for food, we conclude that our findings provide the strongest support yet for the hypothesis that nocturnal communal roosts function as information centres for enhancing foraging success in birds.

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