Anim. Behav., 1991, **41**, 433–438

Evolution of avian roosting behaviour: a test of the information centre hypothesis and of a critical assumption

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(Received 9 January 1990; initial acceptance 15 March 1990; final acceptance 3 August 1990; MS. number: 3511)

Abstract. After a number of carrion crows, *Corvus corone corone*, had fed on a rich food source, many more birds appeared at this source after an intervening visit to the communal roost suggesting that information was transferred between birds. The majority of individuals that appeared on the following days, however, had learnt where food was by themselves the day before, and not by following successful foragers from the roost to their rich food source. The information centre hypothesis contains the important, but previously untested, assumption that the number of birds present at the site at a given time represents the total number of birds so far informed. This assumption can be evaluated only by estimating the daily turnover of birds at the food patch, which necessitates working with marked individuals. The present study, which used marked birds, shows the assumption is unjustified. The apparent information transfer effect was produced by a turnover of birds at the food patch, which resulted in more birds knowing about the food source than were actually present. The following morning the majority of these knowledgeable birds arrived at the food source early, producing the same effect as would be predicted by the information centre hypothesis.

The information centre hypothesis explains avian roosting behaviour as an adaptation for exploiting patchily and unpredictably distributed food. It proposed that by roosting communally less successful birds may recognize successful foragers and follow them to their food patches the next day. The evolution of communal roosting behaviour would thus be explained through the selective advantages given by the transfer of information at the roost, the main advantage being enhanced individual foraging success (Ward & Zahavi 1973). In addition, communal roosts may decrease the risk of predation (Lack 1968). A refined version (Weatherhead 1983) proposed that, of the roost members, the successful foragers benefit by decreasing their predation risk and the unsuccessful foragers benefit by learning where food is. In a recent critical review of the field studies investigating the role of avian roosts as information centres, Weatherhead (1987) concluded that only one field study (Loman & Tamm 1980) demonstrated moderate evidence in favour of the hypothesis. To distinguish between different interpretations of the results of studies investigating the information centre hypothesis, he urged the use of individually marked birds in future studies. In a more general review, Mock et al. (1988) found published evidence of information transfer at breeding colonies of cliff swallows, *Hirundo pyrrhonota* (Brown 1986) and ospreys, *Pandion haliaetus* (Greene 1987), but they reported only one study that gave evidence of information transfer at a roost (Rabenold 1983, 1987). Rabenold (1987), however, was more cautious about the interpretation of her findings on individually marked black vultures, *Coragyps attratus*, and stated that 'even for species such as black vultures whose aggregations satisfy basic predictions of the information centre hypothesis, it has yet to be demonstrated that individuals learn of a new food source at the roost and not by direct experience with the source itself'. For reasons outlined later we consider below only the evolution of communal roosting, and ignore the evolution of communal breeding through the benefits of information exchange at the breeding colony.

Evidence of information transfer is usually considered as positive if, after a number of individuals (*N1*) feed on a rich food source, many more birds (*N2*) appear at this source after an intervening visit to the communal roost (Weatherhead 1987). However, with one exception (Rabenold 1987) all previous studies have used unmarked birds, and they thus make the implicit assumption that the number of birds present at the food patch at a given

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time represents the total number of birds that acquired the information on food location up to that time. This is the same as assuming that there is no turnover of birds at the food patch throughout the day. This assumption is so far untested and it remains to be shown that the number of birds present at the site at a given time actually represents the total number of birds so far informed. Our purpose in this paper is to evaluate the information centre hypothesis and, specifically, to test this assumption by studying individually marked carrion crows, *Corvus corone corone*. For reviews of the information centre hypothesis itself see e.g. Rabenold 1987; Weatherhead 1987; and Mock et al. 1988.

Carrion crows and many other bird species gather every evening at large roosts, sometimes numbering several thousand individuals. Carrion crow roosts are often many kilometres away from their daily foraging sites, and it can therefore be expected that some benefits are associated with communal roosting that compensate for the travel costs. In a previous field study on hooded crows, *C. cornix*, and ravens, *C. corax*, Loman & Tamm (1980) reported that, when food was provisioned on one day, many more birds arrived on the second day than were seen on the first day, and interpreted this as evidence for information transfer at the roost. They assumed explicitly that the birds that found the food source stayed there for the rest of the day. Under that critical assumption the number of birds at the food patch at any one time of day would represent exactly the number of birds who had visited the patch up to that time. Obviously the interpretation of their results regarding information transfer at the roost depends on that assumption, and the validity of the assumption can be assessed only by the use of individually marked birds as in the present study.

METHODS

We studied three feeding flocks (A, B, C) belonging to a large population of several thousand carrion crows near Lausanne, western Switzerland. Over 600 individuals, both adults and juveniles, were individually marked and sexed between 1985 and 1988 (Richner 1989a). Approximately 450 of these birds were caught in a trap, 100 as nestlings and 50 by use of a stupefying bait. During the present study, in 57 counts of different crow groups, 18% of all birds were marked. Breeding and life history characteristics of the population are described elsewhere (Richner 1989b, c). The five principal night roosts in the area, each numbering many hundred individuals, were previously found by radio-tracking marked birds. To assess the natural feeding flock size and daily turnover of marked individuals in each feeding flock, we watched each flock continuously for 2 days without providing food. Then, at a site that was likely to be found by the flock, we provided approximately 40 kg of ground beef mixed with canned dog food each morning before dawn over 3 days. At dusk at least 10 kg of food remained. This large quantity of food was given to ensure that birds that arrived late in the afternoon or in the evening would still find a rich food source. The flock was kept under continuous observation and the times of arrival and departure of all marked individuals were noted. Flock size was counted every 2 h and individually marked birds every hour. We repeated the procedure for three different feeding flocks.

For statistical analysis of the bird counts we computed the 'first differences', i.e. the difference between a given data point and the previous point. This computation was necessary because subsequent counts of animals in the same group, or also cumulated counts, are highly interdependent and thus cannot be used directly for statistical analysis. In contrast, subsequent first differences are practically independent in infinite populations. An interdependence may arise in small populations, but is considered negligible for our population size. The pooled first differences were then analysed by parametric or non-parametric two-sample tests, and the paired first differences by an appropriate paired-sample test.

RESULTS

Flock Dynamics

Without the addition of food the number of birds in the feeding flocks varied little throughout the day (Fig. 1a). The following morning, a number of birds similar to the number observed the previous day returned to the site.

When food was provided at dawn, the number of birds increased rapidly, and more than doubled within a few hours (Fig. 1b). It stayed high until dusk. The following morning many more birds arrived at the food patch than were observed the morning before, and this number further increased

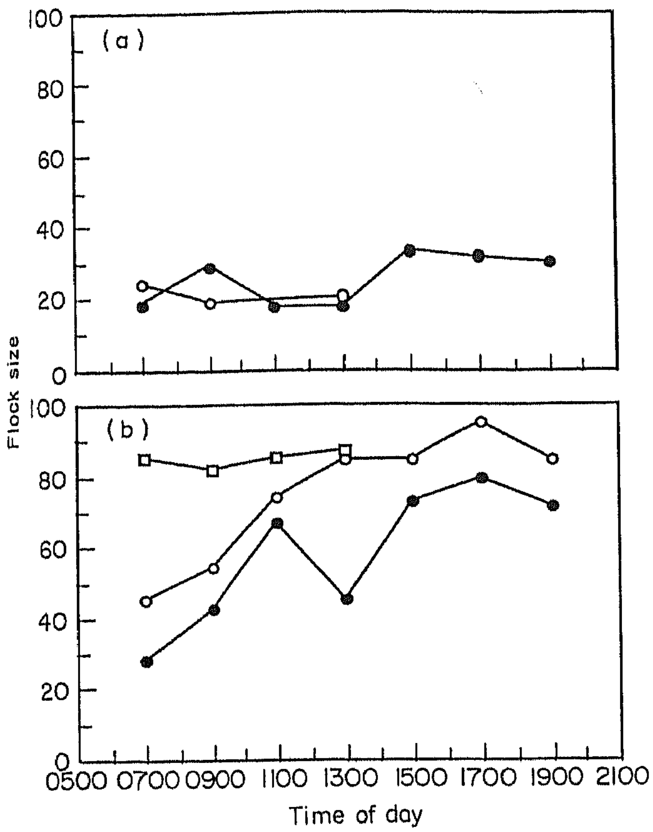


Figure 1. Feeding flock size on 2 subsequent days without food provision (a), and on 3 subsequent days with food provision (b) each morning before dawn for the flock on feeding location B. ●: day 1; ○: day 2; □: day 3.

on the third day. A comparison of the pooled first differences of the number of birds without the addition of food ($\bar{X} \pm$ SE$=0{\cdot}62 \pm 1{\cdot}23$, $N=29$) and with the addition of food ($\bar{X} \pm$ SE$=4{\cdot}28 \pm 1{\cdot}73$, $N=40$) shows that significantly (one-tailed t-test, $t=1{\cdot}72$, $df=65$, $P=0{\cdot}045$) more birds appear at the sites when food is added. Without knowing the identity of the flock members, these findings could be interpreted as evidence for (1) information transfer at the roost, (2) 'local enhancement' (i.e. an increase in flock size through birds being attracted to the feeding flock), or (3) both.

Dynamics of Marked Birds

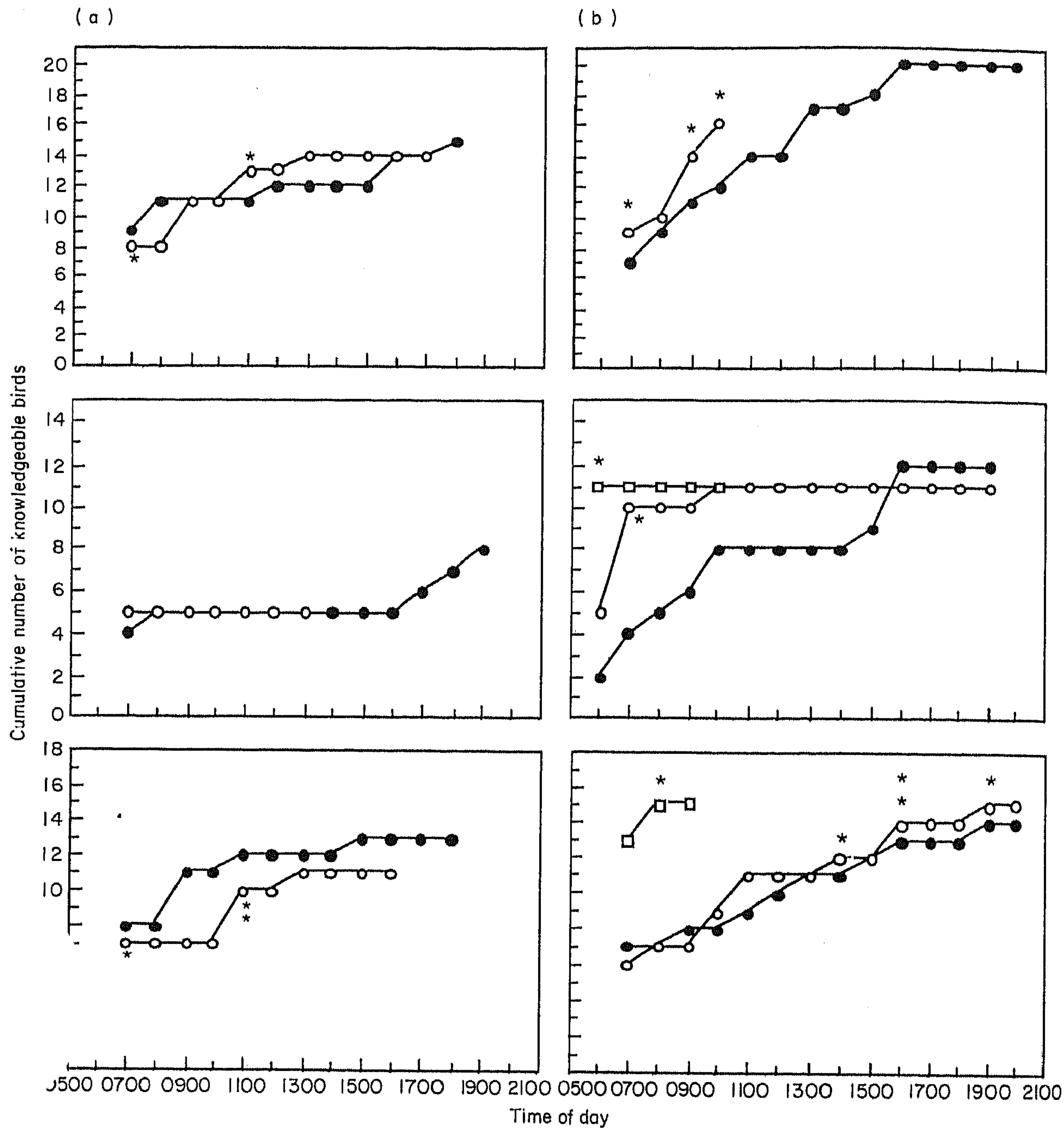
Without the addition of food the cumulative number of marked birds visiting varied little over 2 subsequent days in all three flocks (Fig. 2a), and in flocks A and C a few birds (each of these birds is marked by an asterisk in Fig. 2) which were not seen on the first day arrived throughout the second day.

Compared to the number of marked birds at days without additional food, many more marked individuals arrived over the first day when food was provided, thus learning about the presence of a rich food source (Fig. 2b). Although, after the intervening visits to the roost, the number of marked birds arriving in the early morning of the second and third day more than doubled in flocks B and C, only a very few marked individuals arrived that were not observed at the food patch the previous day. Many arrivals of birds that were not observed the previous day occurred later in the morning and in the afternoon and not, as predicted by the information centre hypothesis, early in the morning, after leaving the communal roost. There is no significant difference between the number of marked birds arriving each hour between dawn and 0900 hours (i.e. the time of leaving the roosts) when no food was provided and that when food was added (Wilcoxon matched-pairs signed-rank test, $z=0{\cdot}734$, $N=15$, $P=0{\cdot}93$, one-tailed). Thus, knowing the identity of the birds provides evidence against information transfer at the night roost, and the findings are consistent with the 'local enhancement' hypothesis.

Turnover of Marked Birds

The difference between the cumulative number of birds that acquired the information throughout a day and the number of marked birds actually present at any given time of day (Fig. 3) indicates the turnover of birds at a food patch throughout a day.

The total number of marked birds that had visited the site up to a given time of day was always higher than the number of marked birds present at that time (Fig. 3). The pooled first differences of the cumulated number of individuals that visited a food patch up to a given time ($\bar{X} \pm$ SE$=0{\cdot}769 \pm 0{\cdot}144$, $N=39$) were significantly different from the pooled first differences of the number of marked individuals actually present at that time ($\bar{X} \pm$ SE$=0{\cdot}205 \pm 0{\cdot}362$, $N=39$; Wilcoxon matched-pairs signed-rank test, $z=1{\cdot}80$, $n=39$, $P=0{\cdot}036$, one tailed). This demonstrates that many birds that find the patch stay for limited periods only, and that the number of birds present at any one time does not reflect the number of birds that have acquired the information so far. The assumption of no turnover of birds at the feeding site allowed the findings of $N2>N1$ in other studies to be interpreted as evidence of information transfer at the communal roost. This important assumption, rarely made explicit in previous studies nor evaluated so far, is thus falsified in the present study.



2. Cumulative number of individually marked birds that learnt (i.e. 'knowledgeable' birds) the feeding location
mselves at the food patch on the first (●) and second day (○) without food provision (a), and on the first (●),
l (○) and third (□) day where a superabundant food source was provided experimentally (b) each morning before
given for each of the three feeding locations. Each asterisk represents the arrival of one individual that was not
ıe day before.

DISCUSSION

hout following individually marked birds, our ı could have been interpreted as evidence for ırmation transfer at the roost. However, work- with marked individuals shows that our obser- ons are consistent with the 'local enhancement' othesis (e.g. Drent & Swiestra 1977; Kushlan 7; Waite 1981), and that an effect similar to the predicted from the information centre hypoth- vas produced by a turnover of birds at the food patch throughout the day. As a consequence, many more birds had learnt the location of the patch by themselves than were present there either by the end of the day, or on a maximum count. The previous study (Loman & Tamm 1980) on unmarked hooded crows and ravens made the critical assumption that the birds that find the food source stay there for the rest of the day. This assumption is unjustified, and thus the findings of $N2 > N1$ cannot be interpreted as positive evidence of information transfer between individuals. It is likely that this hidden assumption

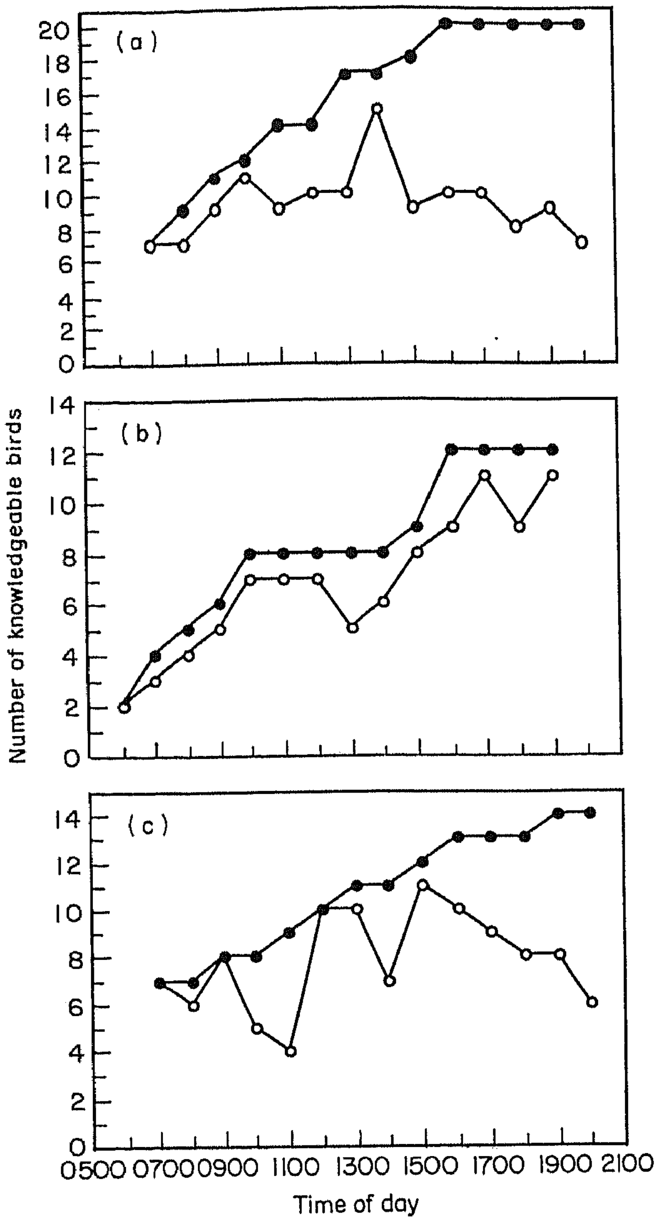


Figure 3. Cumulative number of individually marked birds (●) that learnt (i.e. 'knowledgeable' birds) the feeding location by themselves at the food patch on the first day where a superabundant food source was provided experimentally and the instant (non-cumulative) number of individually marked birds (○) present at different times of day, given for each of the three feeding locations. (a) Feeding site A; (b) feeding site B; (c) feeding site C.

does not hold for many other information centre studies conducted so far.

There may be an important difference between a breeding colony and a roost regarding their potential as sites for information transfer between individuals. Successful birds may return to the breeding colony more frequently or with bigger loads than less successful foragers, and this allows an unsuccessful bird to measure another bird's foraging success by directly observing the bird feeding its chicks. In contrast, food is not usually brought back to the night roost and, for assessing another bird's feeding opportunities, an unsuccessful bird may rely on the physical appearance of successful birds or on other indirect cues. Among carrion crows and probably many other territorial species, the territory owners are the birds in the best physical condition. The territory holders defend their territories all day and all year round, but at night they roost together with the flock birds. Further, many young carrion crows are strongly philopatric over one or several years (Richner 1990). For an unsuccessful forager aiming to follow a successful forager, the task at a night roost would therefore not only consist of discriminating between successful and unsuccessful foragers, but also of recognizing territory holders or their philopatric offspring, since following a territorial bird to its territory would be highly unprofitable. Mock et al. (1988) gave other reasons to believe that the potential for information transfer at a breeding colony is not equivalent to that at a roost.

In conclusion, by working with individually marked birds, we not only found no support for the information centre hypothesis, but we showed that the critical assumption made in studies on unmarked birds is unfounded. Thus, there is so far no evidence from field studies that the advantage that could be gained by information transfer at the roost has been an important selective force for the evolution of communal roosting behaviour in birds.

ACKNOWLEDGMENTS

We are grateful to J. Loman, D. Mock, P. Weatherhead, A. Zahavi and two referees for their helpful suggestions. We thank S. Morgenthaler of the Ecole Polytechnique Fédérale de Lausanne for statistical advice, Mr Guex and Mr Maulaz for permission to operate a trap in the area of a water treatment plant, and P. Vogel for logistic support. We are indebted to Ph. Schneiter and H. Stirniman for their dedicated help in sexing and marking crows.

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