Information transfer determined by association of neighbours in European bee-eater (*Merops apiaster*) colonies

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The Information Centre Hypothesis (ICH) and the Two-Strategies Hypothesis (TSH) predict that foraging success is enhanced by information exchanged among individuals within a colony or roost. Nest location within a colony may be critical in this regard, as individuals with abundant, nearby neighbours likely have greater access to information regarding a new food resource than relatively isolated breeders. To determine how the availability of neighbours influences information transfer, we quantified foraging success in a population of European bee-eaters (*Merops apiaster*) provided with a honey bee (*Apis mellifera*) hive as a new food resource. To quantify potential information transfer we developed a neighbour index that incorporated both the number and proximity of neighbours into a single continuous measure. The change in feeding rate of individual birds after introducing the honey bee hive was positively correlated with our neighbour index, suggesting that information transfer among colony members, at least in part, selects for colonial breeding in European bee-eaters.

KEY WORDS: information centres, bee-eaters, coloniality, cooperative breeding.

INTRODUCTION

The evolution and maintenance of colonial breeding in birds is commonly explained by benefits that accrue via kin selection, reciprocal altruism and direct fitness payoffs associated with group living (HAMILTON 1964, TRIVERS 1971, RICHNER & HEEB 1996). While like resource demands of conspecifics may result in competition, information exchanged among members of a colony or roost may enhance the foraging success of individual group members beyond that experienced by solitary

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breeders. Information transfer at the communal roost or colony site is suggested by several hypotheses, including the Information Centre Hypothesis (ICH, Ward & Zahavi 1973), the Two-Strategies Hypothesis (TSH, Weatherhead 1983), and the Recruitment Centre Hypothesis (RCH, Richner & Heeb 1995). The RCH cannot be applied to colonially-nesting species in its original formulation, however, because it suggests that foragers will refrain from recruiting conspecifics to a food source once an optimal group size is achieved, and costs of recruiting others exceed any benefit that could be derived through group foraging (e.g. dilution effect, optimization of the trade-off between foraging and vigilance). In colonies, breeders are forced to return to the colony to feed their young, and therefore cannot conceal food brought to the nest, which informs others of the presence of food. In a strict sense then, only the ICH and TSH can be applied to colonial breeders, though the uniting principle underlying these hypotheses and the RCH, is that information shared among group members enhances foraging success.

Unambiguous support for information transfer at any aggregation site requires direct evidence that spatial relationships and information sharing among individuals occupying that site influence the foraging success of those individuals when a new food resource becomes available. While this appears to be the case for birds that occupy communal roosts (Sonerud et al. 2001), debate is ongoing as to whether colonies act as information centres despite numerous observational, experimental, and theoretical studies (Mock et al. 1998, Danchin & Richner 2001, Mock 2001).

To test for evidence of beneficial information transfer among colonially-breeding birds, we documented foraging success relative to nesting relationships in a population of colonially breeding European bee-eaters (*Merops apiaster*, hereafter bee-eaters) offered a supplementary local food resource (a honey bee colony, *Apis mellifera*). These bee-eaters typically nest in holes dug in steep sand banks (Cramp 1985) and specialize in foraging on Hymenopterans (Krebs & Avery 1985). Colonies range in size from a few individuals to more than 100 (Hoi et al. 2002). Moreover, within colonies, considerable variation in nest clustering has been documented (Lessells et al. 1994). The presence of this pronounced demographic variation along with the bee-eater's patchily-distributed and ephemeral food resources (Krebs & Avery 1985) renders them well suited to research addressing information transfer hypotheses (ICH and TSH). If coloniality imparts the benefit of information transfer proposed by those hypotheses, we predicted that bee-eaters nesting in closer proximity to conspecifics would more rapidly discover and exploit a novel food source, thereby increasing the rate of food delivery to their nest more rapidly than more isolated nesters.

MATERIALS AND METHODS

From 16 to 22 July 2005, we studied a colony of European Bee-eaters located at Campofelice di Roccella, Palermo, Sicily, Italy (37°58.219'N, 13°50.693'E) on clay-sand banks artificially created by past quarrying activity (Massa & Rizzo 2002). Bee-eaters within that colony were dispersed over a concave surface (about 15 m long × 7 m high), presumably allowing visual contact with neighbouring individuals. The study site was surrounded by citrus, olive and almond orchards and Mediterranean scrubs (Grenci et al. 1997). Our study was carried out during the nestling stage, when bee-eater foraging activity peaks owing to provisioning of young by adults (Inglisa & Galeotti 1993). We carried out a food manipulation experiment (see below) on 18, 21 and 22 July in which we observed feeding rates during two 2-hr periods, from 08:00 to 10:00 and from 15:00 to 17:00 hr (CET). Provisioning events at each bee-eater's nest were recorded

using a tripod-mounted SONY Hi8 camcorder (CCD-TRV238) situated roughly 10 m from the colony. Each entrance of a bee-eater into a nest hole was coded as a feeding visit, and to parallel data presented in earlier studies (LESSELLS 1990, INGLISA & GALEOTTI 1993), we converted these frequency data into Feeding Rate (FR) values as the number of bee-eater visits at the nest per hour. We analysed data only from nests that were active throughout the entire study period. Because the lowest feeding rate reported for nests with dependent young is 12.3 visits/hr (LESSELLS 1990), we assumed that nests were inactive (young deceased or fledged) if fewer than 10 visits occurred during any recording session. Thus, our final dataset included data from 13 nests. To measure distances between nests, we photographed the colony bank with a Sony digital camera (DSC-S40) placing a meter stick beside the bank's face to provide a scale for the photograph. Then, using TechDig 2.0 software (JONES 1998), we digitalized nest locations assigning each a set of Cartesian coordinates. These coordinates were in turn used to calculate the Euclidean (linear) distances between each possible pair of nests. While a variety of indices have been employed to examine dispersion within populations (see KREBS 1989 for a complete review), none of those simultaneously capture both the number and proximity of neighbours, which would most adequately characterize "social richness" and the potential for information transfer among those neighbours. Accordingly, we calculated a Neighbour Index (NI) that provided a continuous measure increasing with the number of neighbours, but weighted the increase in NI by the inverse of the distance to each neighbour. NI thus reflects the relative potential for information transfer, and was calculated for each nest as:

$$\text{NI nest}_n = \sum_{i=1}^{n} (1/\text{dist nest}_n)$$

Where n is the nest label and *dist nest$_n$* is the distance between the nest of interest and each of the other 12 nests in the colony.

To test whether bee-eaters nesting at higher density more rapidly exploit a new food source than those that are more isolated, we introduced a bee hive to our population of bee-eaters at 05:30 hr (CET) on 21 July 2005. This single bee hive, containing about 70,000 workers (based upon two full frames with ca 35,000 workers per full frame in commercial hives; MARCHETTI 1985) was positioned 130 m SSE of the bee-eater colony. The hive was not directly visible from the breeding site as it was positioned opposite a hill adjacent to the colony. Two 7-liter containers of a 50% sucrose solution were established as bee feeders (DELAPLANE 1992) within 2 m of the hive to increase the probability that foraging bees would remain in proximity to the hive, and thus be available to foraging bee-eaters. The sucrose solution was replenished at 06:00 hr on 22 July. Our experiment thus included three levels of the food manipulation treatment: baseline (control) with no new food provided (Food 0; 18 July), a new food source present on the day of hive introduction (Food 1; 21 July), and an existing food source where the hive remained in place for a second day (Food 2; 22 July). We analyzed the daily Feeding Rate (FR) Changes as the differences in the number of visits recorded on each day with supplementary food and that same number during the preceding experimental period within each nest.

To determine whether provisioning behaviour differed among levels of the food manipulations and/or within day, we performed analysis of variance (ANOVA, ZAR 1999) treating food manipulation day (Food 0, Food 1, Food 2) and observation period (AM versus PM) as fixed factors, and Feeding Rate (FR) as the dependant variable on log transformed values (D'Agostino's D-test, all $P > 0.05$ and homoscedasticity $F_{max} = 2.29$, $P > 0.05$). To test whether the food supplementation changed food provisioning rates between the days of food manipulation, we performed a Wilcoxon paired-sample test (ZAR 1999) where the FR Change values recorded between Food 1 and Food 0 days (FR Change 1-0) were compared with those recorded between Food 2 and Food 1 days (FR Change 2-1). We also performed a Wilcoxon paired-sample test to determine whether FR Changes differed between morning and afternoon observation sessions. Finally, to determine whether differential access to information from neighbours within the colony provided disproportionate benefit to those individuals in terms of exploiting a new food resource, we tested for significant relationships between our Neighbour Index (NI) and FR Changes on both the first and second day the hive was present using

simple linear regressions (ZAR 1999). We considered differences statistically significant where $P \leq 0.05$ in analyses performed using STATISTICA 6.0 (STATSOFT, Inc. 1984-2001).

RESULTS

The mean (± SE) feeding rate for the colony across the three experimental days was 38.54 ± 2.60 visits/hr (n = 78, range = 8.81-103.50). Bee-eaters showed a significantly higher FR in the morning (52.63 ± 3.65 visits/hr, range = 14.50-103.50) than in the afternoon (24.45 ± 1.92 visits/hr, range = 8.81-52.93) observation sessions (ANOVA, $F_{1, 72} = 51.19$ $P < 0.001$). FR did not differ, however, among the 3 days of food manipulation (Food 0 = 36.14 ± 4.56 visits/hr; Food 1 = 41.86 ± 4.58 visits/hr; Food 2 = 37.62 ± 4.48 visits/hr; ANOVA, $F_{2, 72} = 0.99$ $P = 0.37$) and no significant interaction was detected between the food manipulation and the time of observation (ANOVA, $F_{2, 72} = 0.10$, $P = 0.91$).

Bee-eaters showed significant differences in feeding rate changes among days (Wilcoxon paired-sample test, $T_{2, 13} = 54$, $P = 0.002$) with an increased feeding rate (5.72 ± 2.26 visits/hr) on the first day supplementary food was offered, but a decreased feeding rate (– 4.24 ± 1.47 visits/hr) from that day to the second day the bee hive was in place. FR Change values did not differ, however, between morning (1.70 ± 2.55 visits/hr) and afternoon (– 0.22 ± 1.64 visits/hr) periods (Wilcoxon paired-sample test, $T_{2, 13} = 152$, $P = 0.55$).

The Neighbour Indices for individual bee-eaters ranged from 3.24 to 10.87, with two pairs of centrally-located nests clustered together with NI > 8.0 and all the others at the periphery of the bank with NI values < 7.00 (Fig. 1). Because the
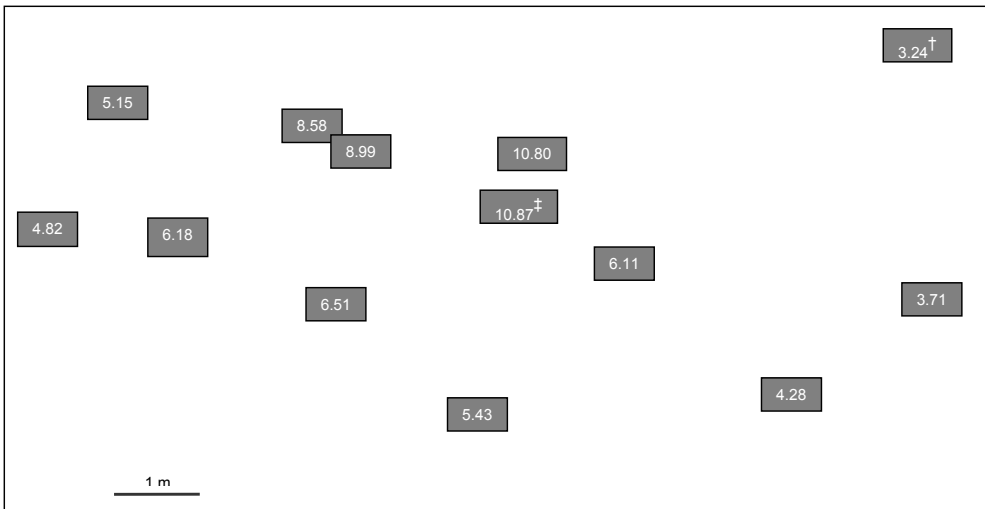

Fig. 1. — Schematic representation of bee-eater nest locations at the colony where labels represent nest locations. Neighbour Index (NI) values for each of the 13 nests are shown. Nests with the lowest (†) and the highest (‡) NI values show that NI is a continuous measure increasing with both the number and proximity of neighbours.
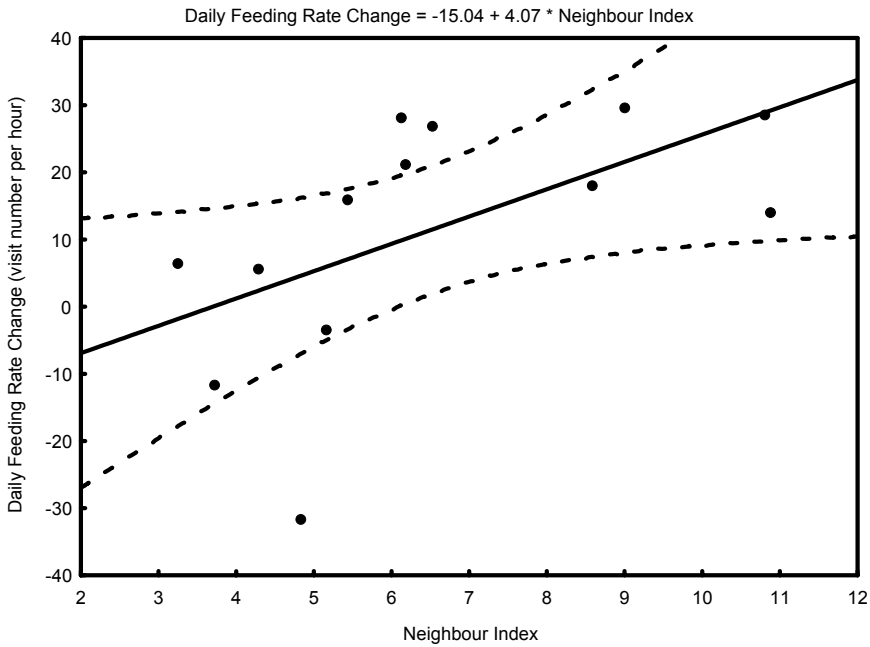
Fig. 2. — Simple linear regression between Neighbour Index (NI) values and the daily FR Changes recorded after the first day of food manipulation (n = 13, r² = 0.323, *P* = 0.04). Dotted lines define the 95% confidence limits. See text for calculation of NI.

FR Changes did not differ significantly between morning and afternoon observation sessions, we pooled FR Changes across sessions to regress daily FR changes against NI values. The relationship between NI and daily FR Change was statistically significant on the first day supplementary food was available (n = 13, r² = 0.323, *P* = 0.04, Fig. 2), with those having higher NI values increasing their feeding rate the most. That effect was transitory, however, and was not detected on the second day the hive was present (n = 13, r² = 0.008, *P* = 0.77).

DISCUSSION

Increases in foraging success with the appearance of a new food source were correlated with the number and proximity of neighbours, suggesting that nesting individuals gleaned information regarding the presence of that food from their neighbours. According to the both ICH and TSH, information transfer occurs at the colony as successful foragers indicate the discovery of food to conspecifics (WARD & ZAHAVI 1973, WEATHERHEAD 1983). In the bee-eaters, neighbours in close proximity returning with prey for their young, or provisioning calls uttered by successful foragers feeding their nestlings (JILKA & URSPRUNG 1980), could have provided the cues underlying this neighbour-dependent enhancement of foraging success. Whatever the case, the more immediate and pronounced increase of FR among closer neighbours is consistent with the prediction of preferential information transfer among colony members (BROWN 1986).

On the surface, the non-significant trend toward decreased FR among colony members on the second day of supplementary food availability may appear to run counter to predictions of the ICH and TSH. On the contrary, such results are expected where information transfer enhances foraging efficiency. A transitory increase in FR, followed by exhaustion of the resource patch, is what we would predict under both hypotheses. Although we estimated that roughly half of the initial number of bees remained at the end of the experiment (S. Falcone pers. com.), further studies with more precise assessment of bee depletion are warranted.

The absence of any relationship between FR changes on the 2nd day and NI may be explained by prey depletion, though our findings do not preclude a contribution of local enhancement whereby foraging colony members are attracted to the new food patch by the presence of conspecifics (Caldwell 1981). That potential contribution, likewise, does not necessarily rule out information transfer occurring at the colony (Buckley 1997). Indeed, the differential enhancement of FR among individuals with higher NI on the 1st day supplementary food was available suggests that information transfer at the colony has primacy over any subsequent contribution made by local enhancement.

More robust documentation, quantifying both foraging efficiency relative to nest location within colonies and reciprocity of information exchange, is necessary to discern between benefits accruing under the ICH and TSH. Further, while the foraging efficiency of individuals with higher Neighbour Indices was significantly enhanced over the relatively small spatial scale employed in our study, the limits of that enhancement must be explored both on larger spatial and temporal scales.

Despite the preliminary nature of this study, our findings confirm that European bee-eater colony members benefit via information regarding food gleaned from neighbours. Replication of our study across colonies showing variation in nest density, as well as marking individuals and recording both their time of arrival at the experimental food source, and synchrony in foraging among neighbours would provide further insight into the limits and mechanisms of information sharing in this context.

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