

Flock foraging at a breeding colony of collared pratincoles *Glareola pratincola*

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领燕 繁殖群体的集群觅食

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摘要 集合点假说 (Assembly-point hypothesis) 认为: 动物局部地区聚群数量的增加有助于不同的繁殖地的个体聚集成群体, 然后一起寻找食物斑块觅食, 这种聚群有助于个体从集群觅食中获得利益。本文通过领燕 (*Glareola pratincola*) 离开和回到繁殖地的先后顺序来验证以上假说。我们在 29 天的观察中, 发现有 4 天该群中个体离开繁殖地的先后顺序不是随机分布的, 尽管这种策略会随着环境条件而改变, 但仍然表明领燕 的觅食群体在繁殖地就已经聚集形成了。食物资源 (飞虫) 的短暂性和波动性以及由繁殖地到觅食地的距离均与所验证的假说的假设相一致 [动物学报 51 (6): 1141-1145, 2005]。

关键词 领燕 局部聚群数增加 集群觅食 群集性

Key words Collared pratincole, *Glareola pratincola*, Local enhancement, Flock foraging, Coloniality

A variety of hypotheses has been adduced to explain why avian coloniality evolves (Wittenberger and Hunt, 1985). The information center hypothesis (Ward and Zahavi, 1973) argues that species that benefit from social foraging should also be able to benefit by following others from a central colony site. According to this hypothesis, the main function of coloniality is transfer of information about the spatial location of food sources. Thus, an unsuccessful forager could follow a successful forager when leaving a communal roost or colony, and will in turn be followed on the occasions when it foraged successfully. However, the empirical evidence available for testing the hypothesis is incomplete and a majority of authors have not been able to confirm it (e. g., Stutchbury, 1988; Caccamise, 1991; Buckley, 1997; but see Sonerud et al., 2001). There are also serious theoretical problems derived from possible assumptions based on group selection (e. g., Richner and Heeb, 1996).

One of the alternatives proposed to the information center hypothesis is the information exchange by the use of local enhancement (Turner, 1964; Pöysä, 1992), the attraction of searching individuals to groups of already feeding birds. This social foraging

strategy can account for the exchange of information at communal roosts and colonies without the problems derived from group selection arguments (Richner and Heeb, 1996). The use of local enhancement can be facilitated at communal roosts and breeding colonies in two ways (Buckley, 1996). First, those sites may make it easier for birds to purposely form foraging groups: the assembly-point hypothesis (Evans, 1982). Second, passively-forming aggregations of birds may result from the time taken by the birds when leaving the roosts or colonies and dispersing over the foraging areas, thus leading to more efficient use of local enhancement than if birds were not grouped (Buckley, 1996). Thus, the birds would profit from the benefits of social foraging by increasing the likelihood of locating food sources.

The collared pratincole *Glareola pratincola* is a colonial, monogamous and mainly aerially feeding insectivorous shorebird (Cramp and Simmons, 1983), associated with semi-desert terrain, poor steppe soils and floodlands which dry out seasonally (Calvo et al., 1993; Calvo, 1994). This species breeds in different countries around the Mediterranean Sea, southern Europe and nations of the former Soviet Union, and spends the winter mainly in Africa

(Cramp and Simmons, 1983).

The studies of the behavior of this species are scarce (Cramp and Simmons, 1983). A singular phenomenon common to some *Glareola* species is the complete, or nearly complete, absence of adults from the nesting colony at certain times of the day. At twilight feeding times the colony's adults are mostly airborne (Pérez Chiscano, 1965; Williams et al., 1989; Calvo and Vázquez, 1995; Tajuelo and Máñez, 2003), as result of the occurrence of a plentiful local food supply near the colonies where the pratincoles forage together (Yeates, 1948). No authors have tried to quantify the individual replacements (departures from and arrivals at the colony), which occurs due to food search by the aerial feeders. This behavior seems to be common among birds where individuals follow others from colony sites or depart in flocks in synchronous waves or in continuous streams in order to search for food sources (e. g., Horn, 1968; Ward and Zahavi, 1973; Gaston and Nettleship, 1981).

The low interference competition at colonies of collared pratincoles, as revealed by a very low frequency of intraspecific aggressions (the author's unpublished data), makes this species a good candidate to exhibit group recruitment behavior, as it should not follow a risk-prone strategy of foraging by departing to the feeding sites in the opposite direction of other birds to avoid competition (Buckley, 1996).

The aim of this study is to measure the frequency of departures and arrivals of collared pratincoles at a nesting colony in order to detect if the sequences of departures follow nonrandom distributions. If foraging with others is advantageous, it might be expected that collared pratincoles would join one another at the colony so as to arrive at the foraging area together. Therefore, it was predicted that if collared pratincoles use local enhancement by joining others at the colony (Assembly-point hypothesis; Evans, 1982), a departure of a bird would be followed by other departure with a higher probability than by an arrival of a bird to the colony. Although passively-forming aggregations of birds are likely to occur in colonies, only the assembly-point hypothesis was tested because those aggregations take place when the birds disperse over the foraging areas surrounding the colonies (see above), which makes them difficult to detect by observing departures in a colony site.

1 Materials and methods

Data were collected in 2000 and 2001 at a breeding colony of collared pratincoles located in Badajoz province (SW Spain, 38°53' N, 6°51' W). The study was carried out during the breeding season of the species (April – July), when all the adult members are present at the colony, and thus not overlapping

with the postbreeding migration period (Cramp and Simmons, 1983; Mascara, 1987; Calvo et al., 1993; Calvo, 1994).

The colony (15 – 18 breeding pairs) was located on an extensive plain on a stubble field that in previous years had been a rice cultivation and was surrounded by maize fields and other rotation cultivations, near the course of the Guadiana river. This is the typical nesting habitat of the species in inland Spain (Calvo et al., 1993; Calvo, 1994; Tajuelo and Máñez, 2003).

The observations were carried out from an irrigation ditch on the edge of the stubble at which the colony was located from an elevated point. The pratincoles did not seem to be affected by the presence of the observer. Data recording took place during the three hours prior to sunset, when the foraging activity of the collared pratincoles is maximum (Tajuelo and Máñez, 2003).

Counts of all the adult members of the colony were made fortnightly during the two years of study.

All the occasions in which a pratincole departed or arrived to the colony were recorded, as well as the time at which it took place. The pratincoles left the colony in two directions (see Results), but successive departures only occurred in the same direction, thus allowing to avoid mixing departures taking place in different directions. Departures and arrivals were easy to detect because of the lack of tall vegetation around the colony site. Furthermore, when a pratincole arrives to the colony from a foraging trip, it calls and sometimes adopts a bowing display posture (Cramp and Simmons, 1983). This call is also issued before departing, and flights in circles around the colony are then often observed. Therefore, a series of sequences of departures and arrivals of individuals was recorded each day. The serial randomness of the sequences of departures was tested with Fisher's exact tests performed along with Markov's analyses (Martin and Bateson, 1986). Thus, 2 × 2 contingency tables were made with the observed temporal distribution of frequencies of departures and arrivals. The null hypothesis tested was that the sequence follows a first order Markov's process in which the probability of a departure does not depend on that the immediately previous event is another departure (Martin and Bateson, 1986). Because the aim of the study was to test the randomness of departures only, the Fisher's exact tests are one-tailed (Zar, 1999). Similar to other authors (e. g., Buckley, 1997), in the analyses only birds departing or arriving within 2 min of each other were considered to be part of a run (i. e., a sequence of birds departing from the colony until the arrival of new birds, and vice versa; Zar, 1999).

To remove the effect of observation time, the

sum the number of birds departing and the number of birds arriving in a sequence was divided by the observation time of each day of study. Thus, it could be determined if the foraging activity of collared pratincoles away from the colony varied along the four months of the study period.

For the analysis of frequencies, G-tests were carried out. Means are expressed with the corresponding standard errors and were compared with Student *t* tests when data was normal distributed. If not, medians were compared with Mann-Whitney *U* and Kruskal-Wallis tests. All these tests are two-tailed (Zar, 1999).

2 Results

There were no significant differences in the number of adult collared pratincoles between the two years of study (2000: 29.3 ± 2.0 , 2001: 31.4 ± 2.6 ; Student *t* test, $t = -0.65$, $df = 14$, $P > 0.05$). Therefore, simultaneous analysis of the two-year data was considered possible.

The colony was visited a total of 29 days, corresponding to 3,990 observation minutes. The number of observation days did not vary between the two years ($G = 0.29$, $df = 1$, $P > 0.05$), nor between the months ($G = 5.31$, $df = 3$, $P > 0.05$). A total of 853 departures and arrivals of collared pratincoles were recorded at the colony during the study period.

The pratincoles always left the colony in the same directions (N and SW), though the frequencies of departures following each direction were not measured. Two groups of foragers were always observed flying in circles to about 1 km from the colony in these directions, over the course of the Guadiana river and over a golf course. The location of these feeding sites did not seem to vary during the two years of study. That means that the pratincoles left the colony mainly to feed.

When the sequences of pratincoles departing from and arriving at the colony were analysed, non-random distributions of departures were found in 3 out of 29 days (Table 1). The probability calculated for another day was marginally significant ($P = 0.054$; Table 1). The median number of departures and arrivals recorded in these four days (42.3 ± 5.9) was significantly higher than those (27.6 ± 6.1) recorded in the rest of observation days (Mann-Whitney *U* test, $U = 82.5$, $n_1 = 4$, $n_2 = 25$, $P < 0.05$; Table 1).

The number of birds departing from and arriving at the colony per hour of observation did not vary between the months (Kruskal-Wallis, $H = 0.68$, $df = 3$, $P > 0.05$, Fig.1).

Table 1 Results of the one-tailed Fisher's exact tests performed along with Markov's analyses on sequences of departures and arrivals of collared pratincoles at a breeding colony during the different observation days of the study period

Observation day	Month	No. departures	No. arrivals	<i>P</i>
1	April	7	24	ns
2	April	4	8	ns
3	April	6	4	ns
4	April	43	13	<0.001
5	April	14	19	ns
6	May	15	17	ns
7	May	10	8	ns
8	May	6	8	ns
9	May	15	13	ns
10	May	10	20	ns
11	May	2	3	ns
12	May	10	5	ns
13	May	22	8	0.008
14	May	21	14	0.001
15	May	29	19	0.054
16	May	5	3	ns
17	May	8	4	ns
18	May	16	4	ns
19	June	3	6	ns
20	June	6	7	ns
21	June	10	5	ns
22	June	13	25	ns
23	June	5	4	ns
24	June	56	104	ns
25	July	16	26	ns
26	July	6	13	ns
27	July	42	11	ns
28	July	8	6	ns
29	July	20	29	ns
Total	–	428	430	–

ns: the test is not significant at the level of $\alpha = 0.05$.

P is the error probability when the null hypothesis is rejected: the sequence follows a first order Markov's process in which the probability of a departure of a bird from the colony depends on that the immediately previous event is another departure (see Martin and Bateson, 1986 for more details on the method).

3 Discussion

The assembly-point hypothesis (Evans, 1982) argues that birds in roosts and breeding colonies that benefit from social foraging should form groups before departing to the feeding sites. Thus, a term better

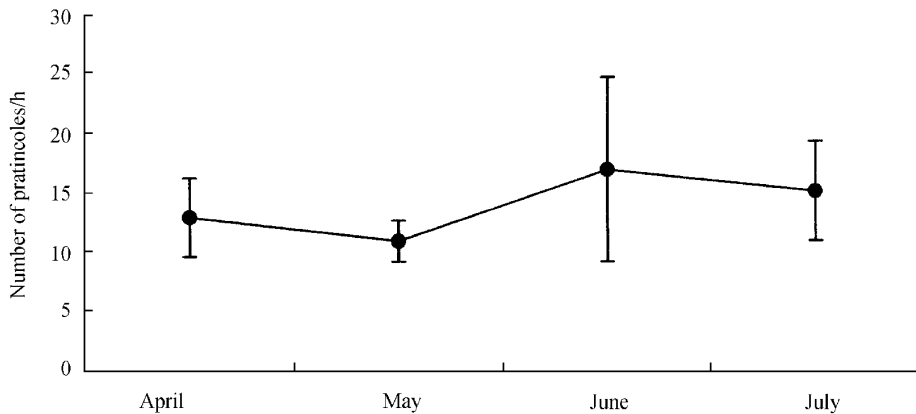


Fig. 1 Number of collared pratincoles departing from and arriving at the colony per hour of observation during the four months of the study period

Data is shown as means \pm SE.

than “local enhancement” for this behavior may be “colony-based recruitment”, as proposed by Richner and Heeb (1996). These authors state that, since aerial displays used to recruit other birds at the colonies in general can be costly (Richner and Heeb, 1996 and cited references), it has the potential to be an honest signaling system. The present study shows that collared pratincoles in fact recruit others at a breeding colony to depart to the feeding sites. Significant results were only obtained in four days, but the frequency of use is not likely to be a good measure of a strategy’s importance (Buckley, 1997), as individuals may not often need to follow other colony members, but only when food is scarce or with other environmental conditions (Buckley, 1997). Furthermore, the total number of departures and arrivals recorded in those four days was significantly higher than in the rest of observation days, indicating non-random distributions of departures which demonstrates that flock recruitment behavior at the colony could be only detected with relatively high numbers of observations on departures and arrivals. Although my findings suggest active group formation behavior, the pratincoles were always seen departing in the same two directions. This could enhance the passively-forming aggregations of birds (Buckley, 1996 and cited references), a behavior that would also facilitate the use of local enhancement (see Introduction). Therefore, this could also account for the fact that nonrandom distributions of departures were only found on some days, as the pratincoles could potentially choose between active and passive grouping (Buckley, 1996).

Alternatively, colonial breeding may not be selectively advantageous for pratincoles, but has been retained as a trait derived from colonial ancestors, since coloniality is a labile trait that has experienced many convergences and reversals in response to vari-

ous environmental pressures (Rolland et al., 1998). Hence, this could also explain that nonrandom distributions of departures were only observed occasionally.

By the other hand, the number of birds departing from and arriving at the colony per hour of observation did not vary between the months, suggesting that the foraging activity was constant through the study period and that the significant results on departure sequences obtained for some days were not caused by different levels of activity.

Spatial clumping of aerial insects often occurs and is associated with localized emergences of aquatic insects (Lewis and Taylor, 1964), and aerial insect abundance fluctuates substantially in response to local weather conditions (Glick, 1939, 1957; Taylor, 1963; Bryant, 1975). Since the collared pratincole is mainly an aerially feeding insectivorous shorebird, this agrees with the assumptions of the colony-based recruitment strategy (“recruitment center hypothesis” in a more general sense; Richner and Heeb, 1996), that is, that food sources are patchily distributed in space, show ephemeral appearance in time, and that food within the patch is relatively abundant (Richner and Heeb, 1996). Although the feeding sites of the collared pratincoles were visible from the colony, the ephemeral and fluctuating abundance of insects could make their exact location vary with time, so that the pratincoles have to control the variance of food intake, one of the aims of social foraging (Flemming et al., 1992 and cited references; Davoren et al., 2003 and cited references). Furthermore, it is impossible to affirm that the groups of pratincoles visible from the colony were the only foraging groups. This fluctuating abundance of insects resembles the spatiotemporal unpredictability of the food of most seabirds (Rolland et al., 1998), which probably made information exchange on food location an important factor allowing for the establishment of

colonies in marine habitats (Rolland et al., 1998). Another possible benefit of recruiting other members of the colony could be a greater ability to detect possible danger, as in other species (Knight and Knight, 1983). Indeed, other birds that feed on aerial insects also follow conspecifics to food patches (Brown, 1988).

Birds can use a variety of strategies for finding food, and the strategy used each time depends on the spatial and temporal resolution of search and current prey conditions. For example, Davoren et al. (2003) found in a seabird species that individuals only use local enhancement when the food sources are visible from the colony, but when the birds have to travel longer distances a memory-based strategy is used instead. At the study site, a river was located 1 km to the north of the colony, where a group of pratincoles was always seen foraging, and the other feeding site was located at the same distance. Therefore, this proximity to the food sources is consistent with the evidence of local enhancement at the colony (Davoren et al., 2003).

Finally, it is important to note that, although local enhancement facilitates the aggregations of birds and can be considered as a benefit obtained by the colony members, it is not necessarily a mechanism leading to the evolution of coloniality (Rolland et al., 1998; Wagner et al., 2000).

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References

- Brown CR, 1988. Social foraging in cliff swallows: local enhancement, risk sensitivity, competition and the avoidance of predators. *Anim. Behav.* 36: 780–792.
- Bryant DM, 1975. Breeding biology of house martins *Delichon urbica* in relation to aerial insect abundance. *Ibis* 117: 180–216.
- Buckley NJ, 1996. Food finding and the influence of information, local enhancement, and communal roosting on foraging success of North American vultures. *Auk* 113: 473–488.
- Buckley NJ, 1997. Experimental tests of the information-center hypothesis with black vultures *Coragyps atratus* and turkey vultures *Cathartes aura*. *Behav. Ecol. Sociobiol.* 41: 267–279.
- Caccamise DF, 1991. European starling fidelity to diurnal activity centers: role of foraging substrate quality. *Wilson Bull.* 103: 13–24.
- Calvo B, 1994. Effects of agricultural land use on the breeding of collared pratincole *Glareola pratincola* in south-west Spain. *Biol. Conserv.* 70: 77–83.
- Calvo B, Mániz M, Alberto J, 1993. The collared pratincole *Glareola pratincola* in the National Park of Doñana, South West Spain. *Wader Study Group Bull.* 67: 81–87.
- Calvo B, Vázquez M, 1995. Field technique suggestions for the study of collared pratincoles *Glareola pratincola*. *Wader Study Group Bull.* 78: 33–35.
- Cramp S, Simmons KEL, 1983. *The Birds of the Western Palearctic*. Volume III. Oxford: Oxford University Press.
- Davoren GK, Montevecchi WA, Anderson JT, 2003. Search strategies of a pursuit-diving marine bird and the persistence of prey patches. *Ecol. Monogr.* 73: 463–481.
- Evans RM, 1982. Foraging flock recruitment at a black-billed gull colony: implications for the information center hypothesis. *Auk* 99: 24–30.
- Flemming SP, Smith P, Seymour NR, Bancroft RP, 1992. Ospreys use local enhancement and flock foraging to locate prey. *Auk* 109: 649–654.
- Gaston AJ, Nettleship DN, 1981. The thick-billed murre of Prince Leopold Island: a study of the breeding biology of a colonial, high arctic seabird. *Can. Wildl. Serv. Monogr.* 6: 1–350.
- Glick PA, 1939. The distribution of insects, spiders, and mites in the air. U.S. Dept. Agric. Tech. Bull. 673: 1–50.
- Glick PA, 1957. Collecting insects by airplane in southern Texas. U.S. Dept. Agric. Tech. Bull. 1158: 1–28.
- Horn HS, 1968. The adaptive significance of colonial nesting in the Brewer's blackbird *Euphagus cyanocephalus*. *Ecology* 49: 682–694.
- Knight SK, Knight RL, 1983. Aspects of food finding by wintering bald eagles. *Auk* 100: 477–484.
- Lewis T, Taylor LR, 1964. Diurnal periodicity of flight by insects. *Trans. R. Entomol. Soc. London* 116: 393–476.
- Martin P, Bateson P, 1986. *Measuring Behaviour*. Cambridge: Cambridge University Press.
- Mascara R, 1987. Confirmed breeding of the collared pratincole *Glareola pratincola* in a crop field of Sicily. *Riv. Ital. Ornitol.* 57: 137 (In Italian).
- Pérez Chiscano JL, 1965. Breeding records of collared pratincoles and little terns on the Guadiana River. *Ardeola* 10: 37–38 (In Spanish).
- Pöysä H, 1992. Group foraging in patchy environments: the importance of coarse-level local enhancement. *Ornis Scand.* 23: 159–166.
- Richner H, Heeb P, 1996. Communal life: honest signaling and the recruitment center hypothesis. *Behav. Ecol.* 7: 115–119.
- Rolland C, Danchin E, de Fraipont M, 1998. The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: a comparative analysis. *Am. Nat.* 151: 514–529.
- Sonerud GA, Smedshaug CA, Bråthen Ø, 2001. Ignorant hooded crows follow knowledgeable roost-mates to food: support for the information centre hypothesis. *Proc. R. Soc. Lond. B* 268: 827–831.
- Stutchbury BJ, 1988. Evidence that bank swallow colonies do not function as information centers. *Condor* 90: 953–955.
- Taylor LR, 1963. Analysis of the effect of temperature on insects in flight. *J. Anim. Ecol.* 32: 99–117.
- Tajuelo FJ, Mániz M, 2003. Collared pratincole *Glareola pratincola*. In: Martí R, del Moral JC ed. *Atlas de las Aves Reproductoras de España*. Madrid: Dirección General de Conservación de la Naturaleza-Sociedad Española de Ornitología, 248–249 (In Spanish).
- Turner ERA, 1964. Social feeding in birds. *Behaviour* 24: 1–46.
- Wagner RH, Danchin E, Boulinier T, Helfenstein F, 2000. Colonies as byproducts of commodity selection. *Behav. Ecol.* 11: 572–573.
- Ward P, Zahavi A, 1973. The importance of certain assemblages of birds as “information-centres” for food finding. *Ibis* 115: 517–534.
- Williams GD, Coppinger MP, Maclean GL, 1989. Distribution and breeding of the rock pratincole on the Upper and Middle Zambezi river. *Ostrich* 60: 55–64.
- Wittenberger JF, Hunt GL Jr, 1985. The adaptive significance of coloniality in birds. In: Farner DS, King JR, Parkes KC ed. *Avian Biology*. Vol. VIII. New York: Academic Press, 1–78.
- Yeates GK, 1948. Some notes on the nesting habits of the pratincole. *Brit. Birds* 41: 301–305.
- Zar JH, 1999. *Biostatistical Analysis*. 4th edn. New Jersey: Prentice Hall.