Effects of distance in central place foraging in Starlings

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Observations of naturally foraging Starlings *Sturnus vulgaris* feeding their young were used to test the prediction that the time spent per visit to a feeding patch will depend on distance from the nest. We recorded the frequency with which the birds returned with food to the nest, and the time spent at the feeding patch. The time per visit increased with increasing distance. But the time spent feeding per unit area was negatively correlated with distance. The Starlings fed longer when alone than when feeding in a group. We suggest that they feed more effectively in a group, because there is less need for vigilance. The abundance of food, measured as the density of earthworms, was higher when the Starlings started to feed than later, and also higher on a more distant than a closer patch at the start of feeding. We conclude that the distance from the nest is an important factor in central place foraging in birds.

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Introduction

A typical example of central place foraging is provided by a bird feeding nestlings. In the recent literature central place foraging has been discussed theoretically (Andersson 1978, Orians & Pearson 1979), most papers being based on the traditional theory of optimal foraging (e.g. Charnov 1976, Pyke et al. 1977, Krebs 1978). There are, however, only a few studies in which theoretical predictions have been tested against field data in cases of central place foraging (Cody 1973, Post 1974, Andersson 1981, Carlson & Mureno 1981, Tinbergen 1981, Bryant & Turner 1982). Orians & Pearson (1979) present a model which predicts that the time spent per visit to a feeding place should increase with distance from the central point, other variables being constant. We will examine this prediction, and other effects of distance, in relation to observations of naturally foraging Starlings *Sturnus vulgaris* L. feeding their young.

Methods and study area

We observed Starlings for two weeks in June 1980 at a time when the birds were very busy feeding their young. Several Starlings nested in the study area, but all the data presented here are for one pair. One person observed the birds at the nest, and another at the various feeding places. It was easy to see whether the birds returned to the nest with food, but neither the amount nor the quality of the food was determined. The frequency with which the birds returned with food was recorded, as were the times spent in the feeding place, flying to and from that place and in the nest.

The pair nested in an agricultural area with cattle pastures, cultivated fields and woods 40 km south of Stockholm, Sweden. They foraged in all directions from the nest, but it was not possible to observe all their feeding places. Each feeding place was visited a number of times by the birds, before they switched to a new place. These feeding places, which were homogeneous with respect to the vegetation, are referred to as patches (Table 1). The patches shown in Table 1 represent only a part of the total feeding area.

Earthworms are known to be an important food for Starlings (Dunnet 1955, Moeed 1980) and the density of earthworms was used as a measure of the abundance of food. The number of earthworms per plot (25x25 cm) was estimated by treating 22 randomly distributed plots on two patches with a 4 % solution of formalin and counting all the earthworms that appeared at the surface.

Results

Two variables were examined in relation to the time spent by a Starling on a visit to a patch. These were: distance from the nest to the patch (Fig. 1), and feeding alone *versus* feeding with other starlings. Together these explained 64 % of the variation in the time spent per visit (Table 2; multiple regression analysis; Bliss 1970).

The Starlings fed significantly longer when they were alone than when other Starlings were feeding with them (Fig. 2; two-factor anova, $F(1, 20) = 8.8$, <0.01 for single-group feeding, the between-patches and interaction terms are not significant). The variable single *vs.* group feeding was independent of the distance from the nest ($r=0.04$, $df=26$, $t=0.23$) and of patch size ($r=0.11$, $df=26$, $t=0.55$).

Table 1. Area and distance from nest of feeding patches used by pair of Starlings.

Patch no.	Area (m^2)	Dist. (m)	No. observ.	
2	800	100	6	pasture
4	2 000	175	4	field
6	2 000	150	11	field
7	1 200	200	6	field
11	100	50	7	ant-hill
12	1 000	300	—	pasture
14	10 000	400	11	pasture

We observed Starlings eating earthworms and many other objects. Significantly more earthworms were found on the test plots when the Starlings had just started to feed in an area than two hours later (two-factor anova, F (1, 18) = 14.0, P<0.01 for before-after, between patches F=13.3, P<0.01, interaction term not significant; Fig. 3). There were also significantly more earthworms on the more distant patch when the birds started to feed than on the closer patch.

The Starlings visited a patch repeatedly. After they had changed to a new patch, they did not return to the old one for at least two hours. The total time (flight time included) for which they exploited a patch was dependent on the size of the patch, and on the distance from the nest (y=0.005 (area) — 0.04 (dist.) + 10.1; R^2=0.99). If we use the patches with the same type of food (the ant-hill, no. 11, excluded), and plot time per unit area against distance from the nest (Fig. 4), we get a negative relationship.

Discussion

Two variables together explained 64 % of the variation in the time spent by a bird in a feeding patch: distance from the nest and single *vs.* group feeding.

The observation that foraging time per visit increases with distance from the nest, agrees with the prediction (Orians & Pearson 1979). Tinbergen (1981) found that the load size in starlings increased with the total time spent on a foraging

Table 2. Regression of time (sec.) spent by Starling at feeding patch on distance from nest and single *vs.* group feeding (multiple regression analysis; Bliss 1970).

	df	F	P
Distance	1, 42	46.2	P<0.001
Single-group	1, 42	0.06	n.s.
Combined	2, 42	37.8	P<0.001

Y=0.50 (dist.) + 4.5 (single-group) — 13.2 R^2 = 0.64

Y=0.51	(dist.)	— 9.1	F (1, 43) = 77.1 P<0.001
Y=80.0	(single-group)	—20.6	F (1, 43) = 14.3 P<0.01

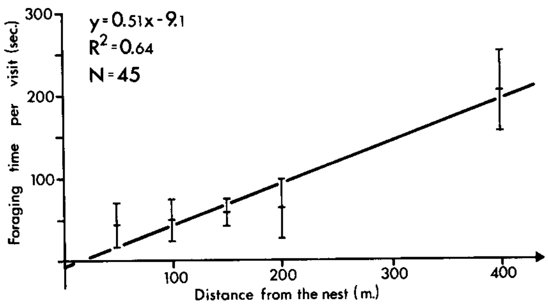

Fig. 1. Dependence of foraging time (sec.) on distance of foraging patch from the nest in Starlings feeding their young. R^2 = coefficient of determination (Bliss 1970).

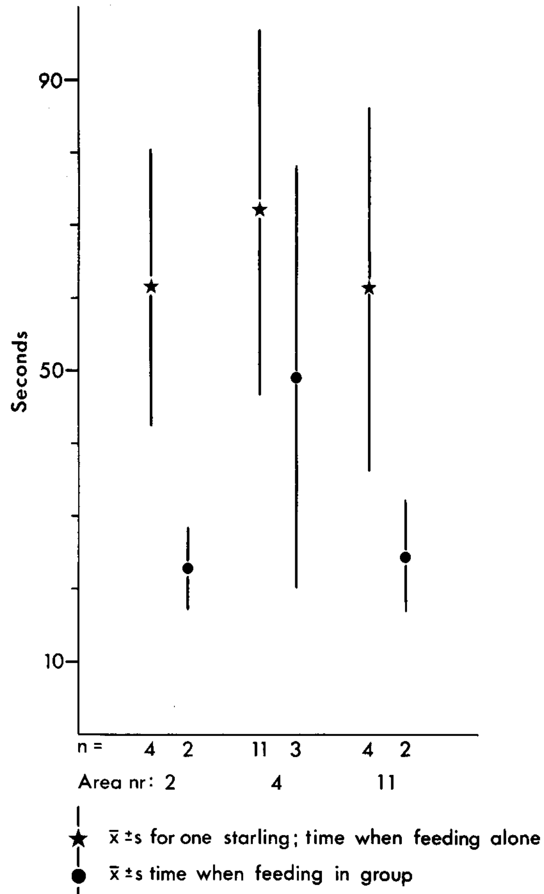

Fig. 2. Time (sec.) spent by a Starling on a feeding patch when alone and in a group (two or more).

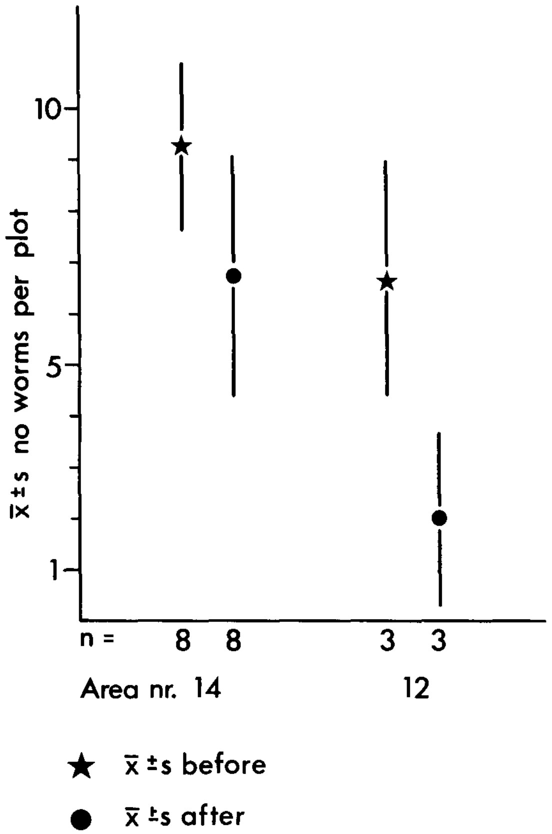

Fig. 3. No. of earthworms per 25-cm^2 plot on a feeding patch before and after visit by Starlings.

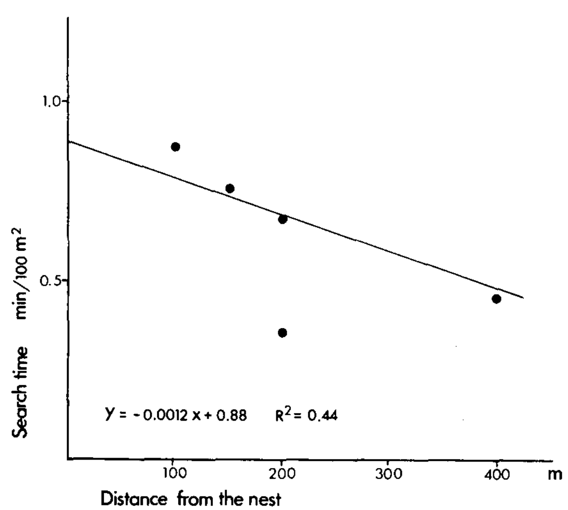

Fig. 4. Searching time (min.) per unit area (100 m^2) in relation to distance from the nest (m) for a pair of Starlings in five patches with the same type of food. R^2 = coefficient of determination (Bliss 1970).

flight, and thus also with distance. In an experimental test with the Wheatear *Oenanthe oenanthe* L., both load sizes and collecting times increased with distance (Carlson & Mureno 1981). Bryant & Turner (1982) examined load size as a function of distance and food density in swallows, and other effects of distance from the nest have been discussed by several authors (Post 1974, Andersson 1978, 1981, Zach & Falls 1979, Tinbergen 1981). Search time per unit area has been shown to decrease with increasing distance, as was also found in this study (Fig. 4), when we compared patches with the same sort of food.

Birds are known to have a marked effect on earthworm populations (Bengtson et al. 1976). Dunnet (1955) showed that earthworms may average 11—14 % of the Starlings' food intake, but occasionally account for as much as 68 % of the total diet. Moeed (1980) obtained the same result when analysing the gizzards of 334 adult Starlings. We found that the density of earthworms was higher when the birds started to feed on a patch than two hours later (Fig. 3). This is probably not caused by depletion of prey in a patch, but rather indicates that a patch is only temporarily favourable as a feeding place. The timing of patch exploitation is thus of importance to foraging Starlings, as pointed out by Tinbergen (1981). Theoretically (Charnov 1976), given the relevant information, a bird should start to feed in a closer patch at a lower prey density than in a more distant one. In fact, we found that the density of earthworms was lower on the closer patch than on the more distant one. But since we have data from only two patches, and earthworm density can vary greatly (Bengtson et al. 1976), no definite conclusions can be drawn.

There is a tendency for Starlings to feed in groups on a larger patch. However, group and single feeding occurred on both small and medium-sized patches. The Starlings fed for longer times when single than in groups (Fig. 2). If this was caused by a lower food density, they would not return to the patch, but the result was obtained from successive visits to the same patch. In a study on Starlings in captivity Feare & Inglis (1979) showed that starlings feeding in groups have higher feeding rates than those feeding alone. Powell (1974) noted that Starlings in groups of ten responded more quickly than single birds to model of a flying hawk. Jennings & Evans (1980) found that Starlings in the centre of a flock spent more time in pecking and less time in being vigilant than peripheral birds. Solitary birds spent even less time picking for food than in the periphery of a flock. This suggests that social feeding in Starlings can be explained as an anti-predator adaptation (Powell 1974, Jennings & Evans 1980), or as a means of learning about good feeding places (Ward & Zahavi 1973), or a combination of these.

Our results were obtained by observing a single pair and we lack information on how much or what they ate. Nevertheless, our observations accord with the predictions of the central place foraging theory, and confirm that distance is an important factor in central place foraging in birds.

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Selostus: **Ruokailualueen etäisyyden vaikutus kottaraisen ravinnonhakukäyttäytymiseen**

Maaseutuympäristössä pesivän kottaraisparin ravinnonhakukäyttäytymistä seurattiin tiiviisti kahden viikon ajan Tukholman lähistöllä. Seuraavat asiat huomioitiin sekä itse pesällä että keskeisillä ravinnonhakupaikoilla ympäristössä (taulukko 1): ruoantuontifrekvenssi pesälle, pesällä vietetty aika, ravinnonhakupaikalla vietetty aika ja lentoon kulunut aika pesän ja ravinnonhakupaikan välillä.

Lähtöolettamuksena oli, että ravinnonhankintaan kulutettu aika on riippuvainen paikan etäisyydestä pesästä. Ravinnonhakuun käytettiinkin sitä enemmän aikaa, mitä kauempana kohde sijaitsi (kuva 1). Yksin ollessaan kottaraisella kului enemmän aikaa ravinnonhakuun kuin ryhmässä (kuva 2), mikä johtunee siitä, että ryhmässä yksilön ei tarvitse käyttää paljoa aikaa varuillaoloon. Nämä kaksi muuttujaa (etäisyys pesään, yksin/ryhmässä ruokailu) yhdessä selittävät 64 % ravinnonhakupaikalla käytetyn ajan pituudessa esiintyvästä vaihtelusta (taulukko 2).

Lierojen, kottaraisten erään pääravintokohteen, runsaus eri koealoilla oli tilastollisesti suurempi kottaraisten vasta asettuessa sinne kuin kaksi tuntia ruokailun aloittamisen jälkeen (kuva 3). Lierojen väheneminen ei luultavasti niinkään johdu kottaraisten saalistuksesta, vaan pikemminkin osoittaa ravintolaikkujen olevan vain hetkellisesti hyviä. Tutkimuksessa havaittiin myös, että lierojen määrä oli suurempi kaukana sijaitsevilla ravintolaikuilla kuin läheisillä.

Kottaraiset käyttivät ravinnonhakupaikkoja toistuvasti. Siirryttyään uuteen paikkaan ne eivät käyttäneet vanhaa paikkaa ainakaan kahteen tuntiin. Paikan kokonaiskäyttöaika (ml. lentoaika) oli riippuvainen paikan pinta-alasta ja etäisyydestä pesään. Lähellä olevia laikkuja kottaraiset käyttivät tehokkaammin (etsintäaika/laikun koko) kuin kaukana sijaitsevia (kuva 4).

References

Andersson, M. 1978: Optimal foraging area: size and allocation of search effort. — Theor. Popul. Biol. 13:397—409.

Andersson, M. 1981: Central place foraging in the whinchat, Saxicola rubetra. — Ecology 62:538—544.

Bengtson, S.-A., Nilsson, A., Nordström, S. & Rundgren, S. 1976: Effect of bird predation on lumbricid populations. — Oikos 27:9—12.

Bliss, C. I. 1970: Statistics in biology, vol. 2. — McGraw-Hill, New York.

Bryant, D. M. & Turner, A. K. 1982: Central place foraging in swallows (Hirundinidae): the question of load size. — Anim. Behav. 30:845—856.

Carlson, A. & Mureno, J. 1981: Central place foraging in the Wheatear Oenanthe oenanthe: an experimental test. — J. Anim. Ecol. 50:917—924.

Charnov, E. L. 1976: Optimal foraging, the marginal value theorem. — Theor. Popul. Biol. 9:129—136.

Dunnet, G. M. 1955: The breeding of the Starling Sturnus vulgaris in relation to its food supply. — Ibis 97:619—662.

Feare, C. J. & Inglis, I. R. 1979: The effects of reduction of feeding space on the behaviour of captive Starlings Sturnus vulgaris. — Ornis Scand. 10:42—47.

Jennings, T. & Evans, S. M. 1980: Influence of position in the flock and flock size on vigilance in the Starlings, Sturnus vulgaris. — Anim. Behav. 28:634—635.

Krebs, J. R. 1974: Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron (Ardea herodias). — Behaviour 51:99—134.

Krebs, J. R. 1978: Optimal foraging: decision rules for predators. — *In* Krebs, J. R. & Davies, N. B. (eds.), Behavioural ecology. Blackwell Scientific Publ., Oxford.

Moeed, A. 1980: Diets of adult and nestling Starlings (Sturnus vulgaris) in the Hawke's Bay, New Zealand. — N. Z. J. Zool. 7:247—256.

Orians, G. H. & Pearson, N. E. 1979: On the theory of central place foraging. — *In* Biosciences Colloq., 3d, Ohio State Univ. 1977. Analysis of ecological systems. Columbus.

Post, W. 1974: Functional analysis of space-related behaviour in the Seaside Sparrow. — Ecology 55:564—575.

Powell, G. V. N. 1974: Experimental analysis of the social value of flocking by Starlings (Sturnus vulgaris) in relation to predation and foraging. — Anim. Behav. 22:501—505.

Pyke, G. H., Pulliam, H. R. & Charnov, E. L. 1977: Optimal foraging: a selective review of theory and tests. — Q. Rev. Biol. 52:137—154.

Tinbergen, J. M. 1981: Foraging decisions in Starlings (Sturnus vulgaris L.). — Ardea 69:1—67.

Ward, P. & Zahavi, A. 1973: The importance of certain assemblages of birds as "information centres" for food finding. — Ibis 115:517—534.

Zach, R. & Falls, J. B. 1979: Foraging and territoriality of male ovenbirds (Aves: Parulidae) in a heterogeneous habitat. — J. Anim. Ecol. 48:33—52.

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