

finch was observed, its sex and its position within a 15 × 15-m grid system were plotted on a map. If the male was heard singing within at least 2 min, this fact was also noted. Both plots were visited during each census so that the activity of the birds in the experimental and in the control area, could be compared.

Six females, all probably mated (judged from their colour-rings and/or their behaviour), were removed from the experimental plot by shooting, between 0515 hours and 0630 hours on 5 May. Nest building in the experimental plot had started in two territories two days before the shooting took place.

No significant differences between the two study areas were found in the numbers of singing males, non-singing males, or females recorded during the censuses made prior to shooting the females (Table I). In this period the birds spent little time in territorial behaviour (most territories were occupied in early April), so that only few records were made per census. Significantly more singing and non-singing males were recorded in the experimental plot than in the control plot during the 5-day period just after the shooting (Table I). Similarly, significantly more singing males ($U = 10$, $N_1 = 8$, $N_2 = 9$, $P < 0.01$, Mann-Whitney U -test) and significantly more males in total ($U = 13.5$, $P < 0.05$) were recorded in the experimental plot during the 5-day period following the removal of the females, than during the 5-day period before. The equivalent differences in numbers for the control plot were not significant ($P > 0.05$).

The increase in singing activity started within 10 min after the females had been shot. In the first half an hour several females were seen. In this period several fights occurred and there was intensive courting of these females by the males. One of the newly-arrived females was colour-ringed in the experimental plot just after the shooting took place, and later bred in the experimental plot with one of the males whose original mate had been shot. Within 3 days after the removal of the six females, six new pairs had become established. It is noteworthy that the previously unmated male was the only one which remained unpaired after the shooting.

From 10 May onwards, no significant differences between the two study plots were recorded in either the frequency of birds present or in the singing activity of the males (Table I).

After the females were shot, the two nests which had been started in the experimental plot were abandoned. However, new nests were later built within both these territories, in both cases at a distance of 2 m from the first nests. Judging from the subsequent behaviour of the pairs and the location of nests, five pairs had nestlings in the experimental area.

The results of this experiment provide evidence for the presence of some non-resident females within the study area. It is most likely that these birds represent surplus individuals which are present at the start of the breeding season, and that those females which became mated after the experimental removal of already-paired females had therefore not been paired previously elsewhere.

A close correlation has been found between song activity and several environmental factors (Slagsvold 1977). This study shows that song activity also depends on the mating status of the males, and that unattached females are readily able to assess the status of the males (cf. Krebs 1971, 1977; Krebs et al. 1978). The failure of one of the males to obtain a mate even after the removal of the original female suggests that females can discriminate between either the territories offered by the males or

the males themselves (Searcy 1979). As suggested by Emlen & Oring (1977), we believe that polygyny has not evolved in our chaffinch population because defence of the food supply is difficult, as the territory is of only minor importance as a source of food (Sæther, unpublished).

We are grateful to Y. Espmark, O. Hogstad, S. Myrberget and T. Slagsvold for critically reading the paper, and to D. Refseth for shooting the birds.

BERNT-ERIK SÆTHER*
TORE FONSTAD†

*DVF Viltforskningen,
Elgesetergt. 10,
N-7000 Trondheim,
Norway.

†Zoological Institute,
University of Trondheim,
Rosenborg,
N-7000 Trondheim,
Norway.

References

- Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*, N.Y., **197**, 215-223.
- Klomp, H. 1972. Regulation of the size of bird populations by means of territorial behaviour. *Neth. J. Zool.*, **22**, 456-488.
- Krebs, J. R. 1971. Territory and breeding density in the Great Tit, *Parus major* L. *Ecology*, **52**, 2-22.
- Krebs, J. R. 1977. Song and territory in the great tit, *Parus major*. In: *Evolutionary Ecology* (Ed. by B. Stonehouse & C. M. Perrins), pp. 47-62. London: MacMillan Press.
- Krebs, J. R., Ashcroft, R. & Webber, M. 1978. Song repertoires and territory defence in the great tit. *Nature, Lond.*, **271**, 539-542.
- Searcy, W. A. 1979. Female choice of mates: a general model for birds and its application to red-winged blackbirds (*Agelaius phoeniceus*). *Am. Nat.*, **114**, 77-100.
- Slagsvold, T. 1977. Bird song activity in relation to breeding cycle, spring weather, and environmental phenology. *Ornis Scand.*, **8**, 197-222.
- Sæther, B.-E. 1980. The composition of the bird community in a grey alder forest in central Norway during a four-year period. *Fauna norv. Ser. C, Cinclus*, **3**, 80-83.
- Watson, A. & Moss, R. 1970. Dominance, spacing behaviour and aggression in relation to population limitation in vertebrates. In: *Animal Populations in Relation to their Food Resources* (Ed. by A. Watson), pp. 167-218. Oxford: Blackwell.

(Received 8 December 1980; revised 16 February 1981;
MS. number: sc-99)

The Ring Dove's Short-Term Memory Capacity for Spatial Information

A factor that may constrain an animal's ability to forage optimally for spatially distributed food sites is its ability to remember which spatial locations it has visited in the recent past (e.g. Orians, 1981; Pulliam, 1981). Accordingly, an animal that could remember (and avoid) the locations of 100 depleted food sites would appear to forage more efficiently than one that could remember only two or three recently visited locations. Thus, infor-

mation about an animal's ability to remember spatial locations, at least for short periods of time, is relevant to models of optimal foraging (e.g. Pyke et al. 1977).

Although birds' foraging behaviour has been studied (e.g. Smith 1974; Kamil 1978), to our knowledge experimental assessment of memory capacity for the spatial locations of food has been conducted only for rodents (e.g. Roberts 1979). Consequently, we undertook the present experiment to assess short-term memory for spatial location in one bird species. We tested adult female ring doves (*Streptopelia risoria*) in a variant of the radial-arm maze (Olton 1979).

Between daily testing sessions the doves were housed individually in stainless-steel cages with ad libitum access to water and granite grit. The birds were maintained at 90% of free-feeding weight by food obtained in the maze and post-testing supplementary feedings. The cylindrical-shaped central area of the maze, constructed of wire mesh, was 82 cm in diameter and 73 cm tall. A mesh screen covered top and bottom. Fourteen cardboard tubes (8 cm in diameter, 14 cm long) served as 'arms' of the maze; these extended through holes cut in the mesh so that the entire length of the tube was external to the central area. The tubes were mounted around the perimeter of the maze forming two parallel levels of seven arms, spaced in such a way that the distance between adjacent arms, both within and between levels, was equal (30 cm). A T-shaped perch was attached to the entrance of each tube; the distal end of each tube contained a food cup mounted in front of a mesh barrier.

At the start of each day's session 0.5 g of budgie mix was placed in the food cup in each tube. Each bird was allowed to make 14 choices (defined as landing on a perch) and was then removed from the maze. The birds were trained for 125 sessions, at which time performance was asymptotic.

The birds flew between perches (birds 1, 2, and 3) or from perch to floor to perch (bird 4) and invariably entered the tube and consumed the food after landing on a perch. The birds generally took about 10 min to make their 14 choices.

A 'correct' choice was defined as selection of a tube containing food: percentage of correct choices for the last 20 days are shown in Fig. 1a. The birds chose more correct tubes than would be expected had choices been random (chance level for a 14-arm maze is 64.5%; see Spetch & Wilkie 1980). Consequently, tube selection was governed by avoidance of tubes that had been entered, and the food depleted.

Figure 1b shows probability of a correct choice for the second through last choice. These probabilities are based on the last 20 days of the experiment and were transformed according to the formulae used by Olton et al. (1977) to take into account the changing chance probability of a correct choice on successive choices. These scores can range from 1.0, indicating best possible performance, through 0, indicating random selection, to -1.0, indicating an error at each opportunity. Performance was considerably better than chance even on the fourteenth choice. Consequently, doves are capable of remembering at least 14 spatial locations.

A factor that may lead to the underestimation of an organism's spatial memory capacities is the tendency to revisit depleted food sites on the chance that they may have been replenished. For example, some birds may have evolved under conditions of recruitment to their prey populations or of movement of prey between locations such that revisiting sites might be fruitful. If so, the

birds could appear to be making more errors because of forgetting than they actually are.

Two reasons, however, make it unlikely that this factor contributed greatly to the birds' performance in the present study. First, the extended training (over 100 tests) provided ample opportunity for the birds to learn that there was no replacement of food in an arm within a test period. Second, ring doves should be less predisposed to revisit depleted food sites than would, say, an insectivorous species, because their food, seeds, does not move between locations. Moreover, substantial recruitment to the prey population usually occurs only during one period of year; during the rest of the year the food is simply depleted. Accordingly, ring doves are good subjects for studies of memory for spatial location. Comparisons of ring doves with other bird species, particularly those with different diets, in regard to spatial memory tasks would also be of interest.

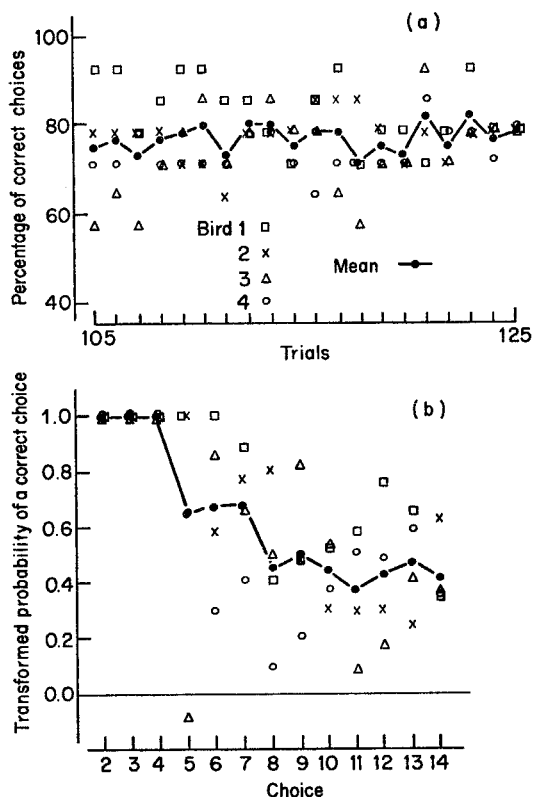


Fig. 1. (a) Percentage of correct arm choices during the last 20 days of training. Chance level of correct choice is 64.5%. (b) Transformed probability of a correct arm choice for the second through fourteenth choices. Scores are based on the last 20 days of training. In both panels, data from individual birds are shown as unconnected points; the group means are shown as connected points.

This work was supported by the Natural Sciences and Engineering Research Council of Canada. D. King and C. Rayner provided valuable assistance.

DONALD M. WILKIE
MARCIA L. SPETCH
LINCOLN CHEW

Department of Psychology,
University of British Columbia,
Vancouver, B.C.,
Canada V6T 1W5.

References

- Kamil, A. C. 1978. Systematic foraging by a nectar-feeding bird (*Loxops virens*). *J. comp. physiol. Psychol.*, **92**, 388–396.
- Olton, D. S., Collison, C. & Werz, W. A. 1977. Spatial memory and radial arm maze performance by rats. *Learn. Motiv.*, **8**, 289–314.
- Olton, D. S. 1979. Mazes, maps, and memory. *Am. Psychol.*, **34**, 583–596.
- Orians, G. H. 1981. Optimal foraging and the evolution of discriminatory abilities. In: *Foraging Behavior: Ecological, Ethological, and Psychological Viewpoints* (Ed. by A. C. Kamil & T. D. Sargent), pp.389–405. New York: Garland Publishing Co.
- Pulliam, H. R. 1981. Learning to forage optimally. In: *Foraging Behavior: Ecological, Ethological, and Psychological Viewpoints* (Ed. by A. C. Kamil & T. D. Sargent), pp.379–388. New York: Garland Publishing Co.
- 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.
- Roberts, W. A. 1979. Spatial memory in the rat on a hierarchical maze. *Learn. Motiv.*, **10**, 117–140.
- Smith, J. N. M. 1974. The food searching behaviour of two European thrushes: I. Description and analysis of search paths. *Behaviour*, **48**, 276–302.
- Spetch, M. L. & Wilkie, D. M. 1980. A program that simulates random choice in radial arm mazes and similar choice situations. *Behav. Res. Meth. & Instrum.*, **12**, 377–378.

(Received 18 August 1980; revised 20 October 1980;
MS. number: AS-104)

'Territorial Song' as a Flocking Signal in Red-Winged Blackbirds

It has been reported that birds sometimes deliver 'territorial advertisement song' outside of the breeding season (Nottebohm 1975). While several studies have shown that song plays an important role in territorial defence, no functional explanation has yet been proposed for pre- and/or post-breeding-season song behaviour. I have commonly observed adult male red-winged blackbirds (*Agelaius phoeniceus*) singing at fall and spring roosts, as well as sometimes while feeding in flocks or resting on temporary perches at these times of the year (also see Orians & Christman 1968). Since redwings aggregate in large numbers before and after breeding, I hypothesized that redwing song outside the breeding season may facilitate group formation and cohesion during roosting and foraging. To test this hypothesis I investigated whether post-breeding-season blackbirds were attracted to playback of male territorial song.

During the breeding season, playback of conspecific song to territorial redwings evoked a strongly aggressive

response (Brenowitz 1980; in press). Females and juvenile males failed to show any consistent, oriented response to playback. Spectrographic analysis indicates that songs produced by males outside the breeding season are identical to those sung by redwings defending territories. In the present set of experiments conducted in an upland field near Ithaca, N.Y., from 23 August to 8 September 1980, I compared the responses of redwings to playback of full song of a conspecific territorial male with those to presentation of the song of a territorial male song sparrow (*Melospiza melodia*). The songs of both species were recorded at the study site with a Sennheiser MKH 415T condenser microphone and a Nagra IV-D recorder at 19 cm/s during the breeding season of 1980.

Preliminary observations indicated that there was a regular flight of redwings, both singly and in groups, over the study site at heights of 30 m or more for about the first 2 h following dawn. After the sun rose above the horizon, playback of either the redwing or sparrow song was initiated, but only when no redwings were visible at the time on the study site or in the air space above. Each signal was played repeatedly at intervals of 3.5 s for 30 min from the Nagra recorder to a Nagra DH speaker-amplifier mounted 1.5 m above the ground at one end of the study field. Maximum root-mean-square sound pressure level of playback for both signals was set at 100 dB 1 m from the speaker. This is equivalent to the pressure level that would result from three redwings each singing at a sound pressure level of 88 dB at 1 m and overlapping in time of song delivery. The mean maximum root-mean-square sound pressure level of 36 songs recorded at the study field from one redwing was 91.3 dB at 1 m ($se = 0.21$, range = 89–94). Both signals were presented sequentially every day, but order of presentation was reversed each day for a series of 12 trials.

During the 30-min playback period, I recorded the number of redwings that landed on perches within 50 m of the speaker (designated as the census area) and the times of arrival and departure for each individual or group of blackbirds, as well as the sex and, where possible, the relative age of each bird. Females, males hatched in 1980, males hatched in 1979 (1-year-olds), and those males hatched in 1978 or earlier (adults) can all be distinguished by plumage pattern following the moult at the end of the breeding season (Wood 1969, page 136).

Redwings landed within 50 m of the speaker in 11 of 12 presentations of conspecific song. Total number counted during the 30-min playback period ranged from 1 to 86 ($\bar{X} \pm se = 26.1 \pm 7.9$). No redwings landed in the census area, however, when sparrow song was played ($P < 0.009$, Wilcoxon matched-pairs signed-ranks test, two-tailed), though they were seen flying over the study site. Blackbirds of both sexes and all age classes described above landed during conspecific song playback. Birds usually entered the census area in groups, ranging in size from 2 to 65. Flocks composed of only one sex or one male age class were more common than flocks of mixed sex and/or age composition. Solitary individuals of all age-sex classes except males hatched in 1980 were seen occasionally. Length of time spent by birds in the census area ranged from 1 to 8 min ($\bar{X} \pm se = 3.53 \pm 0.51$). There was no correlation between group size and length of stay ($r = -0.082$), nor was there a significant difference in length of time spent within 50 m by solitary birds versus groups of birds, or by females versus males ($P > 0.05$, Mann-Whitney *U* test in both cases).

These data strongly suggest that song outside the breeding season in redwings plays an important role in the