

AVIAN COMMUNAL ROOSTING: A TEST OF THE "PATCH-SITTING" HYPOTHESIS¹

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Abstract. Major starling roosts (2,000 to 100,000 birds) cannot be fully explained on the basis of information transfer, predation, migration, or limited habitat. Radiotelemetry has revealed that each starling returns daily to feed on its own stable diurnal activity center (DAC), but stops briefly at supplemental feeding areas (SFAs) on its way to and from distant communal roosts. We test and find supported a new hypothesis (Caccamise and Morrison 1986) that DAC-based starlings select roosts that reduce commuting costs to SFAs far from their DACs. As predicted, DAC-based adults used SFAs that were nearer their roosts than their DACs, and used more distant roosts where SFAs were more widely spaced. In starlings, major communal roosts appear to be aggregations containing large numbers of "patch-sitting" birds roosting near especially rich sources of food.

Key words: Communal roosting behavior; diurnal activity center; European Starling; foraging behavior; roost; staging area; *Sturnus vulgaris*.

INTRODUCTION

Foraging-based explanations for avian communal roosting usually view the roost as a stable base of operation from which the birds disperse to exploit ephemeral patches of food surrounding the roost (Ward and Zahavi 1973). In contrast, radiotelemetry of communally roosting European Starlings (*Sturnus vulgaris*) reveals that individual roost mates are actually far more faithful to their feeding sites than to their roosting sites (Morrison and Caccamise 1985). Each starling returns to feed on its own diurnal activity center (DAC) every day for months, while using a variety of communal roosts surrounding its DAC.

Why do DAC-based birds join communal roosts? Our radio-tagged starlings often joined *minor* roosting flocks (<2,000 birds) close to (<2 km from) their DACs, probably to reduce the risk of nocturnal predation (Lack 1968, Hamilton 1971). However, predation alone cannot explain why DAC-based starlings frequently bypassed nearby roosting flocks in favor of much larger roosts many kilometers away. These *major* roosts (2,000 to 100,000 birds) are orders of magnitude larger than the size at which the antipred-

ator benefits of grouping should be near maximal (Pulliam 1973, Pulliam and Millikan 1982).

Three other selective factors can also be discounted as relatively unimportant at major starling roosts. Major roosts are not simply premigratory aggregations; they begin to form in June, months before migration (Caccamise et al. 1983). Major roosts are not due to a shortage of acceptable roosting sites (Lyon and Caccamise 1981). Finally, since foraging is centered on stable feeding areas (DACs), major roosts do not appear to be "information centers" for daily food finding (Ward and Zahavi 1973).

Here we test a new hypothesis (Caccamise and Morrison 1986) that major roosts form because DAC-based birds aggregate at roost sites that reduce commuting costs to supplemental feeding areas (SFAs); i.e., patches of readily accessible, high energy food located outside their DACs. This patch-sitting hypothesis was suggested by our observations that (a) major roosts are more likely to develop at sites near agricultural fields when grain is available there, (b) radio-tagged starlings feed primarily on soil invertebrates at their DACs, but stop briefly at SFAs (e.g., grain fields, orchards) while commuting between roosts and their DACs (Morrison and Caccamise 1985), and (c) the increase in the number of starlings using major roosts coincides with seasonal changes in foraging-substrate selection (Fischl and

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Caccamise 1985) and diet composition (Fischl and Caccamise 1987).

If our patch-sitting hypothesis is correct, we predict there should be a correlation between the mean commuting distances flown by individual birds and the spacing of SFAs. On average, the greater the distances between SFAs, the farther DAC-based birds will need to fly to get to an SFA. If roosts form near SFAs, then DAC-to-roost distances should be greater where SFAs are more widely spaced.

A second prediction concerns components of the commuting flights of DAC-based birds. Patch sitting reduces total commuting costs to a SFA only if it is closer to the roost than it is to the DAC (Caccamise and Morrison 1986). To explain why, let r represent the distance between the roost and SFA, and d the distance between the DAC and SFA (Fig. 1, inset). A DAC-based bird that stops at an SFA on the way to the DAC in the morning travels a distance ($r + d$). If it stops again at the SFA on the way back to the roost in the evening, it travels another ($r + d$). Therefore the total commuting distance for two stops is $2(r + d)$, or $(r + d)$ per stop. For this to be advantageous, the distance ($r + d$) must be less than that of a simple round trip between the DAC and the SFA. That is, ($r + d$) must be less than $2d$, or r must be less than d . If the patch-sitting hypothesis is correct, then the distance (r) between the roost and SFA should always be less than the distance (d) between the DAC and SFA.

We tested these predictions using radio-tagged starlings. Our results support the patch-sitting hypothesis.

METHODS

The study area was the same 1,000 km² of the piedmont and inner coastal plain provinces of central New Jersey censused for starling roosts by Caccamise et al. (1983). The northern half of the study area is urban/suburban; i.e., it is primarily residential (81%), with some agricultural (4%) and forested areas (2%). The southern half is more rural; i.e., it has more forested area (27%) and agricultural land (18%) and less residential area (29%, Fischl and Caccamise 1985).

Tests of the patch-sitting hypothesis involved 19 starlings radio-tagged during the local roosting seasons (June to November) of 1985 and 1986. In both years, the study period ran from early June through early December, 1 month after the migration south of part of the local starling

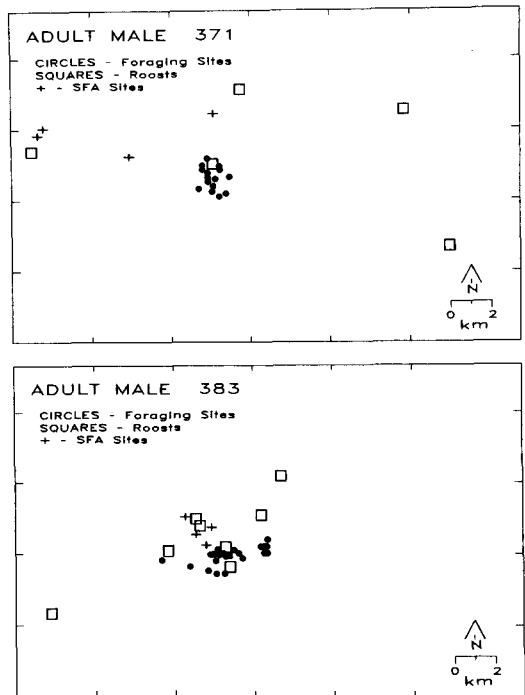


FIGURE 1. Maps of foraging sites (circles), roosting sites (squares), and SFAs (plus signs) used by two radio-tagged starlings in the urban/suburban north (top), and rural south (bottom).

population. Birds for radio-tagging were captured during the day using mist nets or baited walk-in traps. The five adults studied in 1985 (three males, two females) were captured on farms in the southern half of the study area. In 1986, 14 starlings (four adult males, four adult females, and six juveniles) were captured 35 km to the north, on the campus and experimental farms of Rutgers University–New Brunswick. Adults were radio-tagged in June and July. Juveniles were radio-tagged in July and August. Juveniles were young of the year that fledged between late May and mid-July.

A 5-g transmitter package was attached to the back of each starling ($\bar{x} = 76.2$ g, $SD = 5.46$ g) with a “vest” made from cotton shoelace (AVM Instrument Co. 1979). During the 2 to 4 month life of the transmitters ($\bar{x} = 118$ days), we attempted to locate each bird three times daily: twice during the day according to a predetermined, random schedule, and once at its nocturnal roost. Location attempts were successful over 90% of the time, usually to within an area of 100 m \times 100 m.

We defined a bird's DAC as the area of the smallest polygon containing all of the diurnal sightings made on the bird over the life of its transmitter. SFAs were defined as feeding sites visited by the bird on the way to and from a nocturnal roost that were clearly outside its DAC; i.e., more than 2 km from the use-weighted center of the DAC. We calculated the use-weighted center as the mean x and y coordinates of all diurnal sightings on that bird. When the roost was <2 km from the center of the DAC, we did not attempt to distinguish SFAs from feeding areas at the edge of the DAC.

To locate SFAs, we followed individuals as they left their DACs in the evening or as they left their roosts at dawn. Because of the short range of the transmitters and the frequency with which the birds flew to new roosts, it was often necessary to track a bird on two or three evenings before its roost could be found. Each of 17 birds (13 adults, four juveniles) was successfully followed from its DAC to a roost two to six times, for a total of 50. Seven of the birds (five adults, two juveniles) were also successfully followed as they flew from a roost to their DAC. Morning and evening flights did not differ in terms of distances flown or frequency and duration of stopovers, so the data were combined.

RESULTS

All 19 starlings showed a DAC-centered pattern of foraging and roosting like those shown in Figure 1. Mean size of the DACs was 1.02 km². Each bird joined two to nine communal roosts ($\bar{x} = 1.5$ roosts/month, $SD = 0.63$) in several directions from its DAC. There were no significant differences among males, females, and juveniles in either DAC size or the number of roosts used (Morrison and Caccamise, unpubl.).

DAC-TO-ROOST COMMUTING DISTANCES

DAC-to-roost distances for adults (Fig. 2a, b) were significantly greater in the rural south ($\bar{x} = 5.2$ km, $SD = 3.17$) than in the urban/suburban north ($\bar{x} = 2.5$ km, $SD = 1.68$ km; $t = 3.12$, $P = 0.004$). A regional comparison of juveniles could not be made because no juveniles were radio-tagged in the south. For adult starlings in both north and south the daily averages of commuting distance (Y) from DAC to roost increased significantly (1985, $Y = -6.20 + 0.04X$, $P < 0.029$, $r^2 = 0.20$; 1986, $Y = -1.53 + 0.02X$, $P < 0.0001$, $r^2 = 0.35$) with Julian date (X). Adults in the

south began using distant roosts (roosts >4 km from their DACs) in early July; adults in the north first used distant roosts in early August.

We detected no such seasonal relationship in the daily averages of commuting distances flown by juveniles (Fig. 2c). Juveniles rarely used distant roosts even late in the season. Two juveniles did visit distant roosts (8 and 10 km from their DACs) in early October, but this represented a total of only four nights. The juveniles continued to use their DACs for daytime feeding until termination of observations in early December. They roosted near their DACs at least through the end of October.

PROXIMITY OF ROOSTS AND SFAs

DAC-to-roost distances were <2 km in 19 of the 43 commuting flights observed in the urban/suburban north and one of 14 flights in the rural south. We did not attempt to distinguish SFAs in these cases. We were able to record stopovers of 5 to 45 min ($\bar{x} = 22.5$, $SD = 19.32$) during 22 (58%) of the 38 flights to and from roosts >2 km away from the DAC. Additional commuting flights of >2 km may have included stops at SFAs that we did not observe before the bird moved on. Stopovers probably occurred in at least three additional cases in which the time between DAC departure and roost arrival was 20 to 30 min greater than expected, given the distance to the roost and the estimated flight speed of commuting starlings (36.5 km·hr⁻¹; Feare 1984:244, Caccamise and Hedin 1985).

SFAs used by the five birds in the rural south included a 16-ha turf farm and a stand of 10 fruiting wild cherry trees (*Prunus* spp.). The SFAs used by the 12 birds in the urban/suburban north included a 5-ha corn field, a grass-covered athletic field, and a swine feedlot.

The birds stopped at SFAs that were closer to the roost than the DAC on 20 (91%) of the 22 commuting flights of >2 km (the 20 points below the diagonal in Fig. 2). On three of these 20 flights, the bird stopped at two SFAs. In two of these three cases, the first SFA was closer to the DAC than the roost (the two plus signs above the diagonal in Fig. 3); in the third case, the first SFA was closer to the roost (the plus sign below the diagonal).

On only two of the 22 long-distance commuting flights was the SFA closer to the DAC than the roost (the two ovals above the diagonal in Fig. 3). Both involved the same adult female who

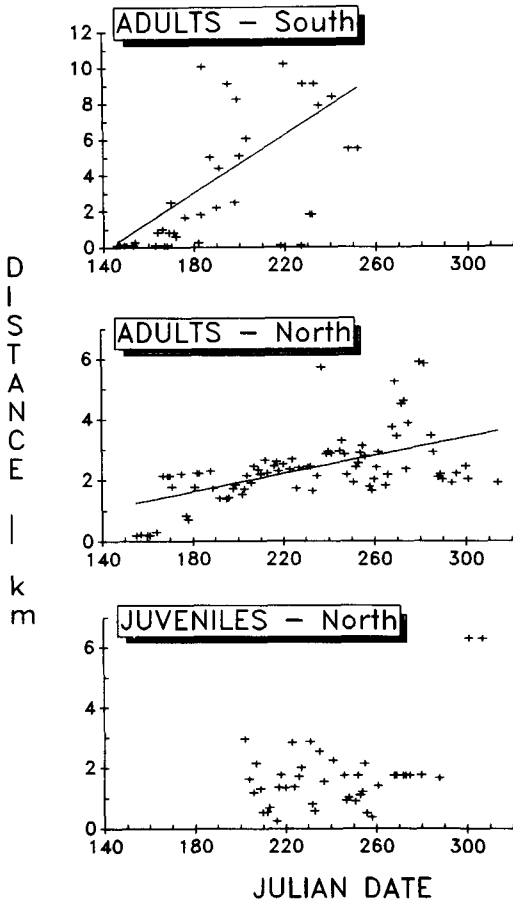


FIGURE 2. Seasonal patterns in commuting distances for southern adults in 1985 (rural), northern adults in 1986 (urban/suburban), and northern juveniles in 1986. Each point represents an average of the DAC-to-roost distances flown by all radio-tagged birds on that day.

habitually stopped at an active garbage dump 1.5 km from her DAC before flying on to a distant roost. It is possible that she, too, stopped at a second SFA nearer the roost, but we were unable to confirm this.

DISCUSSION

Our observations support the hypothesis (Caccamise and Morrison 1986) that communally roosting starlings are patch sitting. Starlings commuting to distant roosts (>4 km from their DACs) stopped at SFAs about 60% of the time. As predicted, starlings commuting to distant roosts used SFAs that were nearer their roosts than their DACs. DAC-to-roost distances in the rural south,

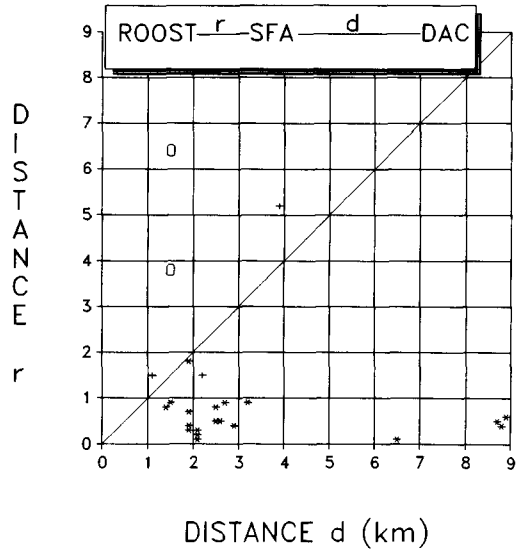


FIGURE 3. A test of the prediction that the distance (r) from roost to the SFA should be less than the distance (d) from the DAC to the SFA. All r and d values are shown for SFAs used by radio-tagged starlings during commuting flights longer than 2 km. Here $r < d$ for all points below the diagonal. The four points above the diagonal are discussed in the text.

where potential feeding areas were more widely spaced, were greater than in the urban/suburban north. Distances to roosts also increased significantly with season.

COMMUTING DISTANCES

Our prediction that commuting distances between the DAC and roost should be longer where potential SFAs are more widely spaced is supported by the observation that DAC-to-roost distances were longer in the southern half of the study area. The types of feeding substrate typically used for SFAs in the rural south (e.g., grain fields, orchards) are larger and appear to be more widely spaced. In the urban/suburban north, the spatial distribution of potential SFAs are finer grained (Fischl and Caccamise 1985).

The prediction is also supported by our observation that adults in both north and south used more distant roosts later in the season. In late August diets shift from primarily soil invertebrates (e.g., in lawns) to less uniformly distributed foods (e.g., wild fruits and agricultural grains) (Fischl and Caccamise 1987). Given the seasonal increase in mean commuting distances, the seasonal increase in mean roost size observed at the population level (Caccamise et al. 1983) appears

to be due to roosts (or the SFAs near them) attracting birds whose DACs are farther away. Unsupported is the alternative explanation that a roost attracts birds from the same area throughout the year and that seasonal fluctuations in roost size only reflect changes in the proportion of the population using the roost.

A seasonal shift from nearby to distant roosts was not observed for juveniles, however. Juveniles were DAC-based, but they rarely used distant roosts even late in the season. The infrequent use of distant roosts cannot be attributed solely to their ignorance of distant roost locations. Two juveniles did use distant roosts for one to two nights, but then returned to minor roosts near their DACs. Juveniles should be able to locate distant, major roosts the same way we do; i.e., by following the conspicuous flight lines of birds converging on the roost site each evening.

ROOSTING NEAR SFAs

As predicted, whenever a SFA was used, it was almost always closer to the roost than the DAC. That is, the distance (r) from the roost to the SFA was less than the distance (d) from the DAC to the SFA. For a bird that visits an SFA twice a day, roosting near the SFA rather than on the DAC reduces the energetic costs of commuting to the SFA by $4d - (2d + 2r)$ or $2(d - r)$. DAC-to-SFA commuting costs are therefore reduced by a factor $2(d - r)/4d$, or (as r approaches 0) by up to 50%.

This cost reduction becomes significant in absolute terms as the DAC-to-SFA distance (d) increases. For a 70-g starling flying at the velocity requiring minimum power ($36.5 \text{ km}\cdot\text{hr}^{-1}$), the energetic costs of flight are about $0.659 \text{ kJ}/\text{km}$ (Caccamise and Hedin 1985). For our starlings the use of roosts near SFAs reduced average commuting distance to the SFAs by 37%. However, since DAC-to-SFA distances were relatively short in our study area, the energetic saving was only $3.8 \text{ kJ}\cdot\text{day}^{-1}$. This represents a saving of 2.4%, assuming a daily energy requirement of $160 \text{ kJ}\cdot\text{day}^{-1}$ for a noncommuting starling (Feare 1984:246, Westerterp and Drent 1985).

However, distances between potential feeding areas may be unusually short because our study area is urbanized. In other environmental settings the energetic savings from patch sitting could be substantial. Roost-to-feeding area distances of 50 to 80 km have been reported for communally roosting starlings in California (Hamilton and Gilbert 1969) and Great Britain (Feare

1984:246). Assuming a DAC-to-SFA distance (d) of 50 km, roosting at the SFA would save a starling 66 kJ, or over 40% of the daily energy expenditure of a starling roosting on its DAC and flying to an SFA two times to feed.

SOME ALTERNATIVE EXPLANATIONS

Patch sitting is an important factor in the formation of starling roosts, but other factors are probably also involved. One third of the birds followed to distant roosts did not stop at SFAs. Some of these birds may have stopped too briefly or at too remote a site for us to observe the stop. Some birds may not stop at the SFA every time they fly to the roost. However, some may fly to distant roosts for other reasons; e.g., to locate or evaluate potential SFAs far from their DACs. This last possibility is suggested by our observations that individuals sometimes stay at the distant roost for just one night (Morrison and Caccamise, unpubl.).

Communal roosting doubtless reduces the risk of nocturnal predation, but predation alone cannot explain the seasonal increases in roost size and commuting distance we observed. There is no a priori reason to hypothesize that the seasonal increase in roost size is due to a seasonal increase in predation pressure. DAC-based birds may join larger, more distant roosts for some as yet unknown reason and stop at SFAs only to offset the cost of the longer commute. However, this alternative does not explain our finding that the SFA was almost always closer to the roost than the DAC.

Other studies have suggested relationships between foraging and roosting. However, their explanations for communal roosting are inconsistent with the DAC-centered roosting and foraging patterns we observed. The information center hypothesis (Ward and Zahavi 1973) and its variations (e.g., Weatherhead 1983) all assume that feeding areas are ephemeral and that an individual's center of operation is the roost. Both assumptions are contrary to our findings.

BENEFITS OF PATCH SITTING

The energetic benefits of roosting near an SFA are clearly greater when the dispersion of SFAs requires long and energetically demanding commuting flights. Nevertheless, energetic benefits may still contribute to patch-sitting behavior even when the energy saving appears trivial. For example, equally trivial energetic savings would appear to be involved in the human practice of

cutting corners to save a few steps, even when this behavior means wearing a path across someone's lawn.

Patch sitting may also have nonenergetic benefits. Reducing commuting distances reduces the time a bird is exposed to in-flight predation. Patch sitting may also facilitate the formation of foraging and commuting flocks. Such flocks might be an important defense against predation while foraging in open habitats or in less familiar surroundings away from the DAC.

Many communally roosting species, including starlings, congregate near a roost at "pre-roosting" or "staging" areas before flying as a group into the roost itself (Wynne-Edwards 1962, Zahavi 1970). Conspicuous prerost assemblies may attract conspecifics to the site and so spread the risk from predators that aggregate around roost sites that are used night after night. Usually, however, prerost assemblies are composed of feeding birds (Feare 1984:235). The observation that communally roosting birds use prerost assembly areas for feeding is consistent with our patch-sitting hypothesis.

Fidelity of individuals to feeding areas (possibly DACs?) has been noted anecdotally in several other communally roosting birds: Red-winged Blackbirds (*Agelaius phoeniceus*; Johnson 1979), Cattle Egrets (*Ardeola ibis*; Siegfried 1971), Great Blue Herons (*Ardea herodias*; Krebs 1974), and Common Grackles (*Quiscalus quiscula*; pers. observ.). The applicability of the patch-sitting hypothesis to roost-site selection by these and other communally roosting species merits further study.

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LITERATURE CITED

AVM INSTRUMENT CO. 1979. Applying transmitter packages to small birds, p. 10-11. In Radiotelemetry equipment and techniques manual. AVM Instrument Company, Livermore, CA.

CACCAMISE, D. F., L. A. LYON, AND J. FISCHL. 1983. Seasonal patterns in roosting associations composed of Starlings and Common grackles. *Condor* 84:474-481.

CACCAMISE, D. F., AND R. HEDIN. 1985. An aerodynamic basis for selecting transmitter loads in birds. *Wilson Bull.* 97:306-318.

CACCAMISE, D. F., AND D. W. MORRISON. 1986. Avian communal roosting: implications of "diurnal activity centers." *Am. Nat.* 128:191-198.

FEARE, C. J. 1984. *The Starling*. Oxford Univ. Press, Oxford.

FISCHL, J., AND D. C. CACCAMISE. 1985. Influence of habitat and season on foraging flock composition in the European Starling (*Sturnus vulgaris*). *Oecologia* 67:532-539.

FISCHL, J., AND D. C. CACCAMISE. 1987. Relationships of diet and roosting in the European Starling. *Am. Midl. Nat.* 117:395-404.

HAMILTON, W. D. 1971. Geometry for the selfish herd. *J. Theor. Biol.* 31:295-311.

HAMILTON, W. J., III, AND W. M. GILBERT. 1969. Starling dispersal from a winter roost. *Ecology* 50:886-898.

JOHNSON, R. J. 1979. Foraging distribution, habitat relationship, and bioenergetics of roosting and flocking Red-winged Blackbirds in central New York. Ph.D. diss., Cornell Univ., Ithaca, NY.

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.

LACK, D. 1968. *Ecological adaptations for breeding in birds*. Methuen, London.

LYON, L. A., AND D. F. CACCAMISE. 1981. Habitat selection by roosting blackbirds and starlings: management implications. *J. Wildl. Manage.* 45:435-443.

MORRISON, D. W., AND D. F. CACCAMISE. 1985. Ephemeral roosts and stable patches? A radiotelemetry study of communally roosting starlings. *Auk* 102:793-804.

PULLIAM, H. R. 1973. On the advantages of flocking. *J. Theor. Biol.* 38:419-422.

PULLIAM, H. R., AND G. C. MILLIKAN. 1982. Social organization during the nonreproductive season, p. 169-197. In D. S. Farner, J. R. King, and K. C. Parkes [eds.], *Avian biology*. Vol. 6. Academic Press, New York.

SIEGFRIED, W. R. 1971. Communal roosting of the Cattle Egret. *Trans. R. Soc. S. Afr.* 39:419-443.

WARD, P., AND A. ZAHAVI. 1973. The importance of certain assemblages of birds as "information centres" for food finding. *Ibis* 115:517-534.

WEATHERHEAD, P. J. 1983. Two principal strategies in avian communal roosts. *Am. Nat.* 121:237-243.

WESTERTERP, K., AND R. DRENT. 1985. Energetic costs and energy-saving mechanisms in parental care of free-living passerine birds as determined by the D₂¹⁸O method, p. 392-398. In V. D. Ilyichev and V. M. Gavrilov [eds.], *Acta XVII Congressus Internationalis Ornithologicae*. Nauka, Moscow.

WYNN-EDWARDS, V. C. 1962. Animal dispersion in relation to social behaviour. Oliver and Boyd, Edinburgh.

ZAHAVI, A. 1970. The function of pre-roost gatherings and communal roosts. *Ibis* 113:106-109.