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COMMENTARY

"Diurnal activity centers" and "information centers": a need for more critical study.—Observations by Caccamise and Morrison (1986, 1988) and Caccamise (1991) have documented the use of preferred feeding sites (which they term diurnal activity centers or DACs) by roosting European Starlings (*Sturnus vulgaris*). They have developed a DAC-centered "patch-sitting hypothesis" of communal roosting as an alternative to the information center hypothesis of Ward and Zahavi (Ward 1965, Ward and Zahavi 1973). Although the observations themselves are interesting, I suggest that the theory developed from them by Caccamise and co-workers lacks explicit predictions which differ from those of the information center hypothesis. My criticisms address two general points (1) that observations by Caccamise (especially 1991) given in support of his hypothesis are consistent with the information center hypothesis and (2) that fidelity to a DAC is not evidence against the role of information exchange in communal roosts.

Caccamise and Morrison (1986, 1988) and Caccamise (1991) reported that starlings used a variety of communal roosts near preferred feeding sites and that such feeding sites (DACs) were attended consistently by individual birds in the post-breeding season (June to early August). Later in the autumn, starlings began to attend larger roosts, farther from their DACs. Caccamise (1991) found that this shift coincided with a decline in food supply (soil invertebrates) on the DACs and with a switch to food from "supplemental feeding areas" (SFAs) which provided mainly fruit. Caccamise (1991) interpreted these observations as evidence against the information center hypothesis which proposes that communal roosts provide centers for the exchange of information about the location of clumps of an unpredictable and patchy food supply. Caccamise and Morrison (1986) suggested that starlings switched to the larger, distant roosts simply because the latter were closer to SFAs or were linked to the DAC via a route which passed over SFAs, thereby minimizing commuting distance and time. However, these arguments appear to contain a number of shortcomings.

First, Caccamise (1991, p. 13) misinterprets the information center hypothesis when he states that it "carries the implicit assumption of a roost-centered foraging distribution . . . the roost should lie at the center of the group of feeding sites used by individual birds". Although central positioning would be advantageous, it is not a necessary assumption of the information center hypothesis; indeed, Ward and Zahavi (1973) pointed out that large communal roosts often occupy traditional sites, which need not be at the center of a feeding area but may rather occupy a conspicuous topographical feature or rare habitat site which provides advantageous roosting conditions (e.g., visibility or protection from weather). Such features may unavoidably be offset in relation to nearby potential feeding sites, and the foraging distribution might then appear to be centered upon a particularly useful foraging site or DAC. Despite the fact that a position central among a group of SFAs is not a necessary characteristic of an information center, it obviously increases foraging efficiency if the information center is close to potential feeding sites. Caccamise and Morrison (1988) found that larger roosts did tend to be nearer to SFAs. This is consistent with both the information center hypothesis and the patch-sitting hypothesis of Caccamise and Morrison (1986) and is not evidence that the latter is true and the former false.

My second point concerns Caccamise's (1991, p. 14) statement that the use of a DAC with a variety of small roosts during the late summer is "clearly contrary" to the roost-centered assumption of the information center hypothesis. There are two faults with this argument. First, since the roost-centered assumption is not essential to the information center hypothesis, these observations need a more cautious interpretation. Second and more serious, although it is true that DAC-based foraging combined with switching between small roosts implies that information centers are not of over-riding importance to starlings during the late summer, this is consistent with the information center hypothesis, not contrary to it. Ward and Zahavi (1973) envisaged species which might require information at certain times of year but not at others, the latter occurring when food was more abundant and/or easier to find. Some European *Turdus* fall into this category and their social organization varies accordingly (Tye 1982). Since starlings in late summer use a DAC, which provides a predictable and stable food supply, they fall into the category of birds which do not require information exchange at that time, as clearly stated by Ward and Zahavi (1973). For this reason, one would not expect them to use a large, traditional communal roost where predation pressure might be higher (Ward and Zahavi 1973) but to switch between less conspicuous roost sites. In these respects, the late summer behavior of the starlings studied by Caccamise is consistent with the information center hypothesis. In other words, Caccamise and Morrison's (1986) patch-sitting hypothesis is not strictly an alternative to the information center hypothesis; it was, in fact, part of the latter as formulated by Ward and Zahavi (1973).

My third point concerns the observation that during the autumn (late August), Caccamise's starlings switched to using larger roosts, farther from their late-summer DACs. Concurrently, they began to forage in a wider variety of habitats (SFAs) and increased their dietary diversity, taking more fruit and seeds. The birds continued to spend much daylight time on, and to obtain some invertebrate food from their DACs, but obtained most of their food from SFAs. Stewart (1978) was the first to notice this fidelity to feeding sites by starlings, although he collected few data on marked birds and did not use the term DAC; he also noted the proximity of winter roosts to SFAs (consistent with both hypotheses). Caccamise (1991, p. 14) suggests that "DAC fidelity provides benefits in addition to those associated with foraging there. Otherwise, there would be no reason to return to the DAC at times when birds travel to SFAs to supplement their diets." However, to Caccamise (1991, pp. 14–15), the "benefits of DAC fidelity [in such circumstances] remain unclear", although Morrison and Caccamise (1990) list several possibilities. I would dispute that DAC fidelity need provide benefits other than foraging ones and suggest two such benefits which were not considered by Morrison and Caccamise (1990) or by Caccamise (1991). First, a DAC may continue to provide a reliable (if scarce) source of invertebrate food as a protein supplement, as in *Turdus* spp. which largely eat fruit in the autumn and winter (Tye 1982). Consistent with this, Caccamise found that starlings continued to obtain invertebrate food from their DACs. Second, a DAC might function as a subsidiary information center, similar to the daytime roosts used by Red-billed Quelea (*Quelea quelea*; Ward 1965), where starlings might take advantage of the foraging knowledge of others by following them to good SFAs of which they had no prior knowledge. Accordingly, Caccamise (1991) found that flock size on the DACs increased in late August, when DAC food declined and roost size and relative use of SFAs both increased. In other words, the patch-sitting hypothesis provides no explicit reason for the continuance of DAC fidelity through periods when the bulk of the food is obtained from SFAs, while the information center hypothesis might do so. However, from my own observations of *Turdus* spp., I believe the major benefit of DAC fidelity is provision of invertebrate food.

A fourth point arises from Caccamise's (1991, p. 14) statement that one prediction of the DAC-based patch-sitting hypothesis is that "foraging substrate quality should decline on DACs as increasing proportions of the local roosting population become associated with large roosting congregations, i.e., when more individuals are leaving their DACs to forage elsewhere". It is true that such behavior is consistent with the patch-sitting hypothesis, but it is also predicted by the information center hypothesis in that when the food supply becomes less stable, less predictable, and more patchy more information is required to track the food supplies, so birds would be expected to congregate in larger roosts (see Zahavi 1971, Ward and Zahavi 1973). Thus, Caccamise's observations of such roost-switching at times of decline

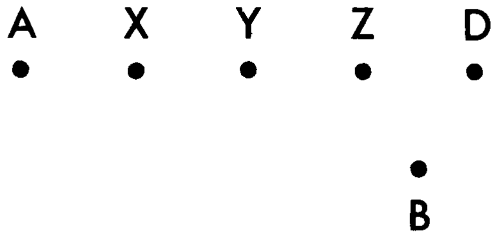

FIG. 1. Relative locations of hypothetical roosting and feeding sites.

in the DAC food supply are consistent with the information center hypothesis. Caccamise's test of this "prediction" of the patch-sitting hypothesis does not therefore permit him to conclude that his observations support the patch-sitting hypothesis and counter the information center hypothesis. His observations of a change in the character of the food supply and a concurrent change in roosting behavior simply do not distinguish between the two.

My fifth criticism lies with the suggestion by Caccamise and Morrison (1986, 1988) and Caccamise (1991) that the use of a large, distant roost combined with continued attendance at the DAC allows starlings to minimize travel time to SFAs while permitting two visits per day to each SFA (but only one to the DAC). This is not necessarily true, even in the special case most favorable to this suggestion where the SFAs lie on a line between the roost and the DAC (minimum daily return trip twice the distance from roost to DAC). In other, more general, circumstances, it is even less likely to be true that a distant roost minimizes travel time; a small roost close to the DAC, such as starlings used earlier in the season (Caccamise 1991), would in most conceivable arrangements of roost, DAC, and SFAs involve travelling a comparable distance or less. Fig. 1 illustrates the situation most favorable to Caccamise's case, where SFAs X, Y, and Z lie on a line between large roost A and DAC D. A small roost B, near D, could clearly result in a *smaller* travel time, while still visiting all but one feeding site twice, depending on the precise locations of A and B relative to the feeding sites (in Fig. 1 both roosts provide equal travel distance and number of visits to feeding sites: 2AD = BD × DB). Whether to use A or B then depends on the balance of advantages of time and distance savings and of visiting a given SFA or DAC once or twice a day. Waltz (1982) presents a discussion of some other aspects of this problem.

In many cases, including communally roosting *Turdus* species (Tye 1982), changes in the location of good food supplies may be such as to prevent birds from adopting Caccamise's ideal roost location (with SFAs on a line between roost and DAC) for much of the time. If so, then the advantage of attending a large distant roost for the purpose of saving commuting time may disappear or apply only intermittently. The fact that large distant roosts were used by starlings clearly suggests some determining factor other than travel time.

A sixth and related point is that even if a roost distant from the DAC does provide the shortest commuting route, the large roosts encountered cannot simply be an adaptation to reduce travel times; small roosts should also serve this purpose (given that the large roosts observed attracted birds from several scattered DACs, which fed at several scattered SFAs). The problem that remains as to why roost *size* increases, a problem dealt with by the information center hypothesis but not by the patch-sitting hypothesis.

A final point is that the relationship between feeding success and roosting population found by Caccamise (1991, his Fig. 4) is clearly consistent with the information center interpretation in that when food is harder to find, roosts should be larger. The decline in roost population during September and October was interpreted by Caccamise (1991) as a switch back to the use of small roosts, although Caccamise apparently obtained no direct evidence that this was so "because the small roosts . . . are difficult to detect" (p. 22). Perhaps an alternative interpretation is that many starlings ceased roosting in the study area altogether; certainly, starling roosts in many parts of the United Kingdom remain large or continue to grow in size through the winter (pers. obs.). Alternatively, if Caccamise is correct and birds do switch back to small roosts, this may be because their food supply becomes easier to track or is more abundant, thereby reducing the need for information. Consistent with this, Caccamise (1991) found an increase in feeding success at that time (his Figs 3 and 4). Further data on roosts in areas surrounding Caccamise's field site and on changes in food availability within it are essential to clarify this point.

In conclusion, many of the observations of Caccamise and Morrison provide the kind of circumstantial evidence for the existence of information centers, on which Ward and Zahavi (1973) based their original proposal, and which has been produced by many studies of communal roosts since. More critical analysis, following the guidelines suggested by Weatherhead (1987), Mock et al. (1988), and Richner and Marclay (1991), would be necessary to determine whether a given set of behavior patterns does or does not facilitate information exchange in the way envisaged by Ward and Zahavi (1973). It might be possible to use a marked population, such as that studied by Caccamise (1991), to investigate experimentally the recruitment of individuals to SFAs as done by Gori (1988). The patch-sitting hypothesis may have relevance for starlings, but proving that it does so does not at the same time prove that information exchange is not important in the same circumstances and that the information center hypothesis is invalid. Circumstances may indeed be envisaged where use of DACs and information centers both carry advantages and where birds may combine a use of both. The two are not mutually exclusive, and evidence for DAC use does not automatically counter the information center hypothesis.

Acknowledgments.—This paper is dedicated to the memory of my late friend and mentor, Peter Ward, who would doubtless have mounted a better defense of his ideas than I have. I thank D. F. Caccamise for his comments.

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The "patch-sitting hypothesis": a parsimonious view of communal roosting behavior.— Tye (1993) points out in his commentary that some predictions of our "patch-sitting hypothesis" (Caccamise and Morrison 1986, 1988; Caccamise 1991) share possible outcomes with the "information center hypothesis" (ICH). I agree with this conclusion, but I maintain that this results mainly from a lack of rigor in the definition of ICH, which in turn leads to predictions so compliant that they may be found consistent with a considerable variety of research outcomes. Furthermore, the "insurance corollary" (Zahavi 1985) of the ICH makes this hypothesis essentially non-falsifiable, and as such ICH provides an exceedingly weak theoretical foundation for examining communal roosting behavior. In an effort to infer support for tenets of ICH from our results, Tye (1993) resorts both to the "insurance corollary" and to a fundamental modification in the basic tenets of ICH—that information exchange takes place away from the communal roost. Neither approach adds to our understanding of communal roosting behavior, while both tend to obscure the real difficulties in applying ICH to our field observations. In his conclusion, Tye calls for critical analyses based on studies of marked populations. Again, I agree, as it was exactly this approach using radio-tagged birds that led us to conclude ICH was unlikely to provide a suitable explanation for our observations of communal roosting behavior.

My reply will show that our results are at variance with two fundamental tenets of ICH. These differences provide very convincing evidence that ICH is unlikely to apply in any important way to the systems we studied. This led us to develop an alternate explanation for communal roosting behavior—the "patch-sitting hypothesis" (PSH). It is based on three explicit assumptions, and by yielding a multitude of falsifiable predictions, provides a robust foundation for examining communal roosting behavior.

Background.—We began looking at communal roosting in 1978 with the specific goal of showing how European Starlings (*Sturnus vulgaris*) employed information exchange to locate feeding sites from their communal roosts. Initially, our work was at the population level (e.g., Caccamise et al. 1983, Fischl and Caccamise 1985, Caccamise and Fischl 1990) which provided a view of regional patterns in communal roosting behavior. In 1979, we began radio-telemetric studies of individual birds to understand patterns of movement between roosting and foraging areas (Morrison and Caccamise 1985; Caccamise and Morrison 1986, 1988; Morrison and Caccamise 1990). Most of our work was with European Starlings (*Sturnus vulgaris*), but we have also worked with Common Grackles (*Quiscalus quiscula*),