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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*), American Robins (*Turdus migratorius*), Red-winged Blackbirds (*Agelaius phoeniceus*), and, most recently, American Crows (*Corvus brachyrhynchos*).

Most important of our findings was that the foraging distributions for all individual birds we studied were centered around their daytime foraging area or diurnal activity center (DAC) and not their roost (Morrison and Caccamise 1985). While birds often changed roosts from night to night, they remained faithful to the same small DACs for months where they spent essentially all of the daylight hours. Our definition of DAC originated from the maps we made of field locations for radio-tagged birds (Morrison and Caccamise 1985). The diurnal locations were consistently very tightly clustered within a small area (2–4 km^2) for up to the 120 day field life of radios. The strict site fidelity displayed by the birds was substantiated by our high rate of success at finding individuals on their DACs (up to 99% of attempts) at randomly determined times during the day. Site fidelity to the DAC remained throughout the entire post-breeding roosting season (June–early November) and through the winter for birds that did not migrate (Caccamise, pers. obs.).

Our observations point to two fundamental contradictions in our results with expectations of birds using roosts as information centers. First, the consistent fidelity to DACs we found for roosting birds is neither predicted by nor consistent with ICH. The very foundation of ICH is built on the assumption that birds roost because food patches are ephemeral. It is this ephemerality that renders information on the location of replacement food patches valuable, thereby giving birds a reason to return to a roost. Our observations show unambiguously that our roosting birds do not switch among food patches. They either forage exclusively on their DAC early in the season, or they forage late in the season both on their DAC's and at food patches associated with roosts. The association of patches (supplemental feeding area or SFA) with roosts in our experience does not change over time. Examples of SFA's we have identified include a land fill, watered turf farm providing invertebrates, corn field, and a patch of fruiting trees. Birds may switch their SFA by switching roosts, but they do not switch among SFAs from a single roost. These observations show that birds cannot be using roosts as information centers in ways consistent with ICH when they (1) use the same stable patches for weeks or months, and (2) do not switch among patches based on a visit to a roost. Despite hundreds of field observations we have never had an individual move from patch to patch over a period of weeks or months as would occur for a bird utilizing information acquired at a roost. If food patches are stable for weeks or months, as our results suggest, then there is no need for information concerning the location of new feeding sites.

Second, another contradiction arises from our observation that the DAC is the center of the foraging distribution, not the roost (Morrison and Caccamise 1990). ICH not only fails to predict a DAC-centered foraging distribution but actually predicts quite the opposite—a roost centered foraging distribution. ICH requires food patches to be ephemeral. An individual returns to a roost or colony when its feeding patch deteriorates, identifies an individual (or group) with a good patch through some form of information exchange, and thereby learns the location of a new patch by following that individual to a new location. ICH gives no basis for suggesting that any one direction from the roost is any better than any other direction. Therefore, over a period of time as an individual obtains new information and uses new patches, a pattern would emerge in which the "information center" (e.g., the roost) would be surrounded by the patches formerly used by each bird. On average, the outcome must be a roost-centered foraging distribution. As Tye (1993) points out, Ward and Zahavi (1973) indicate that, "... roosts often occupy traditional sites, which need not be at the center of a feeding area ...." This, however, they offer as an exception based on local peculiarities of habitat, such as when a roost is at a habitat edge (e.g., lake, forest), or when roosting substrate is limited. This they considered the unusual circumstance and, as such, it does not diminish the legitimacy of the assumption that the information center (the roost), on average, must be at the center of the foraging distribution.

I interpreted these two contradictions as strong evidence that ICH is unlikely to apply in any significant way to the systems and species we examined. As a result, we needed a theoretical framework that applied to our roosting and foraging systems. We developed the PSH, providing a parsimonious explanation for our observations and a theoretical basis for organizing our continuing work (Caccamise and Morrison 1986).

The patch-sitting hypothesis. —We view large communal roosts as passive accumulations of DAC-based (usually) individuals that occur near rich food supplies. The behavior is a response to changes in food dispersion and is the result of individual birds exploiting, in an efficient manner, feeding sites, distant from their DACs. Several key observations led to development of the PSH (1) Fidelity to a single diurnal activity center is common among roosting species. (2) DAC-based roosting birds may change roost sites often, but they change DACs only rarely. (3) When DAC-based birds forage on their DACs, they roost nearby, usually in small local roosts. When they forage away from their DACs they often roost in large associations. (4) When DAC-based birds travel to distant roosts they often feed at an easily identified, high quality feeding area. The PSH hypothesis is based on three assumption: (1) DAC-based roosting birds select roosts and foraging areas in ways that tend to maximize the net rate of energy gain (i.e., they minimize commuting costs). (2) The DAC provides benefits beyond those simply attributable to foraging. (3) Changes in roosting and foraging distribution are responses to changes in food dispersion (e.g., from relatively uniform to relatively clumped).

Since our most complete information is on starlings, I will interpret PSH in terms of their behavior. PSH holds that starlings remain on DACs when food is uniformly dispersed over the landscape and adequately abundant on the DAC. This occurs early in the post-breeding roosting season (June–early August) when their diet is largely invertebrates. There is no reason to commute long distances to feed at other sites because food dispersion is relatively uniform—any small foraging advantage gained by locating a slightly better feeding site would be lost in the costs of commuting. Since birds feed on their DACs, they roost nearby, forming small groups to take advantage of the benefits of group protection. Later in the season, when food becomes clumped into relatively high quality patches (supplemental feeding areas), DAC-based birds can greatly enhance foraging opportunities by leaving the DAC to forage at these patches. Whenever intake rate at a distant patch more than compensates for the cost of commuting, birds would be expected to travel to distant sites. The PSH holds that major roosts are primarily aggregations of birds roosting as closely as possible to these especially rich feeding areas. We assume birds return to DACs because of benefits associated with DAC fidelity. Although we have not yet shown conclusively what the benefits are, we suspect that for starlings they are related to the need to maintain presence near the breeding site. This is more clearly the case for American Crows, as our more recent studies are beginning to show (Stouffer and Caccamise 1991, Caccamise, unpubl. data).

When food becomes clumped, a "patch-sitting" scenario develops naturally from our hypothesis. Birds can efficiently exploit distant food sources while maintaining daily presence on the DAC. Major roosts form when DAC-based birds travel to rich food patches and roost nearby overnight. This allows them to use the patch twice with only one round trip. Since these birds commute daily between the roost and their diurnal activity centers, naive birds can follow knowledgable birds to the roost. Naive birds may locate distant roosts the same way we do, i.e., by following the flight lines of birds that converge on the roost site each evening. Once in the vicinity of the roost, the naive followers may use local enhancement cues (the size and behavior of feeding flocks) encountered en route to pinpoint the food patch.

Replies to specific comments.—Below are (in order of their appearance) replies to each of the major points expressed in the commentary.

(1) Central to the criticisms in Alan Tye's (1993) commentary is his assertion that we misinterpreted ICH by relying on what we consider an implicit assumption—namely that ICH predicts a roost centered foraging distribution. I disagree with Tye's assertion, and, as I indicated above, an "information center" must be, on average, at the center of the foraging distribution. Tye concedes that ". . . central positioning would be advantageous. . . ." Does this imply that ICH, by not requiring central positioning, would have birds engaging in a behavior that is disadvantageous?

Tye incorrectly asserts that our observation of SFAs closer to large roosts than to DACs (Caccamise and Morrison 1988) is consistent with ICH. Here and throughout the commentary, Tye inappropriately compares our results with what he considers predictions of ICH. The comparisons are inappropriate because in each case Tye's prediction is without foundation in the ICH. In the current example, our test has to do with relative distances between roost, SFA, and DAC. ICH does not consider the existence of DACs, so measures of relative distances to them are irrelevant to ICH. It is inappropriate to attempt such comparisons.

(2) Aside from comments on roost centered foraging which I have already addressed, Tye indicates that our observations on DAC fidelity and roost switching for early season starlings are consistent with ICH. He accomplishes this by invoking the "insurance corollary" which holds that birds may travel to roosts as insurance against the possibility their feeding patches will eventually become unsuitable. He reasons that our observations of birds behaving in ways contrary to predictions of ICH did so simply because they did not need information at that time of year. Because this approach renders the ICH essentially non-falsifiable, it is not a suitable tool for evaluating competing hypotheses. Nonetheless, there is a point more important than implications of the insurance corollary. It is that ICH provides no explanation for DAC-based roosting behavior, either early in the season when most roosts are small or later in the season when many roosts are large. DAC-based roosting birds often switch among roosts both early and late in the season while remaining faithful to their DAC. Tye discounts our observations early in the season by invoking the insurance corollary, and he then provides an explanation for late season DAC fidelity (under point 3). However, he does not consider why essentially the same behavior occurs both early and late in the season.

(3) Tye credits Stewart (1978) with first noticing fidelity to diurnal activity centers, suggesting we failed to properly mention this. I believe this is a penurious interpretation of the facts. Stewart's roosting study involved totally anonymous birds. The only observation of a marked individual was a single female banded on her nest in spring and recaptured once in the same area in January. There was absolutely no information on where the bird roosted or how long it remained on its territory. This single observation is hardly evidence for diurnal activity centers. What makes DACs unique and interesting is that birds show persistent fidelity irrespective of where they spend the night. To establish this requires repeated observations of the same individuals over many weeks, both during the day and at night. Stewart's observation has relevance only because it is now possible retrospectively to evaluate this single observation in light of the hundreds of hours of observations we performed over a period of 8 or 10 years on individually marked birds. I should add that we found Stewart's results very interesting because he detected rich food patches near his roost sites just as we did when we formulated the PSH.

Tye (1993) disputes that DACs provide benefits in addition to foraging. If DACs are simply foraging sites, then birds should search for and use the best foraging site. As quality of foraging sites changes through time (as it must), birds would be expected to change foraging sites. They do not do this. Rather they return daily to the same DAC, even from year to year, making it very unlikely that DACs serve simply as foraging sites.

Foraging on DACs does provide a protein source, because, as we have indicated (Fischl and Caccamise 1986, Caccamise 1991), most foraging on DACs involves invertebrates. However, starlings remain faithful to DACs even when the ground is frozen and there would be little opportunity to acquire invertebrates. Furthermore, since invertebrate foraging occurs mainly in grassy habitats (e.g., lawns, old fields), it seems unlikely that birds would often commute long distances simply to use a particular patch of grass on their DAC without some additional benefit associated with DAC fidelity.

Tye (1993) also suggested that DACs might serve as subsidiary information centers. This is an example of just how pliant interpretations of ICH can be. Tye has changed the location of the "information center" from the roost to the DAC, effectively erecting an entirely new hypothesis. This exercise was necessary in order to account for DAC-based roosting behavior, which of course ICH cannot do. I agree with Tye that naive birds likely follow knowledgeable birds from DACs to SFAs and roosts, just as we do when we search for roosts. But this is not information exchange as defined by ICH.

(4) Tye (1993) cites my observations (Caccamise 1991) of declining foraging substrate quality on DACs coupled with increasing size of roosting population as evidence equally supportive of both PSH and ICH. It is true that the test I performed does not distinguish between the two hypotheses, but this was never my intention. My clearly stated goal was to test a prediction of the PSH. I did in that paper, as I have done here, point out the inconsistencies of our observations with tenets of ICH, suggesting that in our system ICH was not likely to apply. Because ICH is functionally non-falsifiable and because of its seemingly infinite malleability, unambiguous and convincing tests have yet to be devised. This leaves "support through preponderance of evidence" as the remaining approach for differentiating ICH from related hypotheses. The necessary outcome of this approach is that not every legitimate test of a prediction for a competing hypothesis will necessarily discriminate between alternate hypotheses. Nonetheless, an acceptable explanation for communal roosting behavior can eventually emerge.

(5) Tye (1993) describes hypothetical spatial relationships between roosts, SFAs and DACs to point out some limitations in a test we performed on a prediction of the PSH (Caccamise and Morrison 1988). However, Tye has made a serious error in not considering an appropriate scale for his invented scenario. This makes the relationships he proposes entirely unrealistic. When starlings fly to distant roosts, the SFA is always (in our experience) very close to the roost. When there are two SFAs involved (we have never seen more than 2), the SFA closest to the DAC has always been along a flight line very close to one that would take the bird directly from the DAC to the roost (e.g., Morrison and Caccamise 1985, p. 800). The birds are so consistent that we can almost without fail take a departure bearing as a radio-tagged bird leaves a DAC in the afternoon and determine which roost it will use that night. In my thousands of hours of observation, I have never seen anything like the pattern Tye invented.

Scale is very important here because it is the scale that determines the dispersion pattern of food patches. In Tye's (1993) example (see Tye's commentary, Fig. 1), dispersion of his SFAs is much less patchy than what we have experienced when birds fly to distant roosts. Nonetheless, I will address the scenario he has presented. If a bird with a DAC at D needed an SFA, according to PSH it would fly to Z and never go on to Y, X or A. PSH says an individual exploits roosts and foraging areas efficiently. It does not require a bird to fly to a distant roost just because it is there. Rather, a bird should fly to the nearest SFA that satisfies its requirements. If its SFA is near the DAC, then it would roost locally and never go on to a large distant roost. It would roost at a distant site only when that was more efficient than returning to the DAC and its local roost. By roosting near the distant SFA a bird can feed twice, once in the evening and again in the morning, for the cost of a single round trip. Distant roosts can be 50 Km from the DAC (Hamilton and Gilbert 1969), although ours are closer (10–15 Km). When SFA's are at such distances, using these sites efficiently can provide distinct advantages to DAC-based birds.

(6) Tye (1993) says "The problem remains as to why roost size increases . . . ," and he then goes on to say that only ICH offers an answer. I refer Tye to our original paper (Caccamise and Morrison 1986) in which we explain that the PSH is based on a change in food dispersion from uniform to clumped. As the uniformly dispersed foods become unavailable (for our starlings it is a decline in invertebrate availability in lawns), increasing numbers of starlings travel to SFAs (the clumps) to feed. The more patchy the food (larger distances between patches and greater difference in food abundance between on and off patch) the larger the area over which an SFA attracts birds and so the larger the associated roost.

(7) Tye (1993) incorrectly asserts that we present no direct evidence that non-migratory starlings return to small roosts late in the season after they leave large roosts. We have presented direct evidence in two papers, but Tye fails to cite both papers (Caccamise et al. 1983, Morrison and Caccamise 1985). Small roosts were not routinely included in our 1000-km^2 censuses. However, until we conducted our radio-telemetric studies, it was not generally known that starlings routinely moved between small local roosts and large communal roosts. Small roosts were readily located and censused after being used by a radio-tagged bird. We estimate that 40–60% of the local population migrates; the rest return to DACs and local roosts.

Conclusion.—PSH is offered as a quantifiable and testable alternative to ICH. PSH is not based on circumstantial evidence but on detailed, long-term observations of the foraging and roosting movements of individually marked birds. In a decade of studying communally roosting birds, we have seen nothing to suggest that they share information at the roost. That Tye (1993) could claim that these observations are consistent with ICH underscores the main problem with ICH as a scientific hypothesis; namely, it is so compliant that it appears to be non-falsifiable.

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