

COMMENTARY

PATTERNS IN ROOSTING FLOCKS: A RE-EVALUATION OF DATA AND CONCLUSIONS

Recently Caccamise et al. (1983) presented data on seasonal roosting patterns of European Starlings (*Sturnus vulgaris*) and Common Grackles (*Quiscalus quiscula*) with the stated goal of providing a descriptive basis adequate for testing hypotheses explaining communal roosting behavior. They concluded that current roosting hypotheses are inadequate to explain their data and that new and more satisfactory hypotheses are required. Herein I argue that much of their data is suspect because of the method of collection and that, even were this not the case, their data provide an inadequate basis for testing current roosting hypotheses, thereby rendering their conclusions unwarranted.

Caccamise et al. presented two types of data—observations of roosting dynamics derived from regular surveys and counts of roosting flocks in the study area, and roosting patterns of individual birds obtained by radio telemetry. My only serious criticism of the former type of data is that some of the observed roosting patterns apparently were due to vegetation manipulations at some unspecified number of roosts (p. 476) and therefore do not reflect natural behavior. However, I have much more serious reservations about the radio-telemetry data. The use of radio telemetry requires that two conditions are known to—or can reasonably be assumed to—have been met. The first condition is that the animals selected to carry transmitters are representative of the population from which they are drawn (and about which inferences will be made). The second condition requires that the animals' behavior be unaltered by transporting a radio transmitter (Weatherhead and Anderka, 1984).

The first condition is unlikely to have been satisfied by Caccamise et al. for several reasons. The age and sex of the birds carrying transmitters were apparently unknown. Because age and sex can affect migration and roosting behavior (Dolbeer 1982, Greenwood and Weatherhead 1982) it was important to the aims of Caccamise et al. that age and sex be known. Certainly their sample sizes were too small for all age/sex cohorts to be well represented ($n = 10$ and 4 for starlings and grackles, respectively). I suspect that their samples were biased toward younger birds, owing to the capture method. An unspecified proportion of their radio-telemetry birds were caught in decoy traps in foraging areas, a method shown by Weatherhead and Greenwood (1981) to catch preferentially younger birds.

Weatherhead and Greenwood (1981) also found that decoy traps caught birds that were in relatively poor condition. If this were true of the birds Caccamise et al. equipped with radio transmitters, then not only would this further violate the assumption that the birds were representative of their population, but additionally, the behavior of these birds could have been seriously affected by the transmitters. Birds in poor condition that are stressed by carrying a transmitter may not show normal migratory behavior because of inadequate premigratory fat reserves (Berthold 1975) and may also have reduced viability. The data are telling in this regard. Of 18 starlings equipped with transmitters five were "lost soon after release," two were found dead and one had an unreported fate, leaving ten birds from which data were collected. Of eight grackles equipped with transmitters, three were lost soon after release and one was found dead, leaving four from which

data were collected. If the birds that disappeared died, then in less than 13 days (the shortest time period for which any of the remaining 14 birds was tracked) the combined mortality for grackles and starlings was 46% (12 of 26). If the birds that disappeared migrated, then overall 70% (16 of 23) of radio-equipped birds had migrated by the end of the study—clearly contradicting the conclusion that "only a small fraction of the total population could have migrated" (p. 480). Collectively, the problems with the telemetry data dictate against any conclusion being drawn from them.

Caccamise et al. used their data on roosting patterns to assess the merits of various hypotheses regarding the benefits derived by members of communal roosts. I consider here only their arguments regarding the hypotheses that potentially have broad applicability. The value of communal roosting as protection against predators (Lack 1968, Gadgil 1972) was dismissed because roost sizes were too large and variable. The expectation that roosts should be uniformly small relies on the assumption that predation randomly affects roost members, thereby making the odds against predation for any individual bird quite high in a relatively small roost (~1,000 birds). Even under that assumption, a predation rate of one bird per night would result in a loss of more than 10% of the roost population of 1,000 during the time covered by the study. If predators differentially attack certain types of individuals (e.g., those in peripheral roosting positions), the odds for those individuals being taken by predators are much worse, making membership in a much larger roost advantageous. More needs to be known about the nature, abundance and distribution of the predators before data on roost sizes can be used to draw conclusions about the predation hypothesis.

Caccamise et al. dismissed the information center hypothesis (Ward and Zahavi 1973) because small and large roosts occurred close together. Another interpretation of this observation is that the small and large roosts were functionally one and were split into two groups because neither site provided adequate roosting habitat of high enough quality. Without knowing a great deal more about the roosting substrate, the species composition of the roosting population, and the nature, abundance and distribution of the birds' food, many other interpretations of the above observation are also possible. Thus, the rejection of the information center hypothesis is unwarranted.

Finally, Weatherhead's (1983) hypothesis, although mentioned earlier in the paper, was not discussed by Caccamise et al. in light of their data but was implicitly rejected by their conclusion that "current hypotheses are inadequate to explain the patterns of roosting behavior we observed" (p. 481). The inadequacy of their data to test either the predation avoidance or information center hypotheses certainly precludes using them to test an hypothesis that incorporates elements of both.

In summary, the radio-telemetry data are too prone to bias to provide any reliable insights into roosting behavior. The general observations of roosting dynamics appear more reliable. However, alone they are inadequate to draw any conclusions about the merits of the general hypotheses about roosting.

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We are responding to the above commentary in order to (a) point out inaccuracies in the commentary concerning goals and objectives of our study, (b) correct errors in interpretation of our data, (c) address criticisms of our methods, and (d) point out inconsistencies and inaccuracies in arguments meant to refute various positions we took in our paper. We will try to show that the criticisms presented are based largely on errors of interpretation and on incorrect assumptions.

1) In the introduction to our paper, we clearly stated that our main goal was to describe patterns of behavior shown by roosting flocks. Nowhere did we promise to perform tests of current hypotheses. Nevertheless, in the first paragraph of the commentary, testing hypotheses is incorrectly stated as one of our goals.

Our results were inconsistent with some assumptions and predictions of current hypotheses. Although we did point these out, we do not purport to have conducted tests of hypotheses. As we stated in the introduction, we believe that meaningful tests of hypotheses will be facilitated by a better understanding of patterns in roosting behavior, and it was our goal to add to this descriptive base.

2) The commentary suggests that we modified roosting patterns through vegetation manipulations at an "unspecified number of roosts." We modified no roost sites before or during the study. All of our roosts were on private land, over which we had no control. We listed the five specific sites (p. 476) that were "cleared" during the study. These activities were all undertaken by private land owners without any participation by us. We consider such occurrences to be a normal condition of the birds' environment, and similar in effect to natural events (e.g., fire, succession) that might render sites unsuitable for roosting.

3) The commentary lists two conditions that must be met in order to use radio-telemetry. We believe these are unrealistic, and if strictly applied would discount most radio-telemetry studies on flying animals. For example, Weatherhead would require that "behavior be unaltered" by a transmitter. However, behavior is always affected because of increased energy demands of carrying a trans-

mitter. A better approach is to estimate cost of transport as we have done (Hedin and Caccamise, *Trans. Northeast Section, Wildl. Soc.* 1982:115) so the importance of the effects can be evaluated.

The commentary suggests that the first condition for telemetry studies (tagged birds representative of population) was not met in our study because age and sex of tagged birds were "apparently unknown." Despite appearances, the information was known (starlings—17 adults, one juvenile [sex unknown], ten males, seven females; grackles—all adults, four males, three females, one unknown sex), and notwithstanding Weatherhead's "suspicions," our sample was not biased toward younger birds. A table describing case histories for all tagged birds was included with the original manuscript, but we deleted it before publication because of its length. However, by our oversight, information on age and sex was not added to the text.

Weatherhead argues that our radio-tagged birds were in poor condition because some birds were obtained with decoy traps. Our losses of radio-tagged birds were also used as evidence to support this position. These conclusions are based on two faulty assumptions and several errors of interpretation. First, it is incorrectly assumed that most radio-tagged birds were obtained from decoy traps, when most (21 of 26) were mist-netted at roosts. We trapped birds on foraging areas in order to show that the radios did not cause the birds to change foraging areas (they did not). Secondly, we do not believe that our losses of tagged birds support the argument that our birds were in poor condition. Experienced telemetry workers realize that high losses often occur during initial studies when patterns of movement are unknown. We lost five starlings soon after release. All losses occurred during initial studies and resulted mainly from our unfamiliarity with the patterns of movement. Once we learned the relationships between foraging areas and roosts, birds were rarely lost (including those that died). The commentary also ignores the importance of the long observation periods for most birds (mean = 89 days, maximum = 139 days); such long pe-

riods from a species as small as starlings certainly support our contention that the birds were in good condition.

Interpreting loss of animals is always a dilemma in telemetry studies. However, we have subsequently accumulated many more telemetry data, and our original interpretations remain supported.

Weatherhead interpreted our data incorrectly in calculating percentages of tagged birds that could have migrated. As we clearly stated (p. 480), our values (five possible migrants of 12) included only birds in the field during the pre-migratory phase. Values in the commentary inappropriately include birds that were not even in the field during this period (mid-August to mid-October). The result is a greatly inflated estimate for the proportion of birds that could have migrated.

Finally, Weatherhead suggests that "problems with the telemetry data dictate against any conclusion being drawn from them." A careful reading of our paper will show that our conclusions were drawn largely from our five years of population studies, not from the telemetry data. We used the telemetry data mainly for corroborating conclusions from population studies, although we also reported some new findings (e.g., local roosts, movement between roosts). We believe that our approach was balanced, and the criticisms of our telemetry work are without foundation.

4) In discussing our treatment of the predation protection hypothesis, Weatherhead incorrectly asserts that the main benefit of roosting results from a simple dilution effect based on numbers of potential prey in roosts. This is an oversimplification, as it ignores benefits of predator detection through group alarm signals. His position carries the implicit assumption that either predators at roosts are seldom detected, or despite detection, they are often successful. We know of no empirical evidence for this assumption. However, the common occurrence of group alarm signals in roosting species would argue for their

effectiveness. When detection of predators is effective in deterring predation, then to maximize predator protection a group need be only large enough to maximize the rate of predator detection. We agree with Weatherhead that more needs to be known about the nature of predation, but we do not believe that his analysis in the commentary contributes to this end.

5) Although we are accused of dismissing the information center hypothesis, in fact we only point out its failure to explain the distribution of roosts we found. Weatherhead's suggestion that the small and large roosts we mentioned (Fig. 1, 2; p. 481) were functionally one is incorrect, although we did find examples of the type he describes. The nearby roosts we referred to were clearly distinct; they were out of view of each other, they occupied distinct patches of habitat, and their arrival and departure flight lines were independent. If roosts serve as information centers, then hypotheses seeking to explain roosting on this basis must also explain the distribution of roosts we observed. Neither the information center hypothesis nor its current derivatives do this.

6) We did not discuss Weatherhead's hypothesis largely because our paper was submitted and reviewed before his paper appeared (in 1983). It was certainly not our intention to "implicitly reject" it. However, we did comment on the two earlier hypotheses (predation, information center) that form the basis for his paper. We found them inadequate to explain the patterns of roosting behavior that we observed, and we remain committed to this conclusion.

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RECENT PUBLICATIONS

Small birds of the New Zealand bush.—Elaine Power. 1970. William Collins Publishers, Ltd. 41 p. Paper cover. No price given. Source: William Collins Publishers Ltd., P.O. Box 1, Auckland, New Zealand. This is a recent printing of an older, thin paperback book of paintings of twenty-one of New Zealand's small birds. Twenty of the paintings are placed opposite text that provides limited information on the habitat preferences, food, nest, and size of the species. A Maori name is given for each. Each bird is shown perching on an appropriate plant. Well-done paintings and informative text make this most suitable for a children's book or a simple introduction to the birdlife.—J. Tate.

The Canvasback on a prairie marsh.—H. Albert Hochbaum. 1981. University of Nebraska Press, Lincoln. 207 p. \$17.95 cloth, \$5.95 paper. Few places in the world have been so central in our knowledge of certain widespread birds as has Delta Marsh, at the southern end of Lake Manitoba. Hochbaum's pioneering study, followed by the results of many workers at the Waterfowl Research Station which he established there, have been seminal in understanding the biology and management of waterfowl. His

book was first published in 1944 and reprinted with updating notes in 1959. The latter edition has now been reprinted, a testimony to the enduring value of the original observations and ideas. The author has written a new introduction gracefully reviewing the changes, as well as the unchanging factors in the prairie wetlands, their waterfowl populations, and hunting pressures over the past forty years. The book contains his pen-and-ink diagrams, maps, and drawings (often in the style of F. Lee Jaques) and bears a new painting by him on the cover. Photographs, references (as of 1959), and index.

Cranes of the world.—Paul A. Johnsgard. 1983. Croom Helm, London. 258 p. \$37.50. Source: distributed by Indiana University Press, Bloomington. Cranes are commonly in the news because of the serious decline of several species and the tentative recovery of a few. Until this book, however, we have not had an up-to-date summary of their biology, distributions, and status. The first third gives a comparative overview of the family: classification and evolution, behavior, vocalizations, ecology, reproductive biology, etc. This is followed by accounts of the fourteen species (combining the crowned cranes into one). The book