

Preroosting aggregations in the American crow, *Corvus brachyrhynchos*

Jeffrey E. Moore and Paul V. Switzer

Abstract: Preroosting aggregations (PRAs), or site-specific gatherings of individuals made prior to flying into a night roost, are frequently associated with avian roosting behavior. We investigated PRAs in the American crow (*Corvus brachyrhynchos*) in order to describe preroosting behavior and test possible hypotheses concerning their function. Crows were aggregated among the available fields and within a field. Although crows in PRAs in fields commonly foraged, in previous studies crow PRAs have been found in the area at sites where little foraging probably took place, such as large rooftops. As the evening progressed, individuals shifted to PRA sites closer to the location of night roosts. Crows left PRAs for night roosts in a highly aggregated fashion, but prior to arriving at a night roost, individuals often separated from those with whom they left the PRA. Those individuals that were still together upon arriving at the night roost rarely settled next to each other. This pattern of behavior, along with characteristics of crow night roosts, is inconsistent with functional explanations based on crow PRAs being information centers for location of either daytime foraging areas or night roosts, nor does it support hypotheses solely related to foraging benefits. Rather, the results suggest that while crow PRAs are probably associated with multiple benefits, lowering predation risk may be a primary function.

Résumé : Les rassemblements avant la nuit (PRAs), qui réunissent des individus à un site particulier avant leur envol vers le dortoir de nuit, sont souvent associés au sommeil en groupe chez les oiseaux. Nous avons étudié ces rassemblements chez la Corneille d'Amérique (*Corvus brachyrhynchos*) afin de pouvoir présenter une description des comportements avant le sommeil et éprouver les hypothèses au sujet de leur rôle. Les corneilles se rassemblent dans les divers champs disponibles ou à l'intérieur d'un champ en particulier. Bien que les corneilles ainsi rassemblées dans les champs se mettent parfois à chercher de la nourriture, des études antérieures ont démontré l'existence de rassemblements à des endroits où il ne peut se faire de recherche de nourriture, comme par exemple des toits à grande surface. À mesure qu'approche la nuit, les groupes de corneilles se déplacent vers des sites plus rapprochés de leurs dortoirs. Les corneilles quittent ces sites en grands groupes, mais avant d'arriver au dortoir, les oiseaux se séparent fréquemment de ceux avec lesquels ils ont quitté le site de rassemblement précédent. Les individus qui arrivent ensemble au dortoir s'installent rarement les uns à côté des autres. Ce type de comportement, de même que les caractéristiques des dortoirs de nuit des corneilles, sont incompatibles avec les hypothèses fonctionnelles qui veulent que les sites PRA soient des plates-formes d'information au sujet des sites de quête de nourriture de jour ou des sites de dortoir de nuit, et ne supportent pas non plus les hypothèses strictement reliées aux bénéfices alimentaires. Les résultats indiquent plutôt que si les rassemblements avant la nuit comportent probablement plusieurs fonctions, l'une des principales est sans doute de réduire les risques de prédation.

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Introduction

Communal roosting is a behavior that occurs in many taxa (Wynne-Edwards 1962), but it has been of particular interest to ornithologists (Eiserer 1984). Numerous studies have investigated avian communal roosting in order to identify its ecological function and aid in the management of bird species that commonly affect or are affected by humans. Descriptive studies have focused on times of entrance to and departure from roosts (Jumber 1956; Schnell 1969; Swingland 1976; Davis and Lussenhop 1970; Michael 1973; Krantz and Gauthreaux 1975; Post 1982), preferred roost characteristics, and site fidel-

ity (Jumber 1956; Eiserer 1984; Engel and Young 1992; Gorenzel and Salmon 1992, 1995). Other studies have sought ultimate explanations for communal roosting, examining the benefits of foraging (Ward and Zahavi 1973; Gochfield and Burger 1982; Caccamise and Morrison 1986; Morrison and Caccamise 1990; Richner and Heeb 1995), predator avoidance (Hamilton 1971; Ludwig and Rowe 1990; Wrona and Dixon 1991; Lima 1995), and thermoregulation (Eiserer 1984).

While avian communal roosting has received a great deal of attention, another common grouping behavior, closely associated with these roosts, has not. Shortly before roosting, individuals of many bird species form large, conspicuous aggregations near the roosting sites (Rhodes 1886; Jumber 1956; Zahavi 1971; Counsilman 1973; Eiserer 1984). These preroosting aggregations (PRAs) consist of many individuals, often on open ground, that are congregated more closely than one would expect from the surrounding, suitable habitat (Zahavi 1971; Counsilman 1973). Because of the dearth of studies on PRAs, we lack even a basic, descriptive understanding of the PRA process in most species, let alone a functional explanation. This is unfortunate, because in addition to PRAs being an interesting phenomenon in their own right

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J.E. Moore.¹ Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616, U.S.A.

P.V. Switzer.² Department of Zoology, Eastern Illinois University, Charleston, IL 61920, U.S.A. (e-mail: cfvs@eiu.edu).

¹ Present address: 1810 H Street, Arcata, CA 95521, U.S.A.

² Author to whom all correspondence should be addressed.

(Zahavi 1971), a better understanding of them would give us insight into the underlying mechanisms and functional aspects of communal roosts (Zahavi 1971; Councilman 1973) and the trade-offs involved between foraging benefits and predation risk (Councilman 1973; Gilliam and Fraser 1987; Lima 1985; Ludwig and Rowe 1990). Recognizing the potential importance of PRAs in avian ecology would also allow us to better assess species' habitat requirements, which would assist us in managing large urban populations (Jumber 1956; Gorenzel and Salmon 1992) and threatened populations of birds.

The few studies that have investigated PRAs differ in their proposed functional explanations for the aggregations. These functional explanations fall into four categories. First, PRAs may serve as information centers for individual birds. If daytime foraging areas (Ward and Zahavi 1973) or night-roosting areas (Zahavi 1971) are ephemeral and difficult to locate, these aggregations may provide information to individuals as to the position of feeding or roosting sites. Second, PRAs may be foraging areas. In this case, for aggregations to result, foraging sites must be limited or patchily distributed, with birds congregating because of a lack of other available foraging locations (Caccamise and Morrison 1986; Stouffer and Caccamise 1991). Third, the risk of predation may lead to the aggregations, because of the dilution effect, an increased chance of noticing a predator, or other predation-related benefits of being in a group (Hamilton 1971; Kenward 1978; Foster and Treherne 1981). A decrease in predation risk may be the sole function of the PRAs, may combine with the benefits of foraging at the site (Councilman 1973), or may apply while the birds are traveling to the roosts. A fourth, "null" possibility is that PRAs do not have a function. That is, they may simply be the result of an increase in the number of birds and a decrease in the amount of available space as birds converge on the night roost. All of these possible functions of PRAs are currently speculative; rarely has any PRA study attempted to test a functional hypothesis. Further, we recognize that PRAs may not currently have a single, exclusive function. However, outlining these possible functions allows us to test them individually, eliminate those that are not supported, and provide possible summary explanations.

We present a study of PRAs in the American crow (*Corvus brachyrhynchos*), a species known for its tendency to form them (Rhodes 1886; Stouffer and Caccamise 1991; Gorenzel and Salmon 1992). Crow PRAs in our study area were easy to identify; they consisted of hundreds to thousands of individuals gathered closely together in fields that were either bare or had very short vegetation (e.g., mown grass). The data we gathered allow us to describe PRA behavior in crows and to test the functional hypotheses proposed above to account for PRAs.

Materials and methods

The study was conducted in Davis, Yolo County, California, from early December 1995 to mid-March 1996 and from mid-October to late November 1996. Roosting in this area runs from approximately July to March (Gorenzel and Salmon 1995). Observations were made of a number of PRAs in open agricultural fields just outside and adjacent to Davis, as well as a number of roosting sites in town. We studied five PRA sites along the north and west perimeter of Davis (Covell Farms, Hutchison Road, North Davis, Sutter Davis West, Sutter Davis East) as well as at two roosting sites within Davis. These

PRAs ranged from 200 m to several kilometres from each other, and were more than 1 km from the nearest roosting site.

At each of these sites we collected data on crow behavior; observation sessions took place in the late afternoon to early evening, beginning prior to individuals leaving a PRA and continuing until the last individual left. Crows were not individually marked. However, it is highly unlikely that we observed the same crow more than once when recording individual behavior; each PRA had from hundreds to thousands of individuals (see Results), and over 10 000 crows roost in Davis (P. Gorenzel, personal communication). Thus, because (i) our data set on individuals is minor relative to the overall number of crows and (ii) we only used one observation from an individual on a given day, the chance of recording data from the same individual was extremely small.

Some of our data were used for purely descriptive purposes (e.g., the pattern of individual movement among PRAs), but most allowed us to test specific predictions resulting from foraging, predation, and information-center hypotheses proposed to account for PRA function. For example, the foraging hypothesis predicts that individuals will commonly forage in PRAs. To examine patterns of foraging in PRAs, we conducted focal observations of individual crows at three different PRA sites on 5 different days. Individuals were located randomly in a flock and observed for 30 s. We recorded birds as foraging if they were observed pecking the ground or eating during the focal observation. Otherwise, they were recorded as not foraging.

To describe crow movement between PRAs, on 1 day we observed the direction of changes between the Sutter Davis East and West PRAs. We noted the numbers of birds flying from Sutter Davis West to Sutter Davis East (toward the town and roosting sites) and from Sutter Davis East to Sutter Davis West (away from the town and roosting sites).

Predator-avoidance hypotheses predict that birds will aggregate in PRAs (if combined with foraging benefits) or when flying into the roost (if swamping or diluting predation effects upon arrival at the roost). By definition, we found crows aggregating in PRAs; hundreds to thousands of individuals were tightly grouped, with much of the available surrounding space unused. To investigate whether they aggregate when departing from PRAs, we recorded data from three different PRAs on 6 different days. We defined the border of the pre-roosting area as the edge of the agricultural fields closest to town, and considered a bird to have left the PRA when it crossed this border. We counted the birds leaving the PRA during 30-s intervals beginning prior to the first individuals leaving and continuing until all birds had left the PRA. If a large group of crows was crossing the border as a given interval terminated, the flock was then divided among intervals. Therefore, one 30-s interval does not necessarily indicate a group, but merely indicates the number of birds leaving in that interval. For analysis, the first interval considered was the interval during which the first bird departed. Data were compared to a Poisson distribution (expected if individuals leave randomly with respect to one another) to examine the temporal dispersion of the crows. To quantify the degree of aggregation within departing crows, we calculated the variance to mean ratio, where a value of 1 for the ratio indicates random distribution, a value less than 1 indicates a more uniform distribution, and a value greater than 1 indicates an aggregated distribution (Zar 1996).

Both information-center hypotheses (for location of either night roosts or daytime foraging areas) predict the following of successful/knowledgeable individuals by unsuccessful/unknowledgeable individuals. To locate night roosts, individuals must follow knowledgeable birds to a roost site from the PRA. To locate daytime foraging areas, individuals must follow knowledgeable individuals to the roost from the PRA and remain together upon arrival at the roost so that they can follow the individual out the next morning.

To examine the extent to which crows leaving the PRA together stayed together as they entered town and roosting sites, we followed pairs of crows leaving the PRA with binoculars until they were out of

Table 1. Temporal dispersion pattern of crows' departure from PRAs.

Location and date	Total no. of crows	No. of 30-s intervals*	No. of crows/interval [†]	s^2/\bar{x}	χ^2
Sutter Davis East					
7 Dec. 1995	1033	59	17.5±25.9	38.4	996 (16)
3 Feb. 1996	2420	129	18.8±26.9	38.5	5217 (19)
11 Feb. 1996	2720	106	25.7±34.2	45.6	2641 (22)
North Davis					
2 Mar. 1996	428	34	12.6±25.1	50.0	515 (12)
14 Mar. 1996	245	18	13.6±24.4	43.7	64.2 (8)
Covell Farms					
1 Nov. 1996	349	36	6.9±12.8	23.8	305 (9)

Note: Chi-squared values are from a goodness-of-fit comparison of the observed departure pattern (number of observed intervals with a given number of crows departing) with a random (Poisson) expected distribution. Categories (number of crows departing per interval) were combined to arrive at expected values greater than 1; degrees of freedom (in parentheses) is the number of categories - 2 (Zar 1996). All $P < 0.001$.

* Number of 30-s intervals between the first and last crows departing.

[†] Values are given as the mean ± SD.

sight. Pairs were defined as two birds leaving the PRA simultaneously, flying within a few metres of each other, either by themselves or as part of a larger flock. Pair observations were taken at four different sites on 16 days. Pairs were recorded as remaining together (i.e., headed the same direction as a pair or remaining part of the same flock; pairs generally remained within 100 m of each other) or splitting before disappearing into town. The number of pairs recorded as staying together represents a maximum value because (i) paired birds in larger flocks were considered to stay together if both remained in the flock, regardless of distance or relative direction of flight between them, and (ii) owing to the distances involved and low levels of ambient light, not all pairs had reached a roosting site before disappearing from the observer's view.

To determine the tendency for birds to land with a partner at a roosting site, we recorded data at two roosting sites on 3 nights (for a description of crow roosting sites see Gorenzel and Salmon 1992, 1995). To ensure that birds had the opportunity to settle with other birds, only crows in pairs or flocks were used. Each crow was categorized as (i) landing independently, i.e., either by itself in the roost or next to an already roosting bird, (ii) landing with a partner, i.e., simultaneously next to an individual that flew in with it as an obvious pair or in close proximity, or (iii) landing with a non-partner, i.e., simultaneously next to a crow other than the one with which it flew in.

Results

PRAs began forming on the ground in the early afternoon. These congregations were clumped both among available fields and within fields. Among fields, the same fields were generally used day after day, with nearby, similar fields (e.g., bare tomato fields, open grassland) rarely being used. While most PRA sites were used during the entire roosting season (e.g., Sutter Davis East), some were used for only part of the roosting season (e.g., Covell Farms), and a few were used sporadically throughout the season (e.g., Sutter Davis West). Within a field, crows were grouped tightly (nearest neighbors generally within 1 m; J.E. More and P.V. Switzer, personal observation), the groups being much smaller than the available space. Within a field, the PRA was often located in a different location from one night to the next.

Flocks and individuals frequently changed PRAs as the day progressed. Eighteen individuals moved from sites farther from the city to sites closer to the city (i.e., toward roosting areas), but none moved from closer to farther sites (χ^2 (Yates' correction) = 16.1, $df = 1$, $P < 0.001$). This strong directional pattern matched the pattern we observed throughout the period. The last major PRAs were in fields directly adjacent to the town. At the PRAs we observed, foraging was common; of 141 focal individuals, 86 (61%) were foraging during a given 30-s period (95% CI: 0.53 < proportion foraging < 0.69). Preening and scanning were also common behaviors at the PRAs.

Around sunset, crows began leaving the PRAs and flying into town to roost. The pattern of dispersal from the PRAs was highly aggregated (Table 1); the data were characterized by periods of time when no crows departed from the PRAs followed by the sudden departure of several birds to hundreds of birds. The number of crows at a PRA was significantly correlated with the total time elapsed between the first and last crows leaving the prerost site (Kendall's $\tau = 0.733$, $P = 0.039$), but was not related to the degree of aggregation found (i.e., s^2/\bar{x}) (Kendall's $\tau = 0.2$, $P = 0.57$). Thus, crows left the PRAs in groups, but did not aggregate more if there were more crows at a PRA.

There was an equal probability that an individual which departed from the PRA with another crow would remain with it or split from it en route to the roosting site. Of 109 observed pairs, 54 (50%) remained together until they were out of sight (95% CI: 0.40 < probability of staying together < 0.59). Thus, at least half of the crows did not arrive at a night-roosting site with an individual from their PRA.

At the time of flock arrivals, roosting areas were very chaotic, often with hundreds of birds flying above the roost trees for several minutes before landing. Many birds called loudly and often as they flew above, frequently changing their direction of flight and commonly moving between trees before remaining perched. Individuals arriving together at roosting sites ("pairs") rarely landed together (of a total of 225 individuals, 187 landed independently, 19 landed with a partner, and 19 landed with a non-partner, $\chi^2 = 251$, $df = 2$, $P < 0.001$). Thus, it was unlikely that pairs arriving from the same PRA perched near each other at the night-roosting site.

Discussion

Our data provide the following description of crow behavior in PRAs. Crows begin aggregating in the early afternoon, forming larger groups as they move toward town and their roosting areas; the last major PRAs are in agricultural fields adjacent to the town. Around sunset, crows begin leaving the PRAs, heading for the roosting sites in groups. Although crows commonly leave together, at least half of the pairs leaving together separate before reaching a roosting site, and very few individuals settle at a roost with the individual with whom they arrived.

This description of crow behavior allows us to test proposed functional explanations for PRAs. First, our observations suggest that the "null" hypothesis (i.e., PRAs are due to a decrease in the amount of space with an increase in the number of birds) does not explain the formation of crow PRAs. The crows are grouped both among similar fields and within a particular field; thus, more suitable space is available than the crows are

occupying on a given day. Therefore, the aggregations are not simply due to a decreasing amount of available space as crows converge on the night roost.

Based on his observations of white (*Motacilla alba alba*) and pied (*M. a. yarrellii*) wagtails, Zahavi (1971) suggested that the function of PRAs is to advertise shifting, ephemeral roosts so that communally roosting birds can gather in one location before flying quietly into the roosting areas together. This hypothesis, which we term the roost-location hypothesis, assumes that (i) roost locations shift nightly and (ii) roosting birds are concealed (e.g., in dense vegetation) and inconspicuous to incoming birds or flocks, so that following other roosting birds is the only quick way to locate a roosting site. Thus, without the more conspicuous PRAs, tight roosting flocks will not form. A clear prediction resulting from the roost-location hypothesis is that individuals will remain together while traveling from the PRA to the roost location.

Our observations of crows do not support the roost-location hypothesis. We found that while some crow pairs remained together while traveling from the PRAs to the roosting site, at least half of the observed pairs separated before reaching the roosting areas. At a more fundamental level, the roosts observed in our study do not conform to the assumptions of the roost-location hypothesis. Unlike wagtail roosts (Zahavi 1971), roosting sites in Davis do not shift nightly but remain traditional, not only throughout the season but from year to year (Gorenzel and Salmon 1995). In further contrast to wagtails, the major crow roosting sites are highly conspicuous, with hundreds of crows flying and calling loudly for substantial periods of time before they fly into roosting sites. These roosting sites include deciduous trees that are bare in winter, i.e., for much of the roosting season (Gorenzel and Salmon 1995; J.E. Moore and P.V. Switzer, personal observation). Thus, PRA advertisement is probably not necessary for crows to find roosts. Although some birds may be following others to roost, roost location is unlikely to be a major function of crow PRAs.

Other studies have proposed that PRAs serve a foraging function. These foraging benefits may be a result of using PRAs as information centers for daytime foraging sites (Ward and Zahavi 1973) or as additional feeding areas that supplement foraging at daytime territories or "diurnal activity centers" (Caccamise and Morrison 1986; Stouffer and Caccamise 1991). Neither of these hypotheses appears to be supported by the results of this study. First, if PRAs were used as foraging-information centers, "hungry" or "unsuccessful" crows should follow "successful" foragers from the PRA to the night roost and then back to the foraging areas. We found that at most half of the crow pairs remained together from the PRA to the night roost, and once at the night roost, incoming pairs almost always split. Further, Stouffer and Caccamise (1991) found that for a population of crows in New Jersey, U.S.A., individuals formed territorial groups during the day that seemed to remain stable throughout the winter (see also Kilham 1984; Chamberlain-Auger et al. 1990). These crows also formed PRAs, and rarely traveled together between the diurnal-activity centers and roosts, which is consistent with our results. If such fidelity to territories or diurnal-activity centers exists in our population, then individuals would not need to use PRAs as information centers for foraging, as their foraging sites would not be ephemeral. Therefore, although we cannot say that no indi-

viduals used PRAs as information centers for daytime foraging sites, the evidence suggests that crow PRAs do not currently function as information centers.

Second, Caccamise and Morrison (1986) (see also Stouffer and Caccamise 1991) proposed that PRAs serve primarily as rich "supplemental feeding areas" to the more stable diurnal-activity centers used throughout the roosting season. Their related hypothesis, the "patch-sitting hypothesis" (Caccamise and Morrison 1986), suggested that the diurnal-activity center, rather than the roost, is the center of the individual's activity. Individuals will join distant communal roosts only when using supplemental feeding areas as well as diurnal-activity centers. Therefore, roosting sites are chosen for their proximity to these rich supplemental food sources, so supplemental feeding areas are between the roost and the diurnal-activity centers, and the distance between the roost and the supplemental feeding areas is less than the distance between the diurnal-activity centers and the supplemental feeding areas (Caccamise and Morrison 1986).

In support of these ideas, we found substantial foraging taking place at the PRAs we observed, and PRAs were located near roosting sites. However, some crow PRAs near our study area are located in places with little to no available food (e.g., large rooftops; Gorenzel and Salmon 1992). Further, even for groups that do forage at PRAs, foraging benefits alone are unlikely to account for the formation of PRAs or the location of crow roosts in the study area. In the vicinity of our study area, crows roost overwhelmingly in urban areas (Gorenzel and Salmon 1992, 1995; J.E. Moore and P.V. Switzer, personal observation), despite an abundance of trees in the surrounding rural areas. According to the patch-sitting hypothesis, the crows would roost in towns because preferred supplemental feeding areas (our PRA locations) are just outside of town, en route to diurnal-activity centers. However, given that agriculture predominates in the entire region of Yolo County and most of the central valley of California, it seems improbable that in this relatively homogeneous foraging habitat, crows would coincidentally choose all of their supplemental feeding areas adjacent to the town on the basis of potential foraging benefits alone. We suggest that some intrinsic quality of urban roosts, rather than just their proximity to foraging areas, makes them preferred roosting areas. Thus, while it may or may not be true that daytime territories or activity areas serve as diurnal-activity centers for crows in our study area during the roosting season, the crows appear to form PRAs according to their location relative to preferred roosting sites, rather than choosing roosts according to the location of preferred supplemental feeding areas.

A lowered predation risk, however, may combine with foraging benefits to favor the formation of PRAs. Councilman (1973) suggested that increased predation risk in the later afternoon encouraged early abandonment of daytime foraging areas and the formation of PRAs. This would allow individuals to minimize predation risk and to forage more efficiently, despite the relative inferiority of PRAs as foraging areas. Aggregating prior to roosting also enables many individuals to fly into the roosting areas at the same time, effectively swamping the roosts and reducing predation risk via dilution or other predation-lowering effect (Hamilton 1971; Wrona and Dixon 1991). The fact that most crows in our study left the PRA in a highly aggregated fashion is consistent with these ideas.

Overall, our results suggest that the formation of crow PRAs is not simply due to a lack of available space, nor are they likely to function as information centers for locating either roosting or foraging sites. Many crows did forage at the PRAs that we observed, but foraging is unlikely to be the sole, or even a primary, function of these congregations. More foraging areas are available than are used for PRAs, and some PRAs occur in areas where foraging is not even possible. Our observations, however, do support hypotheses relating to decreasing predation risk. Thus, we conclude that lowering predation risk likely is at least a partial function of the formation of crow PRAs. For other species, such as wagtails, PRAs may serve different functions, particularly in view of the differences between crow and wagtail communal roosts. Further studies that look at the formation of PRAs by crows and other species, and observing PRAs associated with roosts in rural areas, would be useful in clarifying the function of this interesting behavior.

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References

- Caccamise, D.F., and Morrison, D.W. 1986. Avian communal roosting: implications of diurnal activity centers. *Am. Nat.* **128**: 191–198.
- Chamberlain-Augur, J.A., Augur, P.J., and Strauss, E.G. 1990. Breeding biology of American crows. *Wilson Bull.* **102**: 615–622.
- Councilman, J.J. 1973. Waking and roosting behavior of the Indian myna. *Emu*, **74**: 135–148.
- Davis, J.G., and Lussenhop, J.F. 1970. Roosting of starlings (*Sturnus vulgaris*): a function of light and time. *Anim. Behav.* **18**: 362–365.
- Eiserer, L.A. 1984. Communal roosting in birds. *Bird Behav.* **5**: 61–80.
- Engel, K.A., and Young, L.S. 1992. Movements and habitat use by common ravens from roost sites in southwestern Idaho. *J. Wildl. Manage.* **56**: 596–602.
- Foster, W.A., and Treherne, J.E. 1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature (Lond.)*, **295**: 466–467.
- Gilliam, J.F., and Fraser, D.F. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology*, **68**: 1856–1862.
- Gochfield, M., and Burger, J. 1982. Feeding and enhancement by social attraction in the sandwich tern. *Behav. Ecol. Sociobiol.* **10**: 15–17.
- Gorenzel, W.P., and Salmon, T.P. 1992. Urban crow roosts in California. *Proc. Vertebr. Pest Conf.* **15**: 97–102.
- Gorenzel, W.P., and Salmon, T.P. 1995. Characteristics of American crow urban roosts in California. *J. Wildl. Manage.* **59**: 638–645.
- Hamilton, W.D. 1971. Geometry for the selfish herd. *J. Theor. Biol.* **31**: 295–311.
- Jumber, J.F. 1956. Roosting behavior of the starling in central Pennsylvania. *Auk*, **73**: 411–427.
- Kenward, R.E. 1978. Hawks and doves: factors affecting success and selection in goshawk attacks on wood-pigeons. *J. Anim. Ecol.* **47**: 449–460.
- Kilham, L. 1984. Cooperative breeding of American crows. *J. Field Ornithol.* **55**: 349–356.
- Krantz, P.E., and Gauthreaux, S.A., Jr. 1975. Solar radiation, light intensity and roosting behavior in birds. *Ibis*, **87**: 91–95.
- Lima, S.L. 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the blackcapped chickadee. *Oecologia*, **66**: 60–67.
- Lima, S.L. 1995. Back to the basics of anti-predatory vigilance: the group-size effect. *Anim. Behav.* **49**: 11–20.
- Ludwig, D., and Rowe, L. 1990. Life-history strategies for energy gain and predator avoidance under time constraints. *Am. Nat.* **135**: 686–707.
- Michael, E.D. 1973. Migration and roosting of chimney swifts in east Texas. *Auk*, **90**: 100–105.
- Morrison, D.W., and Caccamise, D.F. 1990. Comparison of roost use by three species of communal roost mates. *Condor*, **92**: 405–412.
- Post, W. 1982. Why do grey kingbirds roost communally? *Bird Behav.* **4**: 46–49.
- Rhodes, S.W. 1886. Crow roosts and roosting crows. *Am. Nat.* **20**: 691–701, 777–787.
- Richner, H., and Heeb, P. 1995. Communal life: honest signalling and the recruitment center hypothesis. *Behav. Ecol.* **7**: 115–119.
- Schnell, G. 1969. Communal roosts of wintering rough-legged hawks (*Buteo lagopus*). *Auk*, **86**: 682–690.
- Stouffer, P.C., and Caccamise, D.F. 1991. Roosting and diurnal movements of radio-tagged American crows. *Wilson Bull.* **103**: 387–400.
- Swingland, I.R. 1976. The influence of light intensity on the roosting times of the rook (*Corvus frugilegus*). *Anim. Behav.* **24**: 154–158.
- Ward, P., and Zahavi, A. 1973. The importance of certain assemblages of birds as “information-centres” for food-finding. *Ibis*, **115**: 517–533.
- Wrona, F.J., and Dixon, R.W.J. 1991. Group size and predation risk: a field analysis of encounter and dilution effects. *Am. Nat.* **137**: 186–201.
- Wynne-Edwards, V.C. 1962. Animal dispersion. Oliver and Boyd, Edinburgh.
- Zahavi, A. 1971. The function of pre-roost gatherings and communal roosts. *Ibis*, **113**: 106–109.
- Zar, J.H. 1996. Biostatistical analysis. 3rd ed. Prentice Hall, Englewood Cliffs, N.J.