

ABSTRACT

E. Duke Whedbee Jr. THE EFFECT OF BEHAVIORAL INTERACTIONS ON THE STRUCTURE AND MAINTENANCE OF BLACKBIRD WINTER ROOSTS. (Under the direction of Andrew N. Ash) Department of Biology, December 1981. The purpose of this study is to seek understanding of the factors controlling the formation and maintenance of winter blackbird roosts in terms of behavioral interactions that exist between the species involved.

The roost is composed of essentially four species; three of which are native resident icterids, and one introduced sturnid. These species are: the common grackle, Quiscalus quiscula Linnaeus; the redwinged blackbird, Agelaius phoenicius Linnaeus; the bronzed-headed cowbird, Molothrus ater Boddaert; and the European Starling, Sturnus vulgaris Linnaeus.

Observations were made of the behavioral interactions that occur, with ancillary data collected concerning roost population size, distribution and composition during 1980 and 1981. Chi-Square analysis of the results indicates that while each species possesses a common behavioral catalogue, as described within the literature, each species also exhibits a new behavior labeled "snub" which is passive in nature and thus is highly important to the formation and maintenance of the roost.

A dominance hierarchy based upon the different roosting strategies utilized by each species to gain and maintain a roost position was established. This hierarchy indicates that accommodation is important in the formation of the roost. The main effect of aggressive behavior is to induce segregation of the species within the roost. Use of accommodative behavior allows those species that are clearly subordinate in dominance

to still attain success in roosting and thus gain any benefit accruing from roost participation at a minimal expenditure of energy.

THE EFFECT
OF BEHAVIORAL INTERACTIONS
ON THE STRUCTURE AND MAINTENANCE
OF BLACKBIRD WINTER ROOSTS

A Thesis
Presented to
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Master of Science in Biology

by
E. Duke Whedbee Jr.

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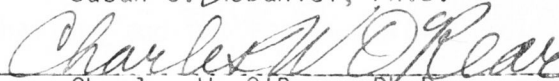


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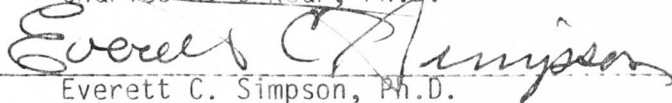
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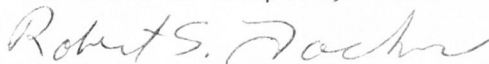
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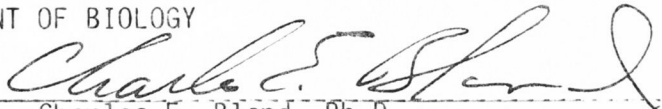


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TABLE OF CONTENTS

	PAGE
LIST OF TABLES	v
LIST OF FIGURES	vi
INTRODUCTION	1
LITERATURE REVIEW	2
The Nature of Blackbird Roosts	2
The Species Involved	3
Roost Structure	3
Behavior	3
Associated Problems	5
Agricultural	5
The Health Hazard	6
Aesthetics	6
MATERIALS AND METHODS	8
Site Description	8
Methodology	10
The Daily Routine	10
The Checklist and Code	11
RESULTS	13
Roost Population Estimate	13
Stratification and Segregation	15
Roost Composition	17
Behavior	17
Encounter Resolution	24
Roosting Strategy Success Index	26

Effects of Time and Temperature	29
DISCUSSION AND CONCLUSIONS	31
Grackles	31
Starlings	32
Redwings	32
Cowbirds	33
The Roost	33
Snub Behavior	37
Some Speculations on the Winter Roost	38
Literature Cited	40

LIST OF TABLES

	PAGE
1. Bird and Tree Density	14
2. Species Composition of the Rich Square Roost	18
3. Roosting Success - Rich Square Roost	30

LIST OF FIGURES

	PAGE
1. The Rich Square Roost Study Site	9
2. Species Segregation within the Roost	16
3. The Snub Behavior	19
4. Frequencies of Active and Passive Behavior	21
5. Frequencies of Intraspecific Behavior	22
6. Frequencies of Interspecific Behavior	23
7. Frequencies of Encounter Resolutions	25
8. Frequencies of Intraspecific Encounter Resolutions	27
9. Frequencies of Interspecific Encounter Resolutions	28
10. The Competition Hypothesis	35

INTRODUCTION

Large concentrations of blackbirds have been roosting in southern North America during winter since before the arrival of Man. In recent years, however, due to the increase in human populations and the subsequent modification of natural habitats, these roosts have become more frequently associated with suburban areas. The resulting increased interest has been focused on applied studies concerning the level of damage, methods of control and eradication. Basic knowledge of the mechanics of winter roosts is largely anecdotal and as a result, no effective and feasible method of alleviating the problems posed for farmers and suburbanites has been found.

This study examined winter roost formation and maintenance in terms of behavioral interactions that take place between and among the species involved. In addition, data on roost composition, roost structure, and total population for 1 typical roost was gathered in order to give an overall picture of the roost as a single entity.

Data collected were interpreted in terms of the evolutionary significance for each of the component species in an attempt to gain some insight into the selective forces behind the origins of winter roosts.

The data produced may enhance the search for control techniques and provide better understanding of interspecific and intraspecific behavioral patterns within the roost.

LITERATURE REVIEW

The Nature of Blackbird Roosts

Each fall, millions of icterid and sturnid birds of various species migrate southward across much of North America and join with resident birds to form large congregations that roost in very high densities (Meanley 1971). As many as 10 different species of birds can be part of roosts depending upon the area in which the roost develops (Meanley et al. 1975). Knowledge of roosts has been an anecdotal by-product of research by government agencies examining damage caused by the birds (P.A. Stewart personal communication).

The daily cycle begins approximately 1 hour before sunrise as the roost breaks up into smaller foraging flocks that range widely in search of food. By late afternoon, the foraging flocks begin to make their way back to the roost site, often stopping at "staging areas" nearby. As sunset approaches, the flocks stream back to the roost site, converging in large circling masses over the roost area and finally dropping back into the roost as night falls. This reformation continues for several hours into the night before the roost settles down and the birds remain relatively quiet until the following sunrise (Meanley et al. 1975, Stewart 1975, 1977).

Information as to how the roost forms is almost nonexistent, but P.A. Stewart (personal communication) believes that resident birds begin to form roosts in late summer and are joined by migrants during their fall arrival. He also believes that the common grackle, Quiscalus quiscula initiates roost formation over much of the Southeastern U.S.,

with other species joining them later, but has no data to substantiate this (Stewart 1977).

The Species Involved

Nationwide, at least 10 species can be associated with blackbird roosts and an estimated 550 million birds in over 700 roost sites may be involved (Meanley and Webb 1965). Of these species, 4 make up close to 80% of all roosts including those in Eastern North Carolina. The species are: the common grackle; the redwinged blackbird, Agelaius phoeniceus; the brown-headed cowbird, Molothrus ater; and the european starling, Sturnus vulgaris. The first 3 species are native icterids and the last is an introduced sturnid that has become part of the roost since its initial introduction in the 1880's (Royall et al. 1975). Because of the predominance of these species in most roosts, the resultant data should have broad application.

Roost Structure

Information on the internal structure of winter blackbird roosts is sketchy at best. Meanley and Webb (1965) observed some vertical stratification among the species in roosts located in Arkansas. Starlings were reported to occupy the highest branches, with grackles and male redwings beneath them, the cowbirds and female redwings occupying the lowest levels. Segregation was also noted in foraging flocks and in lateral location within the roosts.

Behavior

All passerine species share a common background of behavior (Andrew 1961) and icterids, in particular, have certain common behaviors that

allow interaction (Nero 1963, Wiens 1965). Territorial behavior can range from nesting territories to the immediate area in close proximity to an individual (termed "individual space") (Hinde 1966, Wilson 1975). It was a basic assumption of my study that obtaining and defending a perch or roost space could be construed as a form of territorial behavior.

The basic repertoire of agonistic behaviors of icterid species has been studied in terms of individual species (Nero 1956, 1963, Ficken 1963) and interspecific interactions (Crombie 1947, Hinde 1966), giving necessary basic data.

There are 4 basic behavior patterns which differ only in the degree of intensity of the individual's reaction to intrusion. The terms are those used by Wiens (1965) in his study of territorial aggression between and among grackles and redwings in a Wisconsin marsh during breeding season, and are listed in the order of increasing intensity:

1. "Tail flicking" - The bird is observed repeatedly flicking its tail upwards in an erratic manner.
2. "Bill tilt" - The displaying bird bobs its head and points its bill in a vertical direction.
3. "Song spread" - Most typical icterid agonistic behavioral pattern. The bird ruffs out its feathers, spreads its wings horizontally and faces the intruder with an open bill.
4. "Diving" - Actual physical flight at an adversary.

All of these behaviors were observed in preliminary studies of blackbird roosts among and between all species involved. It was clear

from the beginning, however, that "bill tipping" and "tail flicking" were merely precursors to the "song spread" in those cases where a focal individual (individual bird being observed) is reacting strongly to an intruder. Furthermore, the "diving" behavior was not observed in focal individuals at all since all focal individuals were occupying a perch at the time of observation. All intruder birds could be said to have exhibited the "diving" behavior by the very nature of their approach. For these reasons and the discovery of a new behavioral pattern to be discussed later, observations of "song spread" were considered as the only major type of aggressive or "active" agonistic behavior.

Associated Problems

Although not directly related to this study, some examination of the problems associated with blackbird roosts may help shed some light on the necessity for better understanding of roost dynamics beyond the simple curiosity surrounding interspecific interactions.

Agricultural. In those areas of the United States where the maturation of grain crops coincides with winter roost formation, crop depredation has long been considered the main source of concern. Several studies have been conducted to establish the degree of crop depredation (Dolbeer et al. 1978) and to devise means of control of blackbird numbers in affected areas (U.S. Fish and Wildlife Service 1976). There is still some controversy over how much damage is caused by blackbirds to crops such as rice in the South-Central U.S. (Woronecki et al. 1981), but control and prevention remain the major focal point of various governmental agencies.

An additional facet of agricultural damage is the damage that can occur to the roost trees themselves. Earl Raye, Chief Forester for Union Camp Corporation timber interests in Hertford Co., N.C. (personal communication) indicated that pine trees below 30 years of age could be severely damaged by the high concentrations of fecal material which are characteristic of blackbird roosts. My own observations confirm this in several roost areas including the area in which this study was done, where at least 80% of the trees are now dead or dying. Such losses can be devastating to the landowner.

The Health Hazard. Blackbird roosts that occur in close proximation to cities and towns can cause direct health problems. Roosts that occur near airports can endanger aircraft landing and taking off (Caslick and Meanley 1966) by flying over the runways, especially in the case of jet aircraft.

The large amount of fecal material produced by roosting birds that occupy roosts can initiate blooms of the soil fungus, Histoplasma capsulatum which can cause infections in humans ranging from skin and eye irritation to serious infection of internal organs such as the lungs and liver (Chin et al. 1970). It is this danger that has produced the most alarm among residents of areas close to roosts more than any other consideration because of the danger to area children.

Aesthetics. While this consideration is entirely subjective I can state from personal experience that the smell resulting from the droppings and the noise the birds make must be included in any examination of the problems connected with blackbird roosts. Overall the

quality of life enjoyed by residents near roosts is reduced and the property value of homes as well. While this problem is the least serious in nature, it is the most obvious and to the landowners the most economically detrimental. Long before any considerations of the health hazards occur, the residents are faced with the very loss of the use of the outdoor areas around their homes. As one homeowner put it to me, "It's as if we were under seige!"

MATERIALS AND METHODS

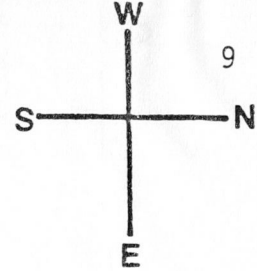
Site Description

All of the observations in this study were made in the roost that is located within the corporate limits of the town of Rich Square, Northampton County, North Carolina. This roost has been in existence since 1975 despite periodic efforts by the 1200 people of Rich Square to drive them off.

The study site was a 7 hectare monoculture stand of loblolly pine, Pinus taeda. The trees averaged 5 to 7 meters in height and density, and distribution was relatively uniform (Figure 1). The western border of the pine stand was a cultivated field, with the eastern edge parralleling U.S. highway 158. On the north, the roost area abuts an open field and a small strip of mixed hardwoods and older pines further separate it from an automobile dealership. The southern edge of the site consisted of older mixed hardwoods and pines which are interspersed among the homes of the Circle Drive subdivision.

At the time of this study, only about 5.8 hectares of the roost site were in actual use by the birds. The easternmost section of the pines had been used in previous years but most of these trees were dead or dying when I first visited the roost in December of 1979.

Field



Mixed Pines / Hardwoods

Water Tower

ROOST

Drainage Ditch

AREA

Mixed Pines / Hardwoods

Circle Drive Residential Area

Garden

UNUSED

QUADRATS

QUADRAT WITH BIRD COUNT

US 158

BLACKBIRD ROOST, RICH SQUARE N.C.

Methodology

Preliminary observations showed that it was possible to observe birds within the roost quite easily as they did not flush once they had settled in. The main problems involved observation of their behavior. For this reason all observations were made at sunset and involved the return of foraging flocks. The morning outflights took place before daylight and observations were impossible. Weather conditions limited the duration of daily observations.

Clothing and protection from the odor and feces were necessary in the form of rain suits and hat at all times. A respirator capable of filtering particles 1 micron or larger removed the odor and provided protection from possible infection by Histoplasma capsulatum microspores.

Boots were also of help within the roost since the concentration of droppings reached depths of 15cm on the ground and rainfall caused collection in depressions and ditches to even greater depths.

During preliminary observations, binoculars and a spotting scope were tested but it was soon apparent that naked eye observation was the most effective since the birds would allow a close approach if the observer remained relatively still once in location.

The Daily Routine

The average day of observation began around 10:00 am with the delineation of a 10 meter square quadrat, the site of all observations for that day. The quadrat was then explored and all dead birds and roost trees within the boundaries counted. If time allowed, other quadrats were delineated for future use.

The quadrat was reentered about an hour before sunset. Observations of the various behaviors and interactions were recorded as long as light permitted accuracy. Observation focused on a perching bird until 15 seconds elapsed or a behavioral interaction occurred. When light no longer allowed accurate observation of behavior, estimates of bird density were made from randomly selected trees within the quadrat to establish some estimate of average birds per tree. The process was repeated each observation day in a randomly selected quadrat.

The Checklist and Code

To insure that the maximum number of observations were recorded each day with accuracy and consistency, a standardized data recording sheet, or checklist (Lehner 1979) was developed.

A standardized alphanumeric code was designed for use on the checklist and its compatibility with Statistical Analysis System ensured. The resulting system maximized efficiency of observation.

For each observation, it was necessary to record certain information to achieve the type and quality of data which would enable me to address the question I sought to answer:

1. Date - A 5 number code, indicating the day, month, and year the observation was made.

2. Time - A 4 number code the time of the observation in.

3. Species - A 2 digit code, the first digit representing the focal species and the second representing the intruder.

4. Behavior - A single digit representing the behavioral pattern observed.

5. Resolution - A single digit was allotted to indicate the resolution of the encounter between the observed birds.

6. Quadrat - A 2 digit field was reserved to indicate the quadrat in which the observation was made.

7. Number of Trees - The 3 digits of this field were used to record the number of trees within the quadrat.

8. Dead Birds - The number of dead birds observed within the quadrat were noted in this 3 number field.

9. Temperature - A 2 digit space was utilized to record the temperature ($^{\circ}\text{C}$) at the time of observation.

10. The checklist also provided a section for comment in the event of any unusual phenomenon.

Using this code, a typical observation would be recorded in the following manner:

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
101180	1610	13	1	1	06	C71	014	21	

A literal translation of the code for this observation would be:

"On October 11, 1980, at 4:10 p.m., a common grackle was observed interacting with a redwinged blackbird, using the song-spread behavior pattern and drove it off. The observation occurred in quadrat 6, which contained 71 trees and 14 dead birds. The temperature was 21°C ."

Once the code was familiar to the observer, data could be recorded almost as fast as events occurred.

RESULTS

Data were collected at the Rich Square roost from November 2, 1980 to January 31, 1981; 777 observations were recorded. A total of 33 quadrats were observed; in 12 of these tree density and bird density were measured. Analysis was for the most part carried out using the Statistical Analysis System through the Triangle Universities Computer Center, with some simple statistics done by hand or on a TSR-80 personal computer.

Roost structure and maintenance are described separately.

Roost Population Estimate

Quadrat data produced estimates of average density of trees in the roost and the average number of birds utilizing each tree (Table 1). The average number of birds per quadrat was derived and number in the entire 5.8 hectares being used by the birds extrapolated. The estimated population was 4,279,240 birds.

The U.S. Fish and Wildlife Service, using a rate of flow technique, in which the number of birds moving into the roost area at sunset was estimated from a small visual sample from one observation point, was 3,000,000 birds. Because of the highly subjective nature of this technique, the estimate taken by me using the quadrat method contains a higher level of inherent accuracy and precision and is, in my opinion, closer to the true numbers. While the quadrat method does require additional equipment and that the observer actually enter the roost area, I feel the results are worth the additional effort in many cases in order to arrive at more accurate figures to use as a basis of future control

Table 1. Bird and Tree Density

Quad #	# Trees/Quad	Estimated Birds/Tree
1	75	110
2	104	120
3	69	90
4	57	130
5	76	120
6	77	100
7	67	85
8	49	100
9	56	120
10	82	100
11	71	90
12	57	100
	\bar{x} 70	\bar{x} 105.4

policies and decisions.

The major problem with the quadrat method may be the assumption of uniformity of distribution of birds within the roost. In the case of the Rich Square roost, the uniformity of the vegetation lends validity to that assumption. In roosts without such uniformity, the accuracy of estimates may be less reliable, but still better than that obtained by the rate of flow technique.

Stratification and Segregation

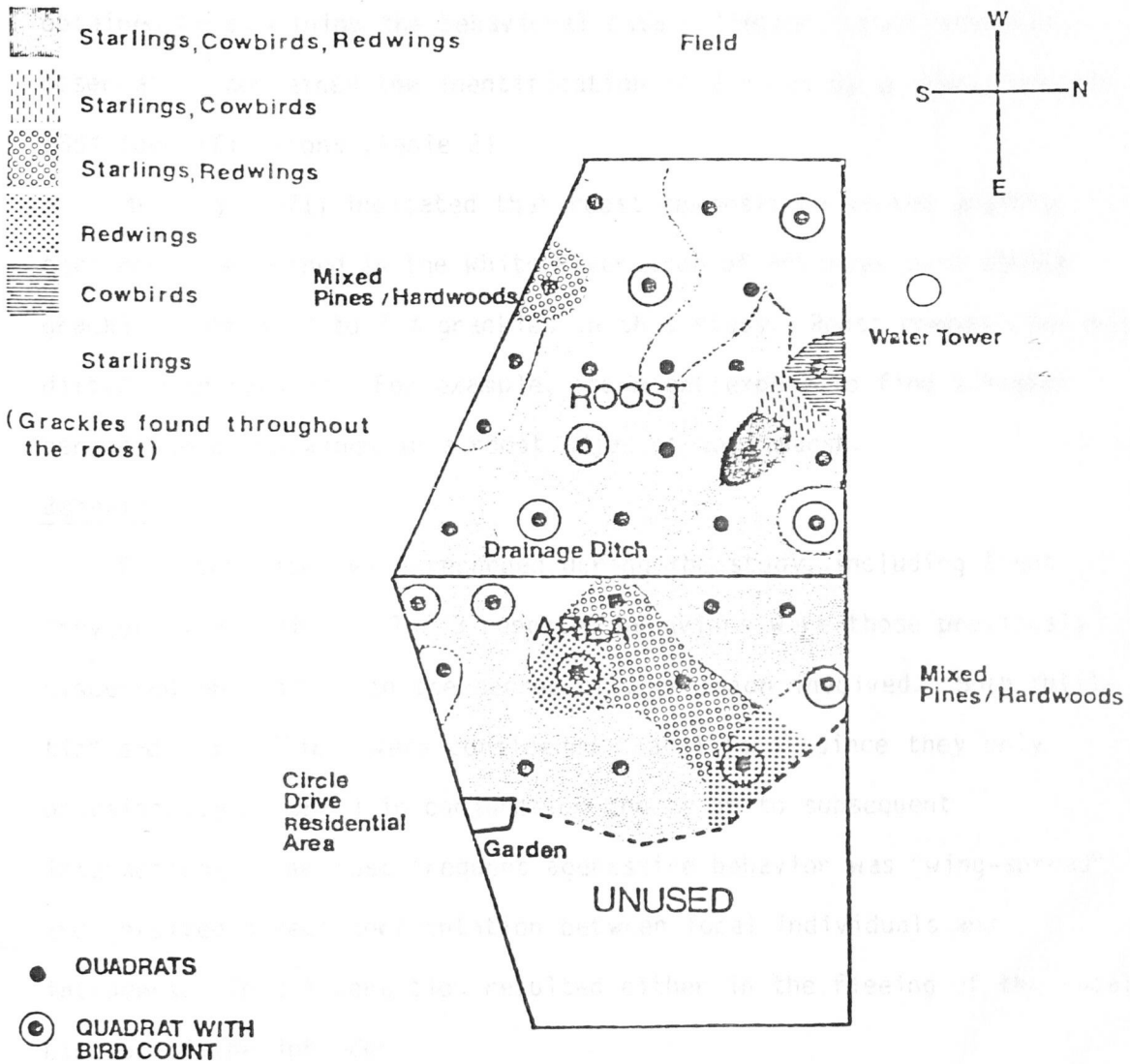
Meanley and Webb (1965) described vertical stratification in Arkansas roosts, but I found no evidence of it in the Rich Square roost. The most obvious reason for this is that the Rich Square roost exhibited no vegetational stratification which probably precluded stratification by the birds themselves.

Horizontal segregation was indicated by the presence or absence of species in each quadrat (Fig. 2). Grackles were found in every quadrat and starlings in most. Redwings and cowbirds were apparently segregated in peripheral areas, though the degree of segregation is not clear due to the coarseness of the sample.

Meanley and Webb (1965) also reported that redwings were segregated by sex, but the scope of my study did not allow determination of sex. It is obvious that there are two distinct concentrations of redwings in the Rich Square Roost.

Figure 2. Species Segregation within the Roost
November 1, 1980 - June 31, 1981

Roost Composition



ROOST COMPOSITION

Roost Composition

Estimates of species composition for the Rich Square roost were obtained by examining the behavioral data collected. Each behavioral observation contained the identification of 2 birds by species, providing 1554 identifications (Table 2).

Meanley (1971) indicated that roost composition varied greatly, but that roosts examined in the White River area of Arkansas were 60-80% grackles, compared to 73% grackles in this study. Roost composition may differ with habitat. For example, one might expect to find a higher percentage of redwings in a roost adjacent to a marsh.

Behavior

Four behaviors were recorded during the study, including 1 not previously described. The 3 reported behaviors were those previously discussed and differ in the degree of aggression involved. Both "bill-tip" and "tail-flick" were considered transitional since they only occasionally occurred in conjunction and prior to subsequent interactions. The most frequent aggressive behavior was "wing-spread" and involved direct confrontation between focal individuals and intruders. This interaction resulted either in the fleeing of the focal bird or of the intruder.

The other observed behavior was not aggressive but consisted of a ritualized accommodation between the focal individual and the intruder. I call this behavior "snub" since it involved acceptance of the intruder on the perch and redirection of both birds' attention to other approaching birds (Fig. 3).

Table 2. Species Composition of the Rich Square Roost

SPECIES	FREQUENCY ^a	PERCENT	POPULATION ESTIMATE
Grackles	1143	73.55	3,147,381
Starlings	286	18.40	787,380
Redwings	77	4.95	211,822
Cowbirds	48	3.10	132,657
Total	1554	100.00	4,279,240

^a Based upon observations of proprietors and intruders for 777 observations of behavior.

Figure 3. The Snub Behavior



...behaviors that this behavior as before reported are self-evident. ...highly ...to it and ...of movement ...must pass before ...more ...for the new ...in a forest ...observations ...of nesting ...was exceptionally ...between ...the behavior of ...blue ...as a ...as the ...according ...in ...10 ...Figs. 5, 6) are ...the birds react ...birds ...there

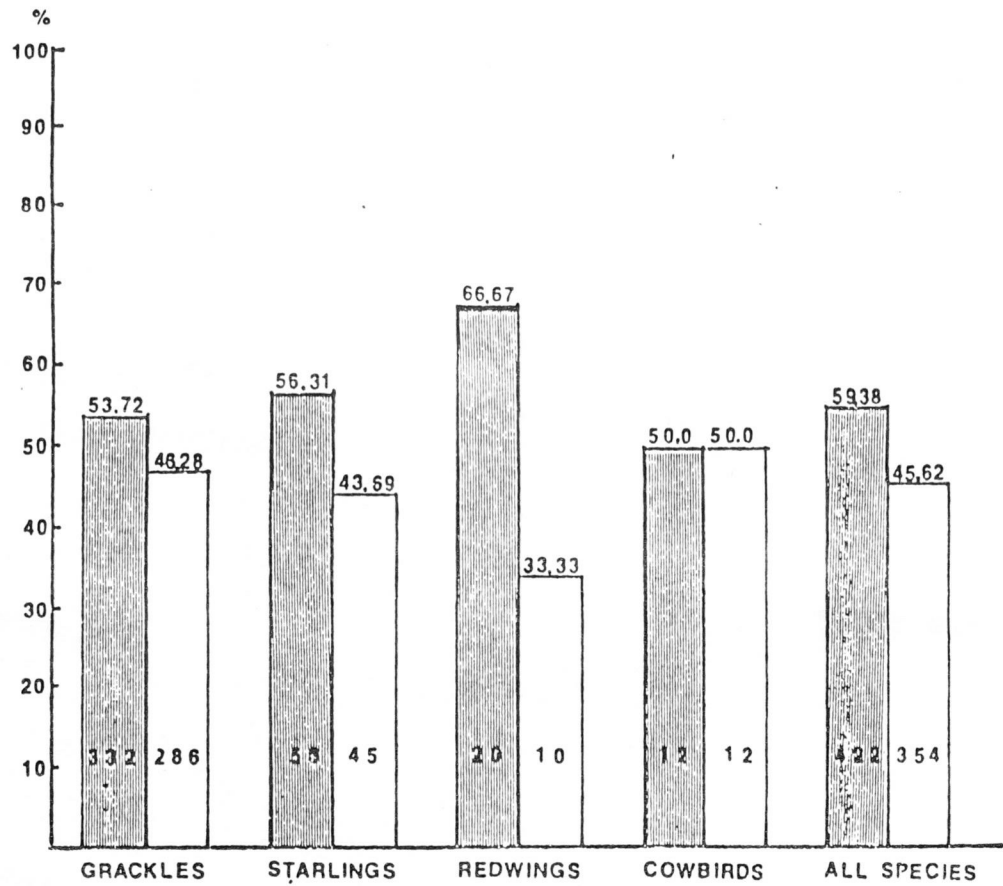
Reasons for this behavior not being reported are self-evident. Since this behavior is passive and occurs within a matrix of highly visible aggressive activities, the eye is not drawn to it and considerable field time is required before the absence of movement becomes clearly recognizable. In turn, sufficient time must pass before the novelty of the new behavior wears off and the observations are more objective. Otherwise, the observer finds himself looking for the new behavior exclusively rather than for behavior that occurs in a focal animal.

The discovery of "snub" behavior did much to clarify interactions involved in the formation and maintenance of roosts. Prior to noting this behavior, the only response possible to a focal bird was aggression, that is, each encounter could only result in the direct conflict between 2 individuals. The inclusion of the "snub" behavior into the behavioral repertoire allowed 2 options instead of 1. A focal individual could actively defend its perch or passively accommodate the intruder. As a result, the behavioral data in this study were categorized as either active or passive.

Basic frequencies of active and passive behavior (Fig. 4) according to the focal species indicates that there is no significant difference in how each of the species reacts to intruders or any other species (Chi-Square analysis: $P > .05$).

However, when intraspecific and interspecific interactions (Figs. 5, 6) are analyzed, there are significant differences in how the birds react to an intruder of the same or different species. In all species, there

Figure 4. Frequencies of Active and Passive Behavior



^a Significant
p < .05

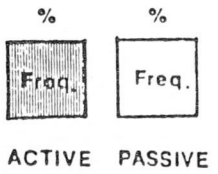
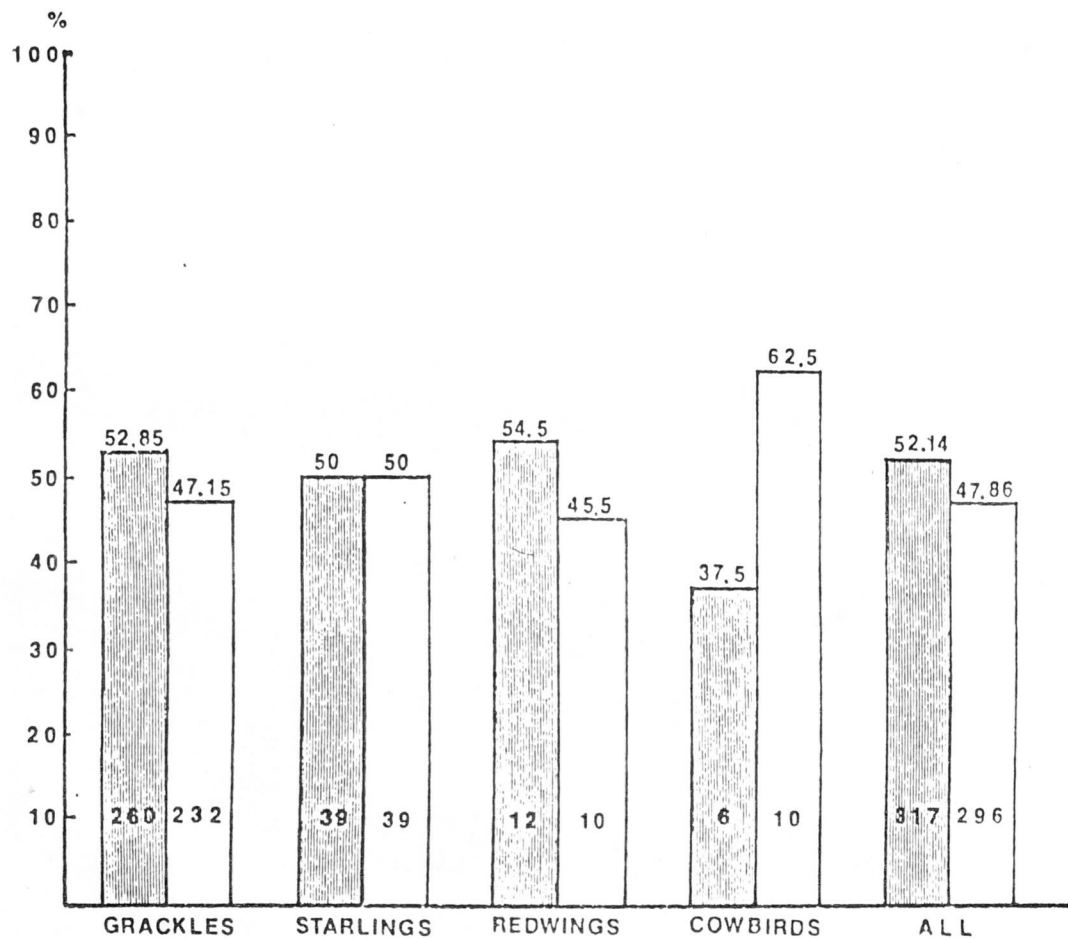
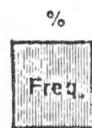


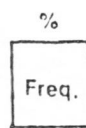
Figure 5. Frequencies of Intraspecific Behavior



^a Significant Difference

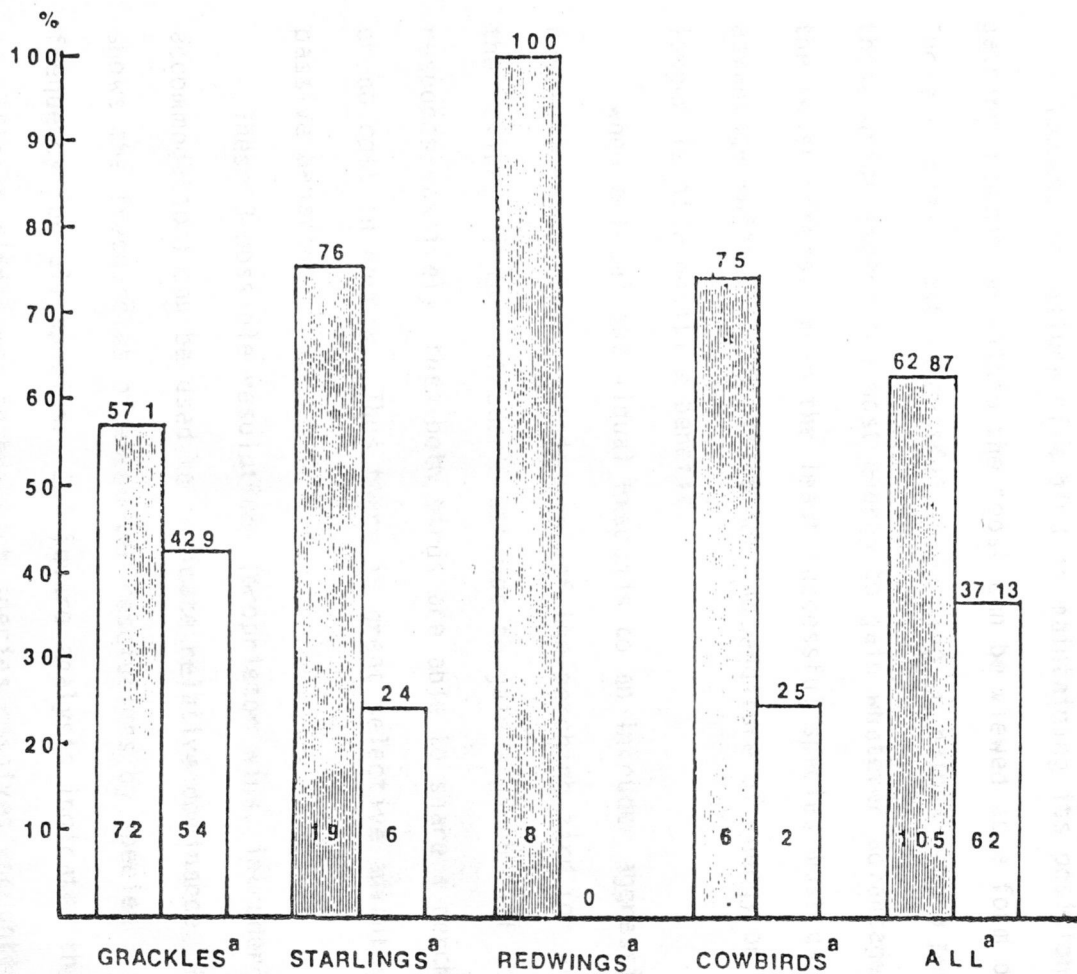


ACTIVE



PASSIVE

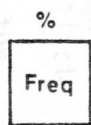
Figure 6. Frequencies of Interspecific Behavior



^a Significant Difference



ACTIVE



PASSIVE

was an interspecific increase in aggressive response and in the case of the redwings there was no passive response to interspecific intruders. While some samples are small, the trend is noted for all species.

Encounter Resolution

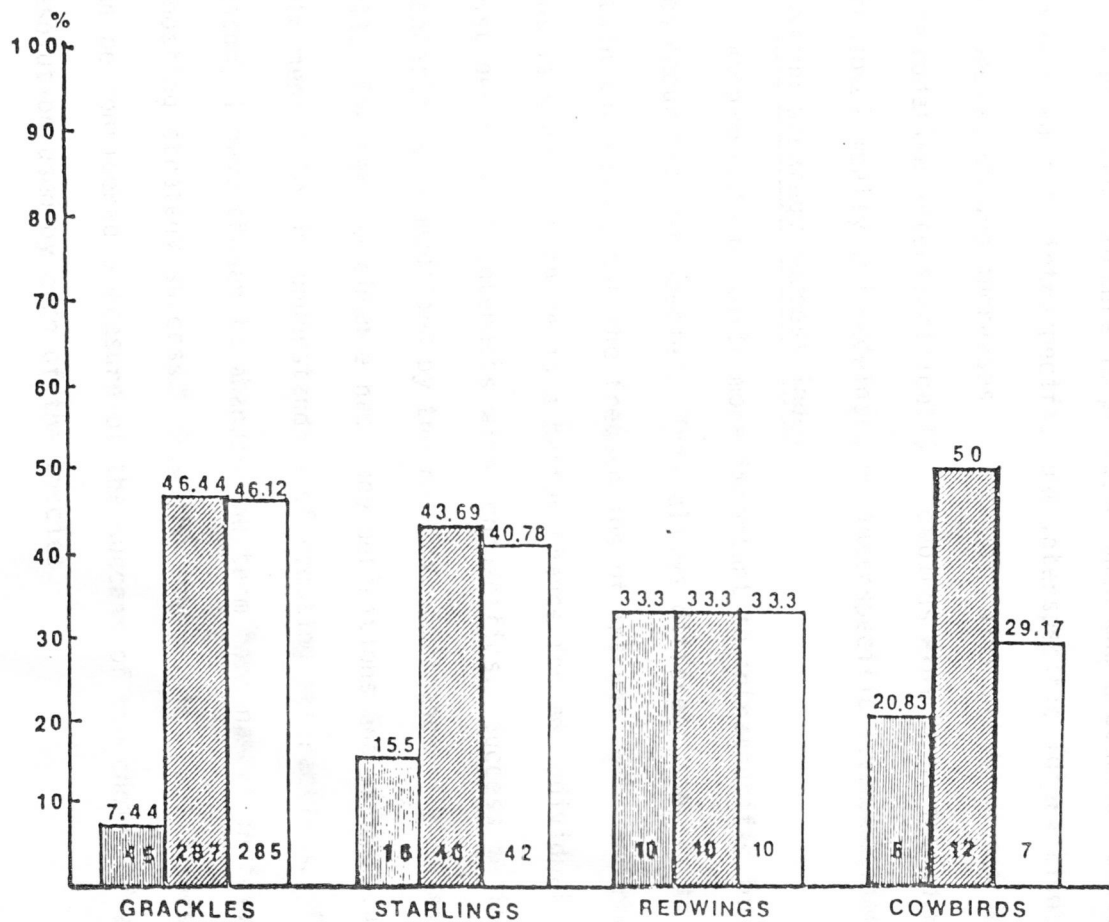
Each focal bird responded to an intruder actively or passively. There were also several possible resolutions to these interactions.

Success or failure of a bird in maintaining its position or in gaining a position within the roost can be viewed as a form of dominance. Those species least successful in gaining or maintaining a perch were those which expend the most energy to gain whatever advantage in survival the roost offers. Even the least successful species must gain an advantage sufficient to offset this expenditure of energy or the roost no longer is of a positive benefit.

When a focal individual responds to an intruder aggressively, the resolution is either dislodgement of the perching bird (or proprietor) or the failure of the intruder's attempt to gain a perch. If the proprietor responds passively, then both birds are able to share a perch at little or no cost in energy. Thus there is great selective advantage in the passive behavior.

These 3 possible resolutions (proprietor wins, intruder wins, and accommodation) can be used to indicate relative dominance. Figure 7 shows the frequencies of encounter resolutions by species and a pooled frequency for all species. Chi-Square analysis indicated that there is a significant difference in how each species resolves encounters ($P < .05$).

Figure 7. Frequencies of Encounter Resolutions



%
 Freq.
 INTRUDER WINS

%
 Freq.
 ACCOMMODATION

%
 Freq.
 PROPRIETOR WINS

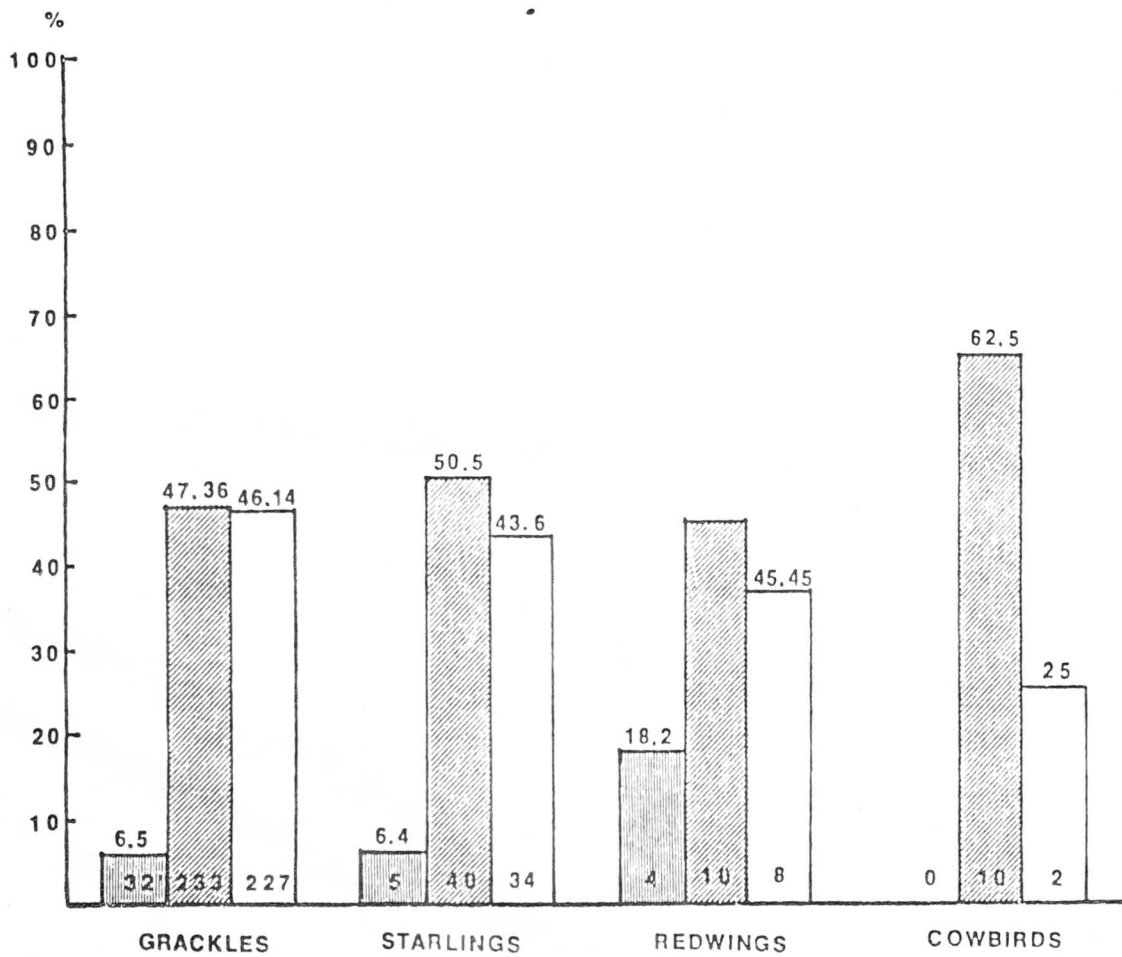
Grackles and starlings resolve encounters similarly, with few intruders successful and most interaction resolutions split evenly between proprietor wins and accommodation. Cowbirds exhibit a larger percentage of encounters resulting in intruder wins and redwings are split evenly.

A different picture is produced when the encounter resolutions are broken down into intraspecific and interspecific interactions (Figs. 8,9). All species showed increases in intruder wins and decreases in accommodation interspecifically. Cowbirds exhibit no intruder wins intraspecifically and redwings, no interspecific accommodation.

Roosting Strategy Success Index

Accommodation, while more important to intraspecific interactions, does occur between species. This allows different species to intermingle within the roost, but the frequencies of intruder wins and proprietor wins is such that there is a better chance for an individual to gain a roost perch if it interacts with conspecifics. Success in interspecific interactions is modified by the relative dominance of each species as well. The term dominance has many definitions and as such can be detrimental to the understanding of roosting interactions. For this reason, I have chosen to abandon the term "dominance" in favor of "roosting strategy success." How the species interact interspecifically can be considered a measure of the success of the choice of encounter resolution used by each of the species.

Figure 8. Frequencies of Intraspecific Encounter Resolutions

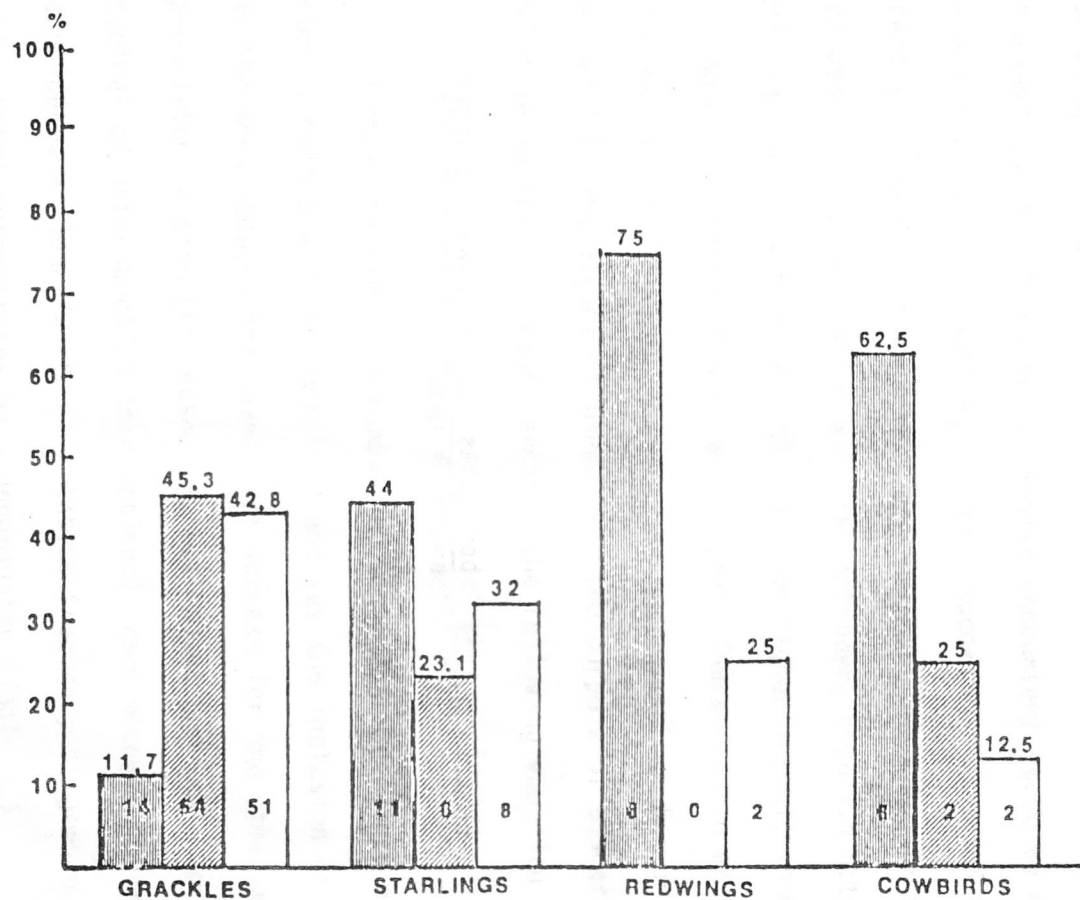


%
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 INTRUDER
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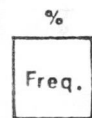
Figure 9. Frequencies of Interspecific Encounter Resolutions



INTRUDER
WINS



ACCOMMO-
DATION



PROPRIETOR
WINS

The simplest measurement of roosting success is a simple frequency based on wins and losses between birds of a particular species, but since each species has a different level of the ability to accommodate other species this can change the success of that species' roosting strategy. For example, a species which seldom retains its perch against intruders of a particular species in aggressive encounters would be considered to have a low index of roosting strategy success in relation to that species. However, if that same species exhibits a higher than expected frequency of accommodation with the intruder, then its actual success in gaining a perch within the roost may be higher overall than indicated by a simple comparison of wins and losses. Therefore, in order to produce a true picture of roosting success, the accommodation factor must be included in any algorithm used. For the purpose of discerning the relative success for each species, the following equation has been used:

$$\text{Success} = \frac{\# \text{wins} + \frac{1}{2} (\# \text{Accommodations}) - \# \text{losses}}{\text{Total } \# \text{ Interactions}}$$

I chose to halve the number of accommodations since each accommodation is both a win for each bird and yet the inclusion of other species in the area reduces the chances of success for the other members of the proprietor species (increased aggression and decreased accommodation is typical of interspecific interactions), thus accommodation cannot be considered a clear "win". A relative frequency is generated by division using total interactions as a denominator (Table 3.)

Effects of Time and Temperature

Chi-Square analysis indicated that neither time nor temperature affected the frequency of behaviors or resolutions for any of the species.

Table 3. Roosting Success - Rich Square Roost

SPECIES	ROOSTING STRATEGY SUCCESS INDEX	RANK	TOTAL INTERSPECIFIC INTERACTIONS
Grackles	0.5634	1	126
Starlings	0.0000	2	25
Redwings ^a	-0.5000	4	8
Cowbirds	-0.3750	3	8

DISCUSSION AND CONCLUSIONS

The structure and maintenance of winter blackbird roosts are the direct result of the roosting strategies used by the species involved. Consequently, examination must proceed from the specific to the conceptual, a natural and logical route to understanding. For this reason; discussion of behavior of each species, the roost in general, accommodation and how it relates to roost maintenance, and possible directions for future research are included here.

Grackles

The grackle was the most numerous (73.55%) and successful species studied. The grackle is found in all parts of the roost with no apparent segregation from the other species, and provides a background upon which all behavioral interactions and encounter resolutions involving other species must be considered.

Stewart (1975), working with roosts of 15,000 birds or less, concluded that the grackles functioned as the nucleus of the roosts and referred to them as the "leader species" in roost formation. The data from this study leads me to conclude that this roost is a "grackle roost" which is being utilized by the other species to varying degrees. How much this situation changes in roosts where grackles are not so overwhelmingly superior in numbers must be left to further study, but I believe that changes in numbers alone will increase other species' chances of competing successfully only slightly and any roost containing sizable numbers of grackles will remain essentially a "grackle roost".

Starlings

Starlings were the second largest group within the roost and were also second ranked in roosting strategy success. It should be noted that the starling is an introduced species that initiates roosts in Europe (Stewart, 1975), and has successfully invaded the grackle roost as an integral part of the roost structure. That an exotic species, moreover one that is of a different family, has been able to establish itself so successfully may indicate that the roost is essentially a response to basic behavioral and ecological factors. It also suggests that the starling possesses an extraordinarily high adaptability and enough common ancestry with the native icterid species to allow it to become so fully integrated.

Redwings

Redwings were the third largest group of birds within the roost and the lowest ranked species in terms of roosting success. Of all species in the roost, they are clearly the most aggressive. Redwings do not exhibit any accommodation interspecifically which compounds the detrimental effects of aggression. Redwings exhibited a relatively large percentage of intruder wins in interspecific encounters and since there was no interspecific accommodation to mollify the intensity of that effect, the result was a segregation of redwings into pockets within the roost. In other words, a redwings' best chance of obtaining a perch is interacting as often as possible with conspecifics, more so than in the case of the other species which do have some chance of accommodation. Obviously, redwings will be more successful in those roosts where they

predominate numerically or in pure redwing roosts which may be the evolutionary direction for this species in the future.

Cowbirds

Cowbirds were the least abundant species and the third most successful species. Cowbirds were second only to grackles in accommodation during interspecific encounters. This relatively high rate was the main reason for being more successful than redwings in roosting strategy. At the same time cowbirds fared poorly in aggressive encounters, losing all interspecific aggressive encounters.

Comparison of redwing and cowbird strategies would indicate the great importance of accommodation to a species' success in roosting. Aggression alone as exhibited by the redwing cannot guarantee roosting success nor can numerical superiority.

The Roost

Winter blackbird roosts are the result of a combination of behavioral characteristics of the species involved. Stewart (1975), in speculating on the development of roosts, noted that there seemed to be conflicting forces in operation that led to roost formation, which he called "communal" and "noncommunal". I believe that the newly discovered "snub" behavior is the major mechanism of the communal force. Without accommodation, any congregation of birds would be in constant turmoil with rates of perch acquisition and loss being equal. It is only when accommodation occurs that eventual stabilization can occur. Accommodation allows birds of low relative dominance to become part of a roost as exhibited by cowbirds and that low levels of accommodation can reduce the

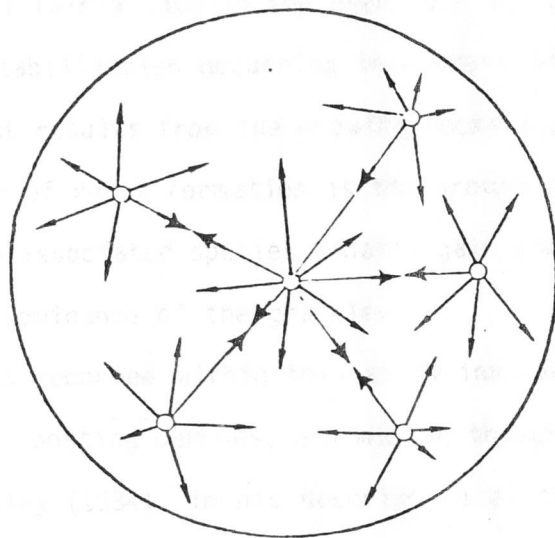
success of an inherently more dominant species such as the redwings.

The control and activation of communal response is seasonal and involves hormones which stimulate territorial aggression and the related behavior patterns that predominate during the breeding season (Hinde 1966). The long term survival value of the winter roost is unknown. B. Meanley (personal communication) stated that there is a general assumption that low temperature and the relatively benign environment within a roost is the major cause of roost evolution. The fact that time and temperature had no significant effect on behavior in this study, while not conclusive, does indicate that we should consider other factors as possible selective forces. One possibility is the role of winter roosts in reducing competition for food. Birds with similar feeding habits dispersing radially from several points within an area are more likely to come into direct competition for food even in areas where food is not a limiting factor (Fig. 10). On the other hand, birds radiating from a central point may face less competition.

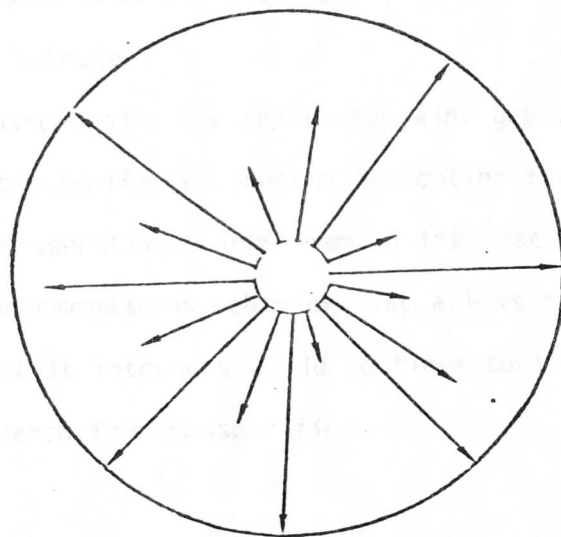
Another consideration is survival rates within the roost. The number of dead birds in each quadrat was noted and these data indicate that the monthly mortality rate within the roost was 0.08%. This does not account for birds that died away from the roost or were hidden by the droppings but does indicate a low death rate within the roost itself.

It is probably safe to assume that the roost is of value to the birds that utilize it, if for no other reason than the fact that an introduced species (starlings) quickly adapted to the roost structure.

Figure 10. The Competition Hypothesis



MANY SMALL ROOSTS



SINGLE LARGE ROOST

What has become apparent is the mechanism of roost formation. It is known that the roost begins to form near sundown but that the birds do not settle down until fairly late in the evening. It is possible to picture the act of stabilization occurring in concert with the increase in accommodation that results from the growing pockets of segregated species. The essence of roost formation is the growth of these pockets of calm in which the associated species finally gain some measure of insularity from the dominance of the grackles.

The interactions recorded within this study involve the establishment or retention of roosting perches, and may be thought of as a form of territoriality. Huxley (1934), in his description of the "elastic disc" and Krebs (1971), in his concept of the "invincible center" proposed that an individual, barring sickness or gross differences in size, is usually undefeatable by conspecifics at the center of its own territory. In the case of blackbird roosts, since each bird is defending a very small area indeed, one could assume that any proprietor would have a higher degree of success than any intruder.

In the Rich Square roost, the proprietor wins greatly outnumber intruder wins in intraspecific encounters indicating that proprietorism was operative. Thus even in the case of the grackles, it is probably the accommodation behavior that allows the roost to stabilize for without it intruders would continue to lose in their attempts to gain a perch from conspecifics.

Snub Behavior

Without some form of accommodation, the roost remains chaotic and unstable, with half of the birds on perches and the other half attempting to join them. It is possible for all birds to eventually gain a perch without accommodation, but it requires more space with larger distances between individuals. Generally, winter roosts do not occupy all of the apparently suitable habitat in an area, indicating some advantage in individual proximity.

The origins of "snub" behavior are not known but there are several obvious possibilities that should be considered. There is a similarity between the general posture of a bird exhibiting "snub" behavior and one exhibiting bill tipping, except for the motion of the head. It is possible that "snub" is at least in part a modification of this low intensity aggressive display through the processes of habituation or displacement.

Another possibility is what I call the individual stimulus horizon. Each proprietor is constantly bombarded with a rich and varied selection of visual stimuli provided by the many intruders that are moving above them. There must be conflict within the proprietor as to which stimuli should be responded to. This conflict could lead to a paralysis of the proprietor's response or in concentration on the most intense stimulus to the exclusion or ignorance of lesser stimuli. There may also be a level or angle below which stimuli are ignored in relation to those stimuli that are occurring above the "horizon". This would allow those intruders which are less stimulating to the proprietor to approach the proprietor

closely and actually land on the perch. Once the intruder has landed, the original proprietor may respond by continuing to concentrate on more intense visual stimuli above him while responding to the perching intruder with a modification of bill tipping ("snub") which allows the intruder to concentrate on the overhead stimulus.

Habituation to intruder stimuli might also play a role in accommodation but since there seems to be no change in the frequency of accommodation over time, it is not likely that it does. Undoubtedly, more research into the nature of accommodation is necessary in order to gain a better understanding of the nature and origins of this behavior.

Some Speculations on the Winter Roost

The fact that 4 species of birds can exist in close proximity for a season, have developed compatible behavioral repitoires and developed a means of accommodation that permits them to overcome their natural tendencies towards aggression warrants continued research into the nature of blackbird winter roosts. Perhaps more important to man is the increasing conflict that occurs when roosts coincide with human habitation. The chances of disease as well as aesthetic and ecological damage to areas valuable to humans only enhances the rationale for such research. To date, we have no data from which to develop control methods to reduce detrimental interactions between these birds and man. As a result, all methods for control have tended to be stopgap or more detrimental than the roosts themselves. We can no longer assume understanding of winter roost dynamics or the reasons that the roosts exist at all. This particular study has raised more questions than it

has answered, but we do know something more about how the roost forms and is held together. New avenues for research exist for the future. It is likely that a simple, successful, and cost effective means of control can be found with continued effort. To destroy the birds or the habitat is not the answer. To decrease the advantages gained by the birds, at least in areas close to human habitation, or the manipulation of behavioral patterns become more viable alternatives. If we can begin to learn more about the ecological and evolutionary facets of the problems in the process, so much the better.

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