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The Role of Predation in the Adaptive Value of Coloniality and Polygyny in the Yellow-headed Blackbird (Xanthocephalus xanthocephalus)

by

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A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science.

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ABSTRACT

The yellow-headed blackbird , *Xanthocephalus xanthocephalus*, is a polygynous, colonial, marsh-nesting passerine. The purpose of this study was to (1) determine the major selective forces limiting yellowhead nesting success, (2) study the anti-predator function of coloniality in yellowheads, and (3) examine the adaptive value of polygyny in this species.

For the population of yellowheads studied, predation was the most important source of nesting mortality, the cause of failure of 51% of all nests over a 2 year period. Further, it was discovered that the most important nest predator was the marsh wren, *Cistothorus palustris*. Yellowheads respond to the potential threat marsh wrens pose and aggressively exclude wrens from the vicinity of their territories, resulting in significantly segregated breeding grounds. Further, the yellowhead colony is significantly synchronized in nesting attempts, which may work to swamp predators.

Several hypotheses proposed to explain the anti-predator value of coloniality were tested. Spatial clumping by female yellowheads has the effect of reducing losses to predators. This probably functions through overlapping sub-territories which allows a more efficient active ~~nest~~ defense.

Predator swamping and dilution on their own do not reduce the impact of predators, but may act to maximize the effectiveness of an active nest defense. Nests in the center of the yellowhead colony enjoy a higher reproductive success through the geometric or selfish herd effects. It is suggested that coloniality in yellowheads may have evolved as a result of predation pressures firstly selecting for marsh-nesting, then predation pressures from marsh wrens which may have promoted reduced neighbor-neighbor distances in the marsh.

Two types of models proposed to explain polygyny, which are based on the nature of interactions between females, the competitive and co-operative female choice models, were tested. Early settling females show a preference for the colony center; male territories tend to be smaller in the center; and female density is greater while inter-nest distances are smaller in the center as compared to the periphery. Despite the decreasing male territory size in the colony center, the average harem size is larger in the center. These all support the idea that yellowheads are competitive to a certain degree. On the other hand, females actively clump their nesting attempts in space as well as time. This supports the idea that females settle co-operatively. Thus both the competitive and co-operative female choice models are compatible with the yellowhead breeding strategy.

GENERAL INTRODUCTION

Natural selection will operate on differences in reproductive success. Therefore an evolved reproductive strategy must be considered as one that has been molded by environmental pressures to maximize inclusive fitness. Specific reproductive traits will evolve that may reduce competition (either intra- or interspecific), improve food gathering abilities, reduce predation or parasitism, improve access to or selection of mates, or most likely some combination of the above.

The adaptive value of colonial nesting in birds has received much attention and a wide variety of hypotheses have been formulated (see Krebs 1978 for a review). However, few have been adequately tested, and little information is available which could allow us to identify which hypotheses are most appropriate for any given species. Generally speaking, coloniality will only evolve if the fitness of individuals within colonies is greater than that of individuals who choose not to be colonial. Selective pressures which render coloniality disadvantageous include: increased competition for resources (food, nest sites, mates etc.), increased conspicuousness of the colony to potential predators, greater opportunity for the transmission of disease and ectoparasites, and finally increased opportunity for interference with reproductive activities (intraspecific killing of offspring, cuckoldry, brood parasitism, and theft of nesting material: Alexander 1974; Hoogland and Sherman 1976; Wittenberger 1981). Alexander (1974) has proposed three evolutionary reasons which may favor coloniality. The first deals with reduced predation through improved anti-predator defense. The second is when food exploitation is maximized through group life. The last reason is simply that suitable breeding grounds are limited.

Mating patterns have also received considerable attention in the literature. Although polygyny in birds is quite rare, occurring in less than 10% of species (Lack 1966), it is perhaps the most heavily studied mating system (Skutch 1935; Verner 1964; Verner and Willson 1966; Orians 1969; Wittenberger 1976, 1979; Altmann et al. 1977; Weatherhead and Robertson 1979; Alatalo et al. 1981; Picman 1981; Lightbody and Weatherhead 1987a, in press). Yet few studies have provided sufficient evidence to support the many hypotheses proposed to explain the occurrence of this strategy and apply these to individual species. Many of these hypotheses are based on the concept of the polygyny threshold (Orians 1969), which proposes that polygyny is favored when a female's fitness in a polygynous mating is as good or better than her fitness resulting from a monogamous mating. In general, most models can be placed in one of two categories which depend upon the relationship between females (Altmann et al. 1977). The first category includes those models that assume females compete for resources that are disproportionately arranged among the male territories (competitive female choice models). The second category of models are those that assume that females obtain an advantage from the presence of other females (co-operative female choice models).

The yellow-headed blackbird (_Xanthocephalus xanthocephalus_), is a polygynous, colonial, marsh-nesting passerine. The occurrence of coloniality and of polygyny in this species have not been adequately addressed. Previous authors have concentrated on the relationship between food, its availability and the method of exploitation, to explain the observed reproductive pattern in the yellow-headed blackbird (Willson 1966; Orians 1980; Gori 1984). More recently, Lightbody and Weatherhead (1987a, 1987b, in press) have concentrated on the interactions between females, female settlement patterns, and mate choice to explain the mating pattern in yellow-headed blackbirds. However, because predation has been found to be a major limiting factor for passerines nesting in the marsh habitat (Ricklefs 1969), it must also be considered. The purpose of this study, therefore, is to determine the role that predation plays in limiting reproductive success in the yellow-headed blackbird (Chapter 1) and then to examine the role of nest predation in the adaptive value of coloniality (Chapter 2) and polygyny (Chapter 3) in this species.

CHAPTER 1

SOURCES OF NESTING MORTALITY AND CORRELATES OF NESTING SUCCESS IN THE YELLOW-HEADED BLACKBIRD

INTRODUCTION

The Yellow-headed blackbird (Xanthocephalus xanthocephalus), is a polygynous, colonial, marsh-nesting passerine. Its breeding range extends roughly through the central and western parts of North America (Orians 1980). For many altricial birds, the period of greatest mortality is the egg and nestling stages (Ricklefs 1969, 1973). For temperate marsh-nesting passerines, the greatest sources of this mortality are predation and nestling starvation (Orians 1961; Young 1963; Willson 1966; Robertson 1972, 1973; Patterson et al. 1980; Richter 1984; Bancroft 1986). It is, therefore, important to look at these sources of mortality in order to gain a better understanding of the observed reproductive pattern in yellowheads.

The purpose of this chapter is to examine the intensity and pattern of nest predation in a yellowhead colony in the Delta Marsh, Manitoba, and to establish which predators operate in this marsh, and their relative importance. Preliminary results suggested predation by marsh wrens (Cistothorus palustris) to be important. Thus I designed several additional studies to (1) specifically assess the impact of marsh wrens on yellowhead nesting success, and (2) establish if yellowheads recognize marsh wrens as a specific nest predator and respond aggressively to them. In addition, to determine the importance of the male territory as a food source to females, the location of foraging grounds for breeding yellowhead females is examined, and the overall foraging effort in these areas estimated. Finally, yellowhead nesting success is examined to determine which variables contribute to its variance.

GENERAL METHODS

General Breeding Information and Nesting Success

This study was conducted in an extensive fresh-water marsh bordering the south end of Lake Manitoba, at the University of Manitoba Field Station, Delta Marsh, between May 1 and mid July 1983, April 20 and July 1, 1984 and between May 20 and 28, 1987. The emergent vegetation of the study area (approximately 5 ha in 1983 and 7 ha in 1984) was dominated by cattail (Typha sp.), and reeds (Scirpus sp. and Phragmites sp.), in that order. The only abundant passerine species breeding in the study marsh were the yellow-headed blackbird and marsh wren. The study was concentrated on 2 yellowhead colonies in 1983 and 3 in 1984, which were separated by narrow strips of reeds. To facilitate the recording of spatial information, the study site was divided into 20 x 20 m quadrats and subsequently mapped. Territorial males were captured early in May using a decoy trap baited with an "intruding" male yellowhead, and were given a unique color band combination. Male territories were determined through observation of male movements, their territorial displays, singing locations, and interactions with neighbors and strange intruders.

In order to determine the importance of the male territory in providing food to females, the following study was undertaken. In 1984, between May 26 and June 13, 22 one hour time budgets for selected breeding females (22) were conducted. Eleven of these females were in the incubation stage, and the remaining 11 were in the nestling stage. Two of the incubating females were later excluded from the analysis because one had laid an egg during the observation period, and the other had an egg hatch. All time budgets were conducted between 06:30 and 11:30 hours. Activities of the females were divided into the following 5 categories:

1) time on the nest;
2) time foraging on the resident male's territory;
3) time foraging in the marsh;
4) time foraging off the marsh;
5) other (perched, preening, sexual chases, mobbing, chasing wrens, interacting with other females).

Bi-weekly searches of the marsh for nests provided the information on the breeding pattern and nesting success of yellow-headed blackbirds. When a new nest was found, a numbered label was attached to surrounding vegetation approximately 1 m from the nest, and its location in a given quadrat was recorded on the map of the study area. At this time, the following nest site characteristics were recorded: (1) water depth below the nest; (2) height of the nest above the floor of the marsh, measured from the top of the nest; (3) vegetation height from the floor of the marsh to the tops of the supporting vegetation; (4) the type of vegetation used for nest support; and (5) vegetation density at the nest. The vegetation density was estimated using a 50 cm long stick with 20 evenly spaced bright red spots (1 cm diameter). This stick was placed on top of the nest and the number of unobstructed dots was counted from a 2 m distance. During these checks, the nest contents of all nests were examined and recorded. A nest was considered active only once a clutch was initiated. If a nest failed, the nest area was examined for possible causes of nesting failure. If a nest lost its eggs or nestlings, it was considered to have been destroyed by a predator. Most often the depredated nests contained egg shell fragments, dried egg contents or dried blood (in some instances these were also found on the nearby vegetation), punctured eggs or dead young with various signs of injuries, or some combination of the above. Nests in which incubation or brooding was discontinued, but with nest contents undisturbed, were all considered to have been abandoned. Other reasons for nesting failure included infertile eggs, nestling starvation, or poorly constructed nests which resulted in the nest contents eventually falling into the water. Finally, those nests that fledged at least 1 young were considered to have been successful.

Recording of Nest Predators Using a Camera Setup

In 1987, 11 camera setups, which photograph the manipulator of a quail (Coturnix coturnix) egg placed in an artificial nest on a trigger (Picman 1987), were placed in the marsh. These setups were distributed along a transect throughout the yellowhead colony for a period of 5 days. Because no predation occurred during this time, the camera setups with nests were placed outside the yellowhead colony (along the edge of the marsh), where marsh wrens were defending their territories, for an additional 2 days. These setups were checked twice a day and if a predation event had occurred, the camera was reset and if necessary a new egg was used.

The Impact of Marsh Wrens Relative to Other Predators

An experimental study of the effect of the spatial distribution of experimental nests on predation patterns, conducted in 1984 (see Chapter 2), offered the opportunity to also assess the impact marsh wrens have on the nesting success of yellowheads and compare it to that of the other predators. In this experiment, 160 yellowhead nests were placed in a marsh where the breeding yellowheads were forced to abandon nesting activities. One yellowhead egg and 1 quail egg were placed in every other nest, while the remaining nests contained 2 yellowhead eggs. Nests were examined for predation 1, 3, 6 and 9 days after the eggs were put out. In addition, 3 transects of a total of 31 experimental yellowhead nests were simultaneously established 10 m apart in an active yellowhead colony. All experimental nests contained 1 yellowhead egg and 1 quail egg, and were examined for predation 1, 3, 6 and 9 days after establishment. For a more detailed description of the methodology, see the methods section in Chapter 2.

Since marsh wrens are rarely able to puncture and destroy quail eggs (Picman 1977, personal observation), experimental nests in which the quail egg was intact, or had small peck holes the size of a marsh wren bill, but from which the yellowhead egg disappeared or was found with various amounts of damage, can only be considered as having been depredated by a marsh wren. Since both types of eggs were collected fresh and were refrigerated for no longer than a week before being used in this experiment, it is unlikely that predators would prefer one egg type over the other.

Response of Yellowheads to Marsh Wren Songs

The response of male and female yellowheads to marsh wren songs was examined through playback experiments. Ten active yellowhead nests were chosen at random in the study area in 1983 and were played 10 minutes of marsh wren songs after a 10 minute pre-playback period of silence. The pre-playbacks began once the local birds resumed normal activities after the intrusion of the observer. As a control experiment, 5 of these nests (randomly chosen) were also played 10 minutes of the common yellowthroat's (Geothlypis trichas) repertoire, again after a 10 minute pre-playback period. These controls were conducted randomly either 1 day before (N=2), or 1 day after (N=3) the experimental trials. All the playbacks were conducted between 0600 and 1100 hours, and none were conducted during inclement weather.

The playback experiments were conducted by placing a speaker on a 2 m high stake, 3 meters from an active yellowhead nest. The observer could control the playback recordings using a portable cassette recorder wired to the speaker at a 20 m distance. Responses of the yellowheads were scored as follows:

0- no response;
1- fly nearby to speaker, but no closer than 3 m, alert;
2- approach speaker from one to 3 m away, agitated;
3- approach speaker less than 1 m away, sometimes hovering over speaker, agitated.

Correlates of Nesting Success

Because nesting success is a binary variable (failed or successful), a BMDP program for a stepwise logistic regression (Dixon 1985) was used to determine the correlates of nesting success. Twenty-two independent variables were originally entered. However, because of inter-correlations and missing values, the final analysis included eleven independent variables. These included distance to the nearest marsh wren nest, harem size, distance to the edge of the colony, distance to open water, water depth at the nest, nest height, relative vegetation density at the nest, vegetation height at the nest, the date the nest received its first egg, the distance to the nearest neighbor, and location within the colony (center vs the periphery, as defined in Chapter 2). The statistical significance was set at $p= 0.05$ level. All nests were included in this analysis.

RESULTS

General Breeding Information

The first male yellowheads arrived onto the marsh in late April (April 20 in 1984) while the first females began arriving in early May (May 4 in 1984). Males established territories in the deeper regions of the marsh, near open water, where they eventually attracted up to 7 females. Most territories were established in cattail-dominated areas of the marsh, and few males defended areas dominated by reeds which are normally associated with the drier regions of the marsh.

Forty-two of a total of 67 territorial males were captured and color banded in 1983. In 1984, in the same area, there were 65 territorial males of which 51 were banded (18 were returning males which were banded in 1983 and 33 were new unbanded males). The third colony, studied only in 1984, included 24 territorial males, none of which were banded. Once males are established in a marsh on a territory, they tend to return to the same marsh and usually to the same territory, or tend to settle very close to their previous territory (unpubl. data). By late June, dispersion from the breeding grounds has already begun, and flocks of feeding birds become prominent outside of the marsh.

Females solely undertake nest building (usually 2 to 3 days) with the first females initiating their nests in the second week of

May. Most nests (82%) were built in cattail and only a small number (6%) were located in bulrush exclusively or different mixtures of cattail, bulrush, and phragmites (12%). Clutch initiation began mid May and the peak of laying the first egg was on May 25 and May 26 in 1983 and 1984, respectively. The number of eggs in a clutch varied from 1 to 5, with most having 3 or 4 eggs. Females alone incubate, and incubation normally requires about 12 days after the second egg is laid. A summary of the mean measure of 4 nest site features is given in Table 1. A between year comparison by means of a t-test, revealed highly significant differences for all 4 nest features measured.

In general, females are highly synchronous in their nesting activities with approximately 60% of clutch initiations occurring within a 5 day period (Figure 1). Females are single brooded, with some re-nesting occurring if a first attempt fails early in the cycle. Inter-nest distances for simultaneously active nearest neighbors varied from 2 to 33 m, and averaged 6.0 m in 1983, and 6.2 m in 1984.

Females feed the young during the nestling stages which normally lasts 12 days. Brooding females spend on average more than 2 times as much time foraging as do incubating females (see Table 2). Most foraging activity for both groups of females was done outside of the marsh (Table 2). Further, the vast majority of these trips were in the direction of a forested dune ridge which separates Lake Manitoba from the marsh, where in fact many adult yellowheads were commonly seen foraging (unpubl. data). This ridge was characterized by its frequent outbreaks of midge (Chironomidae) mating swarms, which provided a superabundant food source to the local insectivorous community. Feeding of young by males was observed in only 7 out of 67 territorial males in 1983.

Nesting Success

In the 2 years of this study, 447 active nests were studied. Of these, 229 (51%) eventually failed due to predation, 182 (41%) fledged at least 1 young and the remaining 36 (8%) were abandoned or failed for other reasons (Table 3). Of the 229 nests which were depredated, 143 (62%) failed during egg stages, and the remaining 86 (38%) failed while containing nestlings.

Which Predators Destroy Yellowhead Nests?

Throughout the 2 years of the study, there were 3 observed cases of nest depredation by a longtail weasel (Mustela frenata), with 6 additional cases where a weasel or some other small mammal was likely responsible. There were also 5 cases when nests were pulled down probably by a larger mammalian predator such as mink (Mustela vison). Finally, there were 48 cases where marsh wrens were either seen leaving a recently depredated nest with punctured eggs, or, were observed singing nearby.

Results from the study during which camera setups were placed around a yellowhead colony in May 1987, indicate that in all 26 cases when a camera was triggered, marsh wrens were responsible.

Assessing the Relative Level of Marsh Wren Depredation as Compared to Other Predators

The establishment of experimental yellowhead colonies with nests containing quail and yellowhead eggs provided the opportunity to assess the relative impact of marsh wrens on yellowhead reproductive success. Out of 80 nests in the artificial colonies with a mixed clutch, 64 (80%) were depredated within 6 days. Sixty-three (98%) of these were considered as to have been depredated by marsh wrens. Similarly, out of 31 nests set out in transects through an active yellowhead colony, 26 (84%) were destroyed by day 9, and 25 (96%) of these were considered as marsh wren depredation.

Indirect evidence of the impact marsh wrens have on yellowhead reproductive success was obtained by relating the distance to the nearest marsh wren nest and the nesting success of yellowhead nests (Table 4). A significant positive correlation emerges for both 1983 and 1984, indicating that yellowhead nesting success decreases with decreasing distance to marsh wrens.

Playbacks

The playback of empty tape did not elicit any response for both the control and experimental categories. The playbacks of the yellowthroat songs (to the control group) also failed to elicit any response from the yellowheads. However, the marsh wren song playbacks elicited aggressive responses from all 10 females and all but 1 male.

Correlates of Nesting Success

Results of the stepwise logistic regression analysis of nesting success against 11 independent variables revealed that, in 1983, distance to the edge of the colony was the only variable entered into the equation ($b=0.059$, $x^2=16.7$, $d.f.=1$, $p<0.001$). The farther a nest was from the edge, the greater the chance that it would survive until fledging. In 1984, the date of clutch initiation ($b=-0.128$, $x^2=27.1$, $d.f.=1$, $p<0.001$), and the distance to the nearest marsh wren nest ($b=0.033$, $x^2=4.3$, $d.f.=1$, $p=0.039$) were the only variables entered into the equation. The greater the distance from marsh wrens, the higher were the chances of nesting success for yellowheads, and the earlier clutch initiation begins, the greater were the chances of success.

DISCUSSION

For this population of yellowheads, predation is the most important source of nesting mortality, accounting for 86% of all nesting failures, and is the cause of failure for 51% of all active nests during the 2 years of this study. Starvation did account for some losses (0.5%) mostly through brood reduction, but in general, food did not appear to be a major limiting factor. Females fed most frequently on a forested dune ridge, where an abundant food source of midges could be found. Further, only 10.5% of males in 1983 were observed feeding nestlings, which is consistent with the observations of Roberts (1909) and Fautin (1941). On the other hand, both Willson (1966) and Gori (1984) have reported frequent feeding of young by males. But in Willson's marsh, starvation was a major cause of nestling mortality and Gori reported that, in general, paternal investment in feeding nestlings is greater in unproductive marshes. Therefore, variation in male feeding of nestlings may in part be related to differences between these studies in food abundance.

Marsh wrens have been identified by other authors as nest predators for both yellow-headed and red-winged blackbirds, Agelaius phoeniceus (Orians and Willson 1964; Burt 1970; Verner 1975; Picman 1977, 1980, 1987; Bump 1983; Ritschel 1985). Picman (1977, 1980, 1987), Bump (1983), and Ritschel (1985) considered marsh wrens as the most important predator operating in their marshes. For this population of yellowheads, marsh wrens are also the most important predator accounting for most cases of nest depredation. Further, indirect evidence from a study of predation patterns on experimental nests, with predation rates of over 80% of all nests, point to marsh wrens which appear to be responsible for the majority, if not all cases of nest failure.

Finally, in addition to the indirect evidence of marsh wren predation, I was also able to obtain photographs of marsh wrens in the act of preying on baited nests, with a camera set-up as described in Picman (1987). In this experiment, the marsh wren was the only predator photographed.

Results of the playback experiments are consistent with the finding that the marsh wren is an important yellowhead nest predator at Delta Marsh. Both male (with 1 exception) and female yellowheads responded consistently in an aggressive manner to the playbacks of marsh wren songs, but failed to respond to playbacks of yellowthroat songs. The yellowthroat is another marsh-nesting passerine, present but not abundant at Delta Marsh, and not known to be a threat to yellowhead reproductive success. This result is similar to the findings of Bump (1983) and suggests that yellowheads recognize marsh wrens as a potential danger. Presumably more aggressive responses could have been elicited from the yellowheads if a visual cue of a marsh wren had been used in addition to the playback of the wren song (Bump 1983). Nonetheless, naturally occurring agonistic interactions between yellowheads and marsh wrens have been well documented (Verner 1975; Bump 1983; Leonard and Picman 1986). Typically adult yellowheads chase nearby wrens (usually singing males) from their perches down into the vegetation, and would either continue the chase in the vegetation, or simply perch above the wrens.

Given that predation is the most important nest mortality factor for yellowheads, and given that marsh wrens and other predators must enter the breeding blackbird colony from the edge, it is no surprise that those nests located closer to, or at the edge of the colony, suffered a higher rate of nesting failure due to predation in one year. Similarly, nesting success is positively correlated with the distance to the nearest marsh wren nest in the other year, and both distance to the edge of the colony, and distance to marsh wrens are significantly inter-correlated in both years. Yellowheads should thus preferentially nest as far as possible from marsh wrens, to reduce the impact of their nest-destroying behavior.

In one year, females nesting earlier suffered on average a lower rate of depredation. This can be explained in at least 2 different ways. First, earlier nesters are often older, more experienced females (Coulson and White 1958; Crawford 1977), who are likely to choose safer nesting sites, and to be more experienced in defending their nests against potential predators (i.e. be more effective in excluding marsh wrens from the immediate vicinity of the nest). Second, since yellowheads are highly synchronous in their nesting activities (Figure 1), early nesters could potentially maximize the benefit from predator satiation and dilution effects, as well as increased group vigilance and predator mobbing during the period of highest vulnerability to marsh wren predation (egg and early nestling stages).

High predation pressures are well documented for temperate zone marsh-nesting passerines (Ricklefs 1969). For many marsh-nesting blackbirds, predation is considered to be an important source of egg and nestling mortality (Orians 1961, 1973, 1980; Willson 1966; Robertson 1972, 1973; Holm 1973; Caccamise 1976; Picman 1980, Picman et al. 1988; Bancroft 1986), and this population of yellowheads is certainly no exception. Selection should, therefore, act on yellowheads to minimize nest predation.

Gregarious nesting, common to many marsh-nesting blackbirds, may reduce predation through group vigilance and mobbing, predator dilution and satiation effects, and through crowding into the center of a colony (geometric effects). The importance of these adaptations for this population of yellowheads is examined in Chapter 2.

CHAPTER TWO

THE ANTI-PREDATOR VALUE OF COLONIAL NESTING IN THE YELLOW-HEADED BLACKBIRD

INTRODUCTION

Alexander (1974) has proposed that, in general, group living may be favoured by one or more of the three following situations:

1- when group life minimizes predation losses through improved anti-predator defense;
2- when exploitation of food resources is maximized through cooperation (information transfer);
3- when suitable breeding grounds are highly restricted.

Gori (1984) has tested whether yellowhead breeding colonies act as information centers by 1) analyzing the timing and identity of colony departures for evidence of statistical non-randomness, and 2) observing the rate and pattern of bird recruitment to an experimental foraging area for evidence of exchange of information about the location of rich food patches. He found that yellowhead colonies can act as information centers. Horn (1968) has also suggested that coloniality is adaptive in the Brewer's blackbird (<u>Euphagus cyanocephalus</u>) because it enhances individual food exploitation. For the Delta Marsh population of yellowheads, food does not appear to be a major limiting factor (Chapter 1), and it is therefore unlikely that this population of yellowheads acts as an information center.

Wittenberger (1976, 1979) has argued that high breeding densities of red-winged and yellow-headed blackbirds in marshes are due to a limited availability of marshes as compared to the population size. This explanation seems unlikely for the local population of yellowheads. The Delta Marsh spans over 20,000 hectares, much of which appear to be equally suitable habitat to those few areas which are colonized: deeper portions of marsh dominated by cattail with areas of open water. But perhaps food varies among these locations, thus making certain areas more desirable because of a better food supply. This also seems doubtful since a very small amount of time spent foraging by both incubating and brooding females is spent in the marsh (Chapter 1). The most convincing evidence for suitable nest site shortages, as an explanation for coloniality, can be found in studies of marine birds (e.g., Nelson 1970; Ashmole 1971).

The third situation that could favour group living, the advantages of group life with respect to predation, is an aspect of yellowhead coloniality that so far has not been examined. Given that predation is a major limiting factor to yellowhead reproductive success (Chapter 1), it would be premature to make generalizations about the adaptive value of coloniality in this species, without further study of its anti-predator value.

The Anti-Predator Value of Colonial Nesting

In general, groups of animals should be more easily detected by predators than solitary individuals (Cullen 1960). Further, once one nest is found, a predator may take advantage of the close proximity of others (Kruuk 1964). But if coloniality is adaptive in its reduction of predation pressures, its anti-predator advantages must outweigh this major disadvantage.

One advantage associated with group living is the enhanced predator detection when there are more vigilant individuals (Pulliam 1973; Hoogland and Sherman 1976; Kenward 1978). Added to this is a reduction of the amount of time spent on the lookout, per individual, as group size increases, thereby leaving more time for other important behaviors such as feeding or courtship (Powell 1974; Siegfried and Underhill 1975; Hoogland 1979).

Associated with predator detection is the alarm call. This behavior can facilitate a quicker response by the group when faced with a dangerous situation. The alarm call may also result in another group benefit: an active group defense such as predator mobbing, which can direct the predator's attention away from the caller or callers (Charnov and Krebs 1975; Owens and Goss-Custard 1976).

Mobbing increases the probability of deterring a predator and is likely to become more effective as the group size increases and therefore as the potential mob size increases (Hoogland and Sherman

1976). The real impact the mob may have on a predator depends largely on the predator size and vulnerability to the mobbers, as well as its mode of attack. Horn (1968) found that Brewer's blackbirds were very efficient in deterring flying birds, mainly ring-billed gulls (Larus delawarensis) through active mobbing. However, he suggested that they could not drive away snakes, mammals, or perched birds. But mobbing may act as a distraction display, luring a predator away from a nest, or may even have a confusing effect on the predator, reducing its effectiveness at finding nests.

The spatial and temporal distribution of nesting attempts in a colony may also confer some reduction in predation pressures, by its swamping effect on predators. Each individual in the colony would have less of a chance of becoming the victim once the group is discovered, than if it were discovered solitarily. This is commonly known as predator satiation and dilution effects (Holling 1959; Pulliam and Caraco 1984). The chances of the group being discovered presumably increase with group size, however, this probability is unlikely to be directly proportional to the group size. Further, the predator may reach its satiation point far before all potential prey are discovered (Hoogland and Sherman 1976). Finally, certain locations within the colony may be less vulnerable than others, the center being more protected, and thus safer than the perimeter (Tenaza 1971; Hoogland and Sherman 1976). This is commonly known as geometric or selfish herd effects (Hamilton 1971).

The most important yellowhead nest predator, at least in Delta

Marsh, is the marsh wren (Chapter 1). Because the nest predation pattern is very simple (i.e. there is only one major predator) and predators' activities may be temporally and spatially predictable, specific anti-predator adaptations could easily evolve. The purpose of this chapter is to test the following hypotheses about the anti-predator role of coloniality, when marsh wrens are considered to be the major predator:

(1) By breeding in close proximity to one another, females may improve anti-predator defense through co-operation with their neighbors, in detection and mobbing of predators;
(2) Colonial nesting may lower the impact of predators through predator satiation and dilution effects;
(3) By breeding in the center of a colony, females may improve their success through geometric effects.

If hypothesis 1 is valid, then the following predictions should hold true: a) Marsh wrens should be forced to breed outside the main colony areas as long as yellowheads are actively breeding; b) Yellowheads with more conspecific neighbors should be more successful in nesting than those with few neighbors. This could be tested by introducing experimental nests near and away from active yellowhead nests. Further, the success of experimentally introduced nests, should increase with increasing density of nearby breeding yellowheads.

If hypothesis 2 is correct, then densely packed colonies should have greater success than sparsely spaced colonies. This can be tested by creating artificial colonies where experimental nests are placed very close to one another and comparing their success to artificial colonies where the nests are placed farther apart.

Finally, if hypothesis 3 is true, then females breeding in the center of an active yellowhead colony should enjoy a higher nesting success than those breeding at the periphery of the colony.

METHODS

Predator Detection and Deterrence

General field observations of responses of yellowheads to various potential predators were made during nest checks, nest watches, experiments, and while mapping male territorial boundaries. These observations were usually of a qualitative nature.

Spatial Segregation Between Marsh Wrens and Yellowheads

Observations of interactions between wrens and yellowheads were made during ongoing studies and experiments. To determine whether wrens and yellowheads were segregated with respect to their breeding areas, the presence or absence of nests of both species was recorded for 10 x 10 m quadrats covering habitable habitat in the study area. Four possible situations arose for any given quadrat: no nests of either species; 1 or more wren nests and no yellowhead nests; 1 or more yellowhead nests and no wren nests; nests of both species present. A chi-square test was used to determine if nest locations for wrens and yellowheads were significantly segregated.

Temporal Synchrony in Female Settlement

To determine the pattern of distribution of female settlement with time, the following test was performed. Nests were divided into categories of date of nest initiation, each representing a period of 1 day, excluding nests initiated after 3 June for both years, to eliminate re-nests. Because the date of first egg laid, and the date of female settlement on ~~a~~ territory are highly correlated (Lightbody and Weatherhead 1987b), the date of first egg was used as an indicator of female settlement. The observed distribution was compared to the expected Poisson (random) distribution (based on the observed mean) using a chi-square goodness of fit test. Next, a population variance (s^2) was calculated for the distribution of actual nest initiations. If: $s^2/x = 1$ (x = mean number of nests initiated per day), then the distribution is random; $s^2/x < 1$, then the distribution is uniform; $s^2/x > 1$, then the distribution is clumped (Smith 1980).

Marsh Wren Satiation Experiment

To assess whether or not there is an upper limit to the abilities of marsh wrens at destroying nests with eggs, 2 wrens were each offered 15 artificial nests constructed of grass resembling the redwing nest, which contained two quail eggs that had been soaked in a 20% acetic acid solution for 10 minutes then thoroughly washed in running water (after this treatment marsh wrens can break quail eggs).

Nests were attached to clumps of cattail, and located 2 m apart along 3 transects throughout the wren territories. These nests were then monitored for predation 2, 4, 19 and 24 hours after being set-up, at which time the condition of the eggs was carefully noted.

The Effect of Nest Density on the Survival of Experimental Nests

In 1984, in an area where yellowheads had begun to breed, 13 of 21 territorial males and all active nests were removed during a 2 day period (May 31 and June 1). Then, on June 4, 160 experimental yellowhead nests (nests collected in the experimental area as well as elsewhere) were placed throughout the experimental area in 2 groups of 40 nests, each with an inter-nest distance of 5 m (i.e. high density colonies) and another 2 groups of 40 nests, each with an inter-nest distance of 15 m (i.e. low density colonies). These groups of nests were alternated in placement as shown in Figure 2. The following day, 1 yellowhead egg and 1 quail egg were placed in every other nest, and in the remaining nests, 2 yellowhead eggs were placed (see Chapter 1 for an explanation of why this mixed clutch was used). Since both types of eggs were collected fresh and were refrigerated for no longer than a week before being used in this experiment, it is unlikely that predators would prefer one egg type over another. Finally, the experimental nests were examined for predation 1, 3, 6 and 9 days after the eggs were put out.

As a control for this experiment, 3 transects of a total of 31 experimental yellowhead nests were simultaneously established on June 4, 1984, in an active yellowhead colony. These transects were placed 40 m apart and the experimental nests placed along these transects at 10 m intervals. All nests along the 3 transects contained 1 yellowhead egg and 1 quail egg, and were examined for predation 1, 3, 6 and 9 days after establishment.

The Effect of Female Density on the Survival of Experimental Nests

Forty experimental yellowhead nests with 2 yellowhead eggs each (collected outside the study area), were placed throughout an active yellowhead colony under study. Ten nests were placed in each of the 4 following situations of local active yellowhead nest density:

(1) no active yellowhead nest within 10 m;
(2) 1 active yellowhead nest within 10 m;
(3) 2 active yellowhead nests within 10 m;
(4) 3 active yellowhead nests within 10 m.

For all experimentally introduced nests, the distance to the nearest marsh wren nest was kept between 20 and 30 m. The experimental nests were examined for predation 1, 3, 6 and 9 days after the initiation of the experiment.

Geometric Effects

To study the effect of location in the colony on the nesting success of yellowheads, male territories were divided into two different groups; those that formed the outer perimeter of the breeding colony and those that were buffered from the outside of the colony by at least 1 other male territory. The first group of territories was termed peripheral, and the second group as central territories. All nests contained within these territories were likewise named either peripheral or central nests and compared for differences in nesting success. To determine if there are any inherent physical differences between central and peripheral nests that may reflect differences in habitat suitability with regard to predation, four nest site features (nest height, vegetation height, water depth, and relative vegetation density) were compared by a t-test. In addition, five other nest features which might explain differences in nesting success between central and peripheral nests were compared (distance to the nearest marsh wren nest, distance to the edge of the colony, date of clutch initiation, stage of nesting at which depredated nests failed, and the number of eggs laid).

RESULTS

Predator Detection and Deterrance

In this study area, there were many opportunities to observe responses of the yellowhead colony to a variety of potential avian predators; the Northern Harrier (Circus cyaneus), the Great Horned Owl (Bubo virginianus), the Great Grey Owl (Strix nebulosa), the Short-Eared Owl (Asio flammeus), the American Crow (Corvus brachyrhynchos), the Blue Jay (Cyanocitta cristata), the Great Blue Heron (Ardea herodias), and the American Bittern (Botaurus lentiginosus). In general, these birds were detected very quickly, eliciting a general alarm call throughout the colony. In addition, intensive mobbing from both male and female yellowheads, in the general region of the intruder, usually resulted in its rapid departure from the area. On rare occasions an owl might land and perch near the colony. Although the blackbirds seemed quite effective in mobbing a flying owl, once it was perched many blackbirds ceased mobbing and only those nesting nearby remained agitated but ineffectual in driving the perched predator away.

In general, mobbing intensity seemed to increase with increasing breeding activity, and slowly subsided towards the end of the breeding period (pers. obs.). The only observed cases of depredation by a large aerial predator occurred in late June 1984, when on 3 occasions a Northern Harrier was seen leaving the study area with a yellowhead fledgling in its talons. This was at a time when the majority of colony members had dispersed and only a few late breeders remained.

Terrestrial and semi-aquatic predators observed near or in the study area include mink (Mustela vison), the longtail weasel (Mustela frenata) and the striped skunk (Mephitis mephitis). In 1 observed case of a weasel preying on yellowhead nestlings in at least 2 nests, mobbing did occur but did not apparently deter the predator. The only other sighting of a weasel occured when this predator was seen leaving a nest in which the eggs had been freshly depredated. In this case no adult yellowheads were nearby and no alarm calls or mobbing occurred, but this was not surprising since the nest was rather isolated from the main part of the colony (i.e. the nest was located in a drier area dominated by Phragmites). The only sighting of a mink occurred in an open water pool, near where a nest on the water's edge was later found torn down and depredated. Minks have been observed by others as nest predators of blackbirds (Knight et al 1985; Picman, pers. comm.).

The only other known nest predator is the marsh wren, which is known to destroy yellowhead eggs (Willson 1966; Burt 1970; Verner 1975; Bump 1983; this study). Marsh wrens can also kill or seriously injure small blackbird nestlings up to several days old (Picman 1977; unpubl. data). Marsh wrens breed in close proximity to yellowheads in Delta Marsh and have an important negative effect on yellowhead reproductive success (Chapter 1). Yellowheads are exposed to marsh wrens on a regular basis and they don't respond to nearby wrens with alarm calls and or mobbing. Individual yellowheads will however chase very effectively nearby wrens away from their nests and territories. In fact, on several occasions, female yellowheads were observed guarding their nesting areas by perching in cattail between the colony edge and the nearest marsh wren nests, from where they would chase approaching wrens. However, marsh wrens (especially females) are cryptic and will move about low in the vegetation, often without detection by yellowheads. Nonetheless, there are other potential benefits of group life that could further reduce the impact of wrens.

Spatial Segregation Between Marsh Wrens and Yellowheads

Yellowheads exhibit a high level of aggression towards marsh wrens as shown by observations of agonistic interactions in this study and Orians and Willson (1964), Burt (1970), Verner (1975), Bump (1983), and Leonard and Picman (1986). In addition, yellowheads will aggressively approach speakers used in marsh wren song playback experiments (Bump 1983 and this study). Presumably as a result of these behavioral interactions, the nesting sites of these 2 species are significantly spatially segregated (Table 5). This is supported by the observation that following the yellowhead departure late in June, marsh wrens expanded their territories into the yellowhead breeding areas (Leonard and Picman 1986). As well, in an experiment where male yellowheads were removed and females were forced to abandon their nests, the surrounding population of male marsh wrens quickly expanded their territories to include much of the newly vacated areas

(Leonard and Picman 1986).

Synchrony in Female Settlement

The pattern of nest initiation dates was significantly non-random in both years. When the population variance (s^2) is analyzed, the results indicate a clumped distribution in both 1983 ($s^2/x=17.09$, $x^2=96.99$, d.f.=12, $p<0.0001$) and 1984 ($s^2/x=5.38$, $x^2=34.83$, d.f.=12, $p<0.001$).

Marsh Wren Satiation

In 1987, two neighboring male marsh wrens were offered 15 nests with 2 quail eggs each. After 2 hours, 2/3 of these nests had at least one of the 2 eggs destroyed and after 24 hours all nests had been attacked (Table 6). The majority of eggs had small peck holes and as the experiment proceeded, these holes were enlarged until eventually many of the eggs were completly destroyed.

Nest Density

A comparison of the predation rate on experimental nests placed in high and low densities in an area of yellowhead removal revealed that nests placed in closer proximity suffered slightly less than those that were more dispersed (this difference was significant on day 3 only; Table 7). Thus, in the absence of an active nest defense behavior, higher nest density is not particularly advantageous. Further, the generally high rates of predation suggest that the predators operating in this marsh are essentially insatiable. The most likely predator, given the overwhelming preferential selection of yellowhead eggs over quail eggs (63 out of 64 cases), is the marsh wren (see Chapter 1). It is not surprising that the wrens capitalized on the absence of adult yellowheads and managed to discover and destroy 81.9% of all experimental nests within 6 days.

Transects Through an Active Yellowhead Colony

Of the nests placed along 3 transects through an active yellowhead colony, nests placed at the extremities of the transects were destroyed most quickly (Figure 3). These nests were closest to marsh wren nests and farthest from active yellowhead nests. Further, yellowhead eggs were preferentially destroyed over quail eggs (25 (96%) yellowhead vs 1 (4%) quail), strongly suggesting marsh wren activity. When compared to the experimental colonies established in an area of yellowhead removal (see previous section), predation on experimental nests placed near yellowhead nests was delayed, although most nests were eventually destroyed (Figure 3 and Table 8).

The Effects of Female Density on the Survival of Experimental Nests

As the local density of active yellowhead nests increased, predation rates on nearby experimentally introduced nests decreased (Table 9). This trend was evident throughout the duration of the experiment and was statistically significant. Since the distance to marsh wrens in all cases was kept at between 20 and 30 m, any bias due to the proximity of wrens was minimized.

Geometric Effects

A comparison of nests that were located in male territories that formed the periphery of the colony, with nests in centrally located territories, revealed that peripheral nests suffered significantly higher predation in both 1983 and 1984 (Table 10). A comparison of 4 nest site features, which reflect quality of nesting sites with respect to predation, revealed no significant difference between centrally and peripherally located nests (Table 11). Thus the difference in nesting success between peripheral and central nests cannot be explained by differences in physical features of nesting sites alone. However, an analysis of 5 other variables (distance to the nearest marsh wren nest, distance to the edge of the colony, date of clutch initiation, stage of nesting at which depredated nests failed, and the number of eggs laid) revealed significant differences between central and peripheral nests, in all but one variable (Table 12). Central nests were located farther from marsh wrens as well as the edge of the colony, failed in later stages of nesting, and contained larger clutches. Finally, the central nests were also initiated on average 1 day earlier than peripheral nests, however this difference was not significant (Table 12).

DISCUSSION

These results suggest that a yellowhead colony is quite effectual in deterring most large aerial predators, but perhaps only during the most active parts of the breeding season and before colony dispersion has proceeded too far. This is consistent with the result of the multiple logistic regression analysis (see Chapter 1), which in 1984 revealed that the most successful females were in part those who initiated nesting early, thus coinciding more closely with the peak of breeding activities. Synchrony could act to reduce predation by increasing the efficiency of communal mobbing by birds at the same stage of nesting (Patterson 1965) and/or through Hamilton's (1971) selfish herd effect.

However, yellowheads probably have very little chance of effectively deterring most mammalian predators once a nest is found, but may reduce overall impact through predator confusion and distraction, or through predator satiation or dilution effects. However, the predation pattern exhibited in the experimental nest studies (see Chapter 1) suggests that, in general, mammalian predation occurs at generally low levels in this marsh. Therefore mammalian predation may not pose a consistently strong pressure to influence the yellowhead reproductive strategy, other than favoring breeding in deep water marshes.

As for reducing marsh wren predation pressures, yellowheads aggressively exclude wrens and this evidently results in the spatial segregation of their breeding areas. The spatial segregation of yellowhead and marsh wren nesting areas has also been observed in other geographic regions (Orians and Willson 1964; Burt 1970; Verner 1975). But this in itself is clearly insufficient, since wrens can penetrate yellowhead territories often without detection.

Temporal synchrony and spatial clumping are two possible mechanisms through which colonial species can reduce predation. In the first case, prey animals can periodically swamp predators, which cannot fully exploit extreme fluctuations in prey abundance. In the second case, if predators remain dispersed, then spatial clumping can have a similar effect to temporal synchrony.

Yellowhead females initiate nesting highly synchronously and this temporal clumping is highly statistically significant. However, as was shown in the nest presentation experiment (Table 6), marsh wrens are virtually insatiable in their egg destroying capacity, and therefore temporal synchrony on its own is not effective in reducing predation caused by this predator. Spatial clumping by itself is also ineffectual in reducing predation, as was shown when experimental nests were placed in colonies of high and low densities with perfect temporal synchrony. These two situations differ very little in terms of losses to predators. Therefore, the dilution principle (whether spatial or temporal) on its own is untenable. Predator swamping may, however, be effective against mammalian predators, but cannot be validated with these results. But in the presence of an active nest defense, temporal synchrony and spatial clumping can have indirect benefits. The close proximity of nests that are synchronized could, for example, maximize both predator detection and deterrence.

An obvious strategy for avoiding predation in colonial or gregarious species is to remain in the center of the group or colony. For yellowheads, this holds true since centrally located nests are less likely to be depredated than peripheral nests (Table 10). Ritschel (1985) has also found geometric effects to be important in the reduction of predation on redwing nests. But the mechanism behind this effect is poorly understood.

The habitat is essentially homogeneous throughout the yellowhead breeding colony (Table 7), however the central regions do differ from peripheral areas in two important ways (Table 8). First, marsh wrens and the edge of the marsh are both farther from central nests, thus rendering these nests less vulnerable to both mammalian predators entering the marsh, and marsh wrens nesting around the colony. This is supported also by the result that as compared to peripheral nests, the depredated central nests are destroyed in the later stages of nesting (Table 8), suggesting an overall lower or delayed predation in the center. Second, central nests had on average larger clutches, which may indicate that either the females nesting in the center are older and/or more experienced, or that the females nesting there benefit from the closer proximity of neighbors via an improved nest defense, thus allowing for more foraging time which could lead to larger clutches.

If older females are nesting preferably in the center of the colony, then the central nests should be initiated earlier than peripheral nests, assuming that older females initiate nesting earlier (Crawford 1977). The central nests were initiated on average one day earlier than peripheral nests, but the difference was not significant (Table 12). But given the extreme synchrony in breeding, a one day difference may be important. Additional work is necessary for a more complete understanding of why centrally located females lay larger clutches.

The idea that neighboring females benefit from one another's presence, through overlaping sub-territories, is supported by reduced predation on experimental nests placed along three transects through an active yellowhead colony, compared to nests placed in an area where yellowheads were essentially absent. Here, experimental nests enjoyed a greater chance of survival when near active yellowhead nests, at least until day six of the experiment (Table 8). A more convincing support for the suggestion that female nest clumping reduces predation comes from the experiment where the distance to marsh wrens was controlled, while the density of active yellowhead nests around experimental nests, was varied from low to high. Here a highly significant correlation between the number of active nests within 10 m of an experimental nest and its survival (Table 9) strongly suggests that females benefit from each other's nest defense effort. These findings are similar to those of Picman et al (1988) and Ritschel (1985), who found that redwings could also reduce the impact of marsh wrens by breeding close together. Whether this benefit is the result of true active co-operation (suggesting altruism), or rather a passive mutualism, where the members of a group share an advantage more or less equally, is difficult to assess.

In summary, my results strongly suggest that coloniality in yellowheads may be an adaptation to strong predation pressures favoring increased female density. The yellowhead colony exhibits a high degree of temporal synchrony, which may swamp certain predators, but not marsh wrens. To reduce the impact of this important nest predator, yellowheads aggressively exclude wrens from their territories, which results in a spatial segregation of nesting sites of these species. The temporal and spatial clumping by female yellowheads seem to further reduce predation by improving the efficiency of active nest defense. Finally, nests in the center of the yellowhead colony may enjoy higher success through the geometric or selfish herd effects. The antipredation role of the yellowhead colonial nesting pattern is likely to have important implications for the mating pattern in this species. This problem is examined in the third chapter.

CHAPTER 3

THE ROLE OF PREDATION IN THE EVOLUTION OF YELLOW-HEADED BLACKBIRD POLYGYNY

INTRODUCTION

Polygyny entails a cost to both males and females. However, it is generally accepted that the costs associated with males becoming polygynous (intrasexual competition and territoriality) are less important than those that females may encounter (increased competition for food, increased conspicuousness to predators, and reduced non-shareable male parental assistance; Wittenberger 1981). Hence, polygyny is likely to evolve when its advantages to females outweigh or at least balance its disadvantages (Orians 1969).

The Polygyny Threshold Model was proposed to explain how females could overcome the costs of mating with an already mated male, and therefore how polygyny may have evolved (Verner 1964; Verner and Willson 1966; Orians 1969; Altmann et al. 1977; Garson et al. 1981). The original form of this model assumes that females depress one another's fitness by competing for critical resources (Verner 1964; Verner and Willson 1966; Orians 1969). However, an alternative assumption is that females could benefit from settling close to other females through co-operative nest defense and/or foraging (Altmann et al. 1977; Garson et al. 1981). These two versions of the Polygyny Threshold Model, which differ dramatically with respect to how females behave towards one another, have been respectively termed the competitive female choice model and the co-operative female choice model (Altmann et al. 1977).

A third, more recent model, proposed to explain polygynous mate choice is the neutral mate choice model (Lightbody and Weatherhead, in press). In this model, female reproductive success is unaffected by mate choice, and therefore random settlement of the females is the optimal choice (Lightbody and Weatherhead 1987a). Lightbody and Weatherhead (in press) distinguish their "neutral" mate choice model from the null hypothesis by stating that in their model, random mate choice is optimal, while for the null hypothesis, mate choice is also random, but not optimal (i.e. not maximizing fitness). Regardless of whether interactions among females and variation in male or territory quality affect female reproductive success, and can or cannot be predicted at settling time, the neutral mate choice model predicts random mate and territory choice, which is essentially a null hypothesis against which all other models should be tested.

The Competitive Yellowhead

It has been previously shown that marsh wrens are a major source of yellowhead nesting mortality (Chapter 1). As a result, yellowheads seemed to have developed several anti-predator strategies, the most important of which is improved nest defense which is achieved through increased female density (Chapter 2). However, a consequence of this strategy is that some locations within the colony are safer than others, because: (1) they are farther from marsh wrens; (2) they benefit from more neighbors due to improved nest defense and predator dilution and satiation effects (Chapter 2). Thus, central locations within the colony should be preferred, because nesting success in these areas is greater. But since not all yellowheads can settle in the center, some level of competition must exist, enabling a partitioning of the breeding grounds.

If competition for centrally located breeding sites within a colony is important, the following predictions can be made: (1) the speed of settlement of yellowheads should be faster in the center of the colony, i.e. the majority of the first settling birds should colonize the center; (2) male territories should be smaller and female density higher in the colony center; (3) depending on the amount of variation in male territory size, male harem size could possibly increase towards the center of the colony.

The Co-operative Yellowhead

It has been shown earlier that yellowheads can reduce the impact of marsh wrens through active nest defense (Chapter 2). This lends support to the hypothesis that yellowheads may derive a benefit from co-operative nest defense. Therefore the prediction that yellowheads should actively clump because of the positive effects this has on nest defense and hence reproductive success should be tested.

Clumping can occur both spatially as well as temporally. In

Chapter 2, yellowheads were found to be clumping nesting attempts in time. Although this result is consistent with the idea of active grouping, temporal clumping by itself cannot be used to discriminate between individuals that are co-operative, competitive or perhaps even act independently of one another. This is because rapid settlement could also result from a keen competition for the preferred nesting sites, or, alternatively, from temporally highly clumped food supplies. Both of these situations would result in a high level of synchrony of nesting.

In contrast, female spatial settlement patterns can be used to establish whether females actively co-operate, act independently of one another, or compete, by testing the following predictions: (1) If females are co-operative, then we should expect females to settle throughout the breeding colony such that the nearest neighbor distance at the time of settlement is maintained consistently short from the first settlers to late settlers. (2) If females act independently of each other, then we could predict a purely random female settlement pattern which would result in inter-nest distances decreasing over time as the colony fills up. (3) Finally, if females are competitive, they should attempt to reduce competition for limited resources by spacing themselves out. Therefore, the nearest neighbor distances should be generally large for initial settlers, but as colonization proceeds, these distances become forcibly smaller due to limited breeding space, although a lower limit set by female territorial behavior is likely.

The predictions above could be re-stated in terms of a correlation between the date of settlement and the nearest neighbor distance at the time of settlement. Thus for co-operative females the correlation coefficient should approach 0, for randomly settling females an intermediate value (near -0.5), and for competitive females the correlation coefficient should be high (i.e. approach -1; see Figure 4).

The purpose of this chapter is to test the above predictions made from the 3 polygyny models and then to discuss the implications of nest predation by marsh wrens for the polygynous mating pattern exhibited in yellowheads.

METHODS

Male and Female Preferences for Location Within a Colony

To analyse the spatial distribution of female yellowheads on a temporal basis, four successive time periods of female settlement were created such that a similar number of nests were initiated in each period. Then, within these time periods, the number of females that settled in the center of the colony were compared to the number that settled in the periphery. Since the date of first egg and the date of female settlement on a territory are highly correlated (Lightbody and Weatherhead 1987b), the date of first egg was used as an index of female settlement.

To determine whether the ultimate yellowhead population density is greater in the center, the male territory size, the minimum inter-nest distance (for simultaneously active yellowhead nests during the incubation stage), and the relative female density (as measured by the number of simultaneously active yellowhead nests within 10 m of a focal nest during the incubation stage) were compared for central and peripheral locations by t-test.

Effect of Location Within a Colony on Male Harem Size

To establish whether or not male mating success is influenced by a male's location within a colony, the harem size of central and peripheral males was compared using a t-test. The male territories that formed the outer perimeter of the breeding colony were considered as peripheral territories, and those that were buffered from the outside of the colony by at least 1 other male territory as central territories.

Spatial Pattern of Female Settlement

To determine the spatial pattern of female settlement relative to the nearest neighbor, the settlement dates (as estimated by date of first egg; see Lightbody and Weatherhead 1987b) were divided into 5 cohorts of approximately equal size in terms of the number of nests initiated within each time period. Next, the nearest neighbor distance was measured for each nest (only nests initiated within that same cohort or in a previous cohort(s) and still active were included). The nearest neighbor distance was categorized in 3 m intervals for a total of 10 categories of increasing distance. Finally, a Spearman rank correlation was run to establish how the nearest neighbor distance varies over time throughout the settling period. The same analysis was also performed for a set of nearest neighbor distances which were calculated for a hypothetical randomly settling population of yellowheads. The constraints applied to this simulation were identical to those experienced by the 1983 population (i.e. the same marsh area was used, the same number of settlers were created for each cohort and a minimum inter-nest distance of 2 m was maintained). This simulated random settlement is a useful way to test the validity of the prediction for random settlement made in the introduction.

RESULTS

Male and Female Preference for Location Within a Colony

When the rate at which females settle in the center versus the periphery of the colony is analyzed, a preference for the center emerges for the first group of settling birds (Table 13). In 1983, 72% of the first 60 females to settle, and in 1984 59% of the first 61 females to settle, did so in the center of the colony. However, the settling rate between the center and the periphery of the colony was significantly different only in 1983 (Table 13).

In both 1983 and 1984 male territories were significantly smaller in the center than in the periphery of the colony (Table 14). This supports the idea that male yellowheads compete to secure territories in the center of the colony. The relative density of females is significantly greater and inter-nest distance is significantly smaller in the center, as compared to the periphery of a colony (Table 15), indicating that females also seem to prefer the central regions of the colony.

Effect of Location Within a Colony on Male Harem Size

Male harem size was larger in the center of the colony, although this was significant only in 1984 (Table 16). When both years are combined however, the difference between harems of central and peripheral males is highly significant (Table 16).

Spatial Pattern of Female Settlement

In both 1983 and 1984, small, nonsignificant correlation coefficients for inter-nest distances vs time were obtained (for 1983: $r_s = -0.095$, d.f.=226, p(1-tail) >0.05; and for 1984: $r_s = 0.060$, d.f.=221, p(1-tail) >0.10). In addition, an intermediate, highly significant correlation coefficient for the relationship between inter-nest distance and time, for a simulated randomly settling yellowhead population was obtained ($r_s = -0.421$, d.f.=226, p(1-tail) <0.0005), thus corroborating the validity of this test. These results strongly suggest that female yellowheads preferentially settle close in space to other conspecifics, and that this female tendency is consistent throughout the settling period.

DISCUSSION

Competitive Female Choice Model

Nest defense capabilities in yellowheads was increased through female clumping (Chapter 2). A result of this is that geometric effects as well as predator dilution and satiation effects may also operate such that the center of the colony is safer from predators, given that predators enter the colony from outside. Therefore, a potential competitive situation is established among both male and female yellowheads. Evidence for preference of earlier settling females for the colony center, smaller male territories in the center, and higher female density resulting in smaller inter-nest distances in the center supports the idea that yellowheads compete for the high quality (i.e. centrally located) breeding situations.

Competition for high quality breeding grounds has also had a significant effect on the mating pattern in the breeding population in one of the two years of the study, when centrally located males acquired, on average, larger harems. The lack of difference between harem size of central and peripheral males in 1983 could be explained by a larger number of females breeding in this marsh (i.e. 209 in 1983 and 143 in 1984). Therefore, it is conceivable that in 1983, a year of a larger female population, a surplus of breeding females overflowed into the peripheral parts of the colony, thus masking differences in harem size between these 2 regions of the colony.

Three different hypotheses that have been proposed to explain the evolution of polygyny in marsh-nesting birds and that are consistent with the competitive female choice model, are worthy of discussion in relation to the yellowhead case. The first proposes that a high degree of heterogeneity in food distribution within marshes may favor resource defense polygyny (Verner and Willson 1966; Orians 1969). This hypothesis is unlikely, because yellowheads forage mainly away from their territories (Lightbody and Weatherhead 1987b; Chapter 1), and therefore food heterogeneity in the male territory is unimportant. The second proposes that higher predation rates in upland habitats may favor polygyny in better quality marsh territories (Wittenberger 1976). Although this hypothesis is applicable to redwings, it does not provide a plausible explanation for polygyny in yellowheads, which generally breed only in deep water marshes. Finaly, the sexy son hypothesis proposes that females may settle on a low quality territory but with a sexy male, suffering an immediate reduced fitness which would be offset ultimately by producing sexy sons that would eventually attract large harems (Weatherhead and Robertson 1979). This hypothesis has received considerable criticism, the most damaging of which is a demonstration that forfeiting immediate for ultimate reproductive success is evolutionarily unstable (Kirkpatrick 1985).

Co-operative Female Choice Model

The study of settlement patterns of female yellowheads in time and space suggests that females actively clump. These data lend a strong support to the co-operative female choice model. In contrast to these results, Lightbody and Weatherhead (1987b) found no evidence to support the idea that female yellowheads within a harem are co-operative. However, several of the predictions they proposed for testing the co-operative female choice model are debatable and are therefore discussed below.

Firstly, Lightbody and Weatherhead (1987b) state that the co-operation hypothesis predicts that females should be attracted to each other, a reasonable prediction. However, when testing this prediction, they limited their analysis to a comparison of female settling patterns between harems. There is no reason to restrict this analysis to the male territory, because if co-operation occurs, it should be exhibited throughout the population. It is, therefore, at the population level that female settling patterns should be analyzed. To further illustrate this point, there is no evidence to suggest that females discriminate between neighbors from the same harem and those from neighboring harems. In fact, for many females, neighboring harem females (from which co-operative benefits could be obtained), are just as close or even closer than female neighbors from the same harem.

Second, Lightbody and Weatherhead (1987b) predict that females should not be aggressive to potential settlers, also a reasonable prediction. However, when testing aggression to a perched female mount, they placed the stimulus only 1 meter from the nest. It is, however, unreasonable to assume that intrasexual aggression should never be exhibited, even in the most co-operative animals. On the contrary, because there is likely to be an optimum degree of clumping, which may represent a compromise between benefits and costs of group life, female-female aggression, the most likely mechanism setting an upper limit to female density, is to be expected. Therefore, by placing the stimulus too close to the nest (the average nearest neighbor distance observed in this study is more than 6 times greater, and the minimum is twice as large), Lightbody and Weatherhead (1987b) have certainly increased the chance of provoking a response in an unnatural situation. In addition, their results indicate that the most aggressive response obtained was "agitation and vocalization by a female within 5 m of the mount", and this occurred in only 8% of the cases. Such relatively low levels of aggression should not be used to falsify the co-operative female model.

Next Lightbody and Weatherhead (1987b) predicted that if the co-operation hypothesis is correct, then, on territories of the same size and quality, females settling in large harems should have higher reproductive success than those settling in smaller harems. Again, restricting this analysis to just the harem is underestimating any potential benefit that could be derived from co-operation, because females from neighboring harems could also have a significant effect. This would not, however, be recognized given Lightbody and Weatherhead's assumption. But, in spite of these unrealistic conditions, results on percent nests successful as a function of harem size do not contradict the co-operative female model. When I re-analyzed their data (harems of 6 and 7, for which there is only 1 harem in each category were combined with harems of 5) and ran a Pearson correlation between proportion nests successful and harem size, a significant positive relationship ($r= 0.947$, $d.f.=3$, $p(1\text{-tail})<0.01$) between nest success and harem size emerges. This correlation is consistent with the co-operative female choice model.

Finally, Lightbody and Weatherhead examined the prediction that female reproductive success should increase with increasing nest density and with increasing synchrony in nest initiation, if females are co-operative. Again, this analysis was based on the assumption that co-operative benefits can only occur within individual harems. An analysis at the population level for synchrony in nesting is necessary, because of the potential increase in female reproductive success that may be attributable to predator swamping and dilution, and improved predator detection and deterrence which need not be restricted to females within a harem. In Chapter 2, temporal synchrony at the population level was demonstrated for yellowheads at Delta Marsh. However, to be able to establish an association between increased synchrony and reproductive success, we would have to compare asynchronous colonies with synchronized ones, something which may not be feasible for yellowheads.

A possible confounding factor, causing an underestimate of the benefits resulting from co-operation is territory tenacity. This phenomenon has been observed in both male redwings (Nero 1956; Case and Hewitt 1963; Searcy 1979; Picman 1987) and female redwings (Picman 1981). For yellowheads, males return very close to their previous territories (Isabelle, unpubl. data), but no information is available on females. But by exhibiting site tenacity, returning birds will not be able to benefit as much from previous breeding experience. More data on returning females are needed to better understand the effects of territory tenacity.

Co-operative Vs Competitive Female Choice Models

It is more realistic to expect that under different sets of selective pressures, competitive as well as co-operative interactions among individuals within a species could co-occur. In fact, if co-operative interactions are favored, competition must also exist as a mechanism setting an upper limit to grouping. Thus, the competitive and co-operative female choice hypotheses need not be mutually exclusive.

The Role of Male Emancipation in the Evolution of Polygyny

Male assistance in feeding does not affect the number of young that fledge (Fautin 1941; Willson 1966; Patterson et al. 1980; Lightbody and Weatherhead 1987a) and therefore is unimportant in yellowheads (Chapter 1). Further, the male territory is not an important food source for yellowhead females (Chapter 1; Lightbody and Weatherhead 1987b). Finally, because female yellowheads breed close to each other, male parental assistance in nest defense is likely to be a shareable resource. Therefore, female yellowheads are probably not compromising their reproductive success by accepting an already mated male. In fact, by mating polygynously, female yellowheads may even be facilitating increased female density, which has been shown to be advantageous in reducing predation pressures.

Conclusions

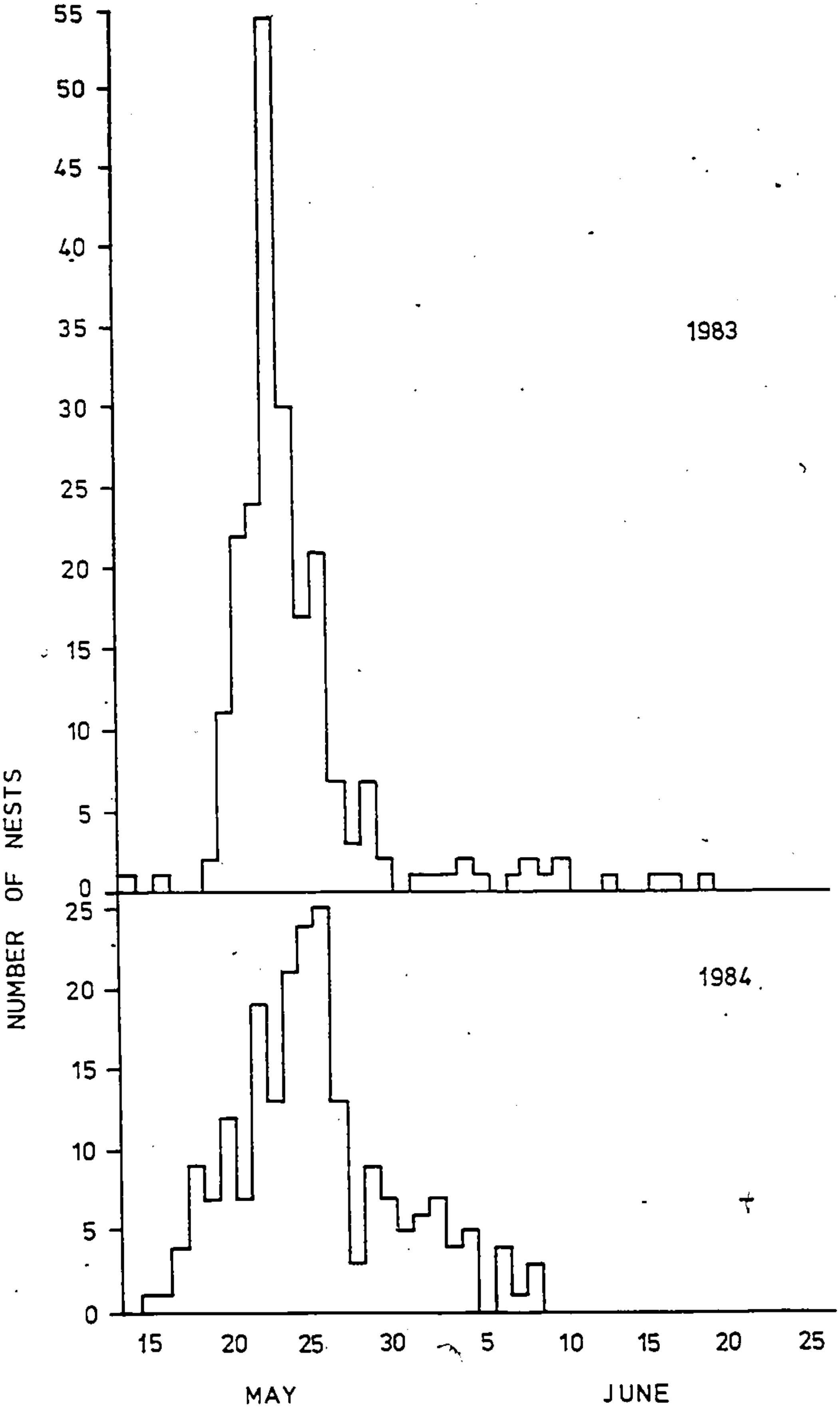
Predation and competition may play an important role in determining colony organization, and can potentially lead to specific behavioral strategies that will minimize their effects.

For yellowheads, predation pressures, mostly due to marsh wrens, have probably led to co-operative nest defense strategies which include temporal clumping of nest initiation, and increased female densities. These strategies, in turn, are likely to maximize predator detection and mobbing, and may also reduce predators' impact through dilution and satiation as well as geometric effects. However, the benefits of these strategies are maximized in the center of the colony. Therefore, competition among males to monopolize the center and among females to settle in the center must exist as the mechanism which allows a partitioning of these prefered areas.

I suggest that polygyny in yellow-headed blackbirds can be explained by both the co-operative and competitive female choice models. These two models need not be mutually exclusive although the co-operative female is probably a greater driving force behind the observed mating pattern.

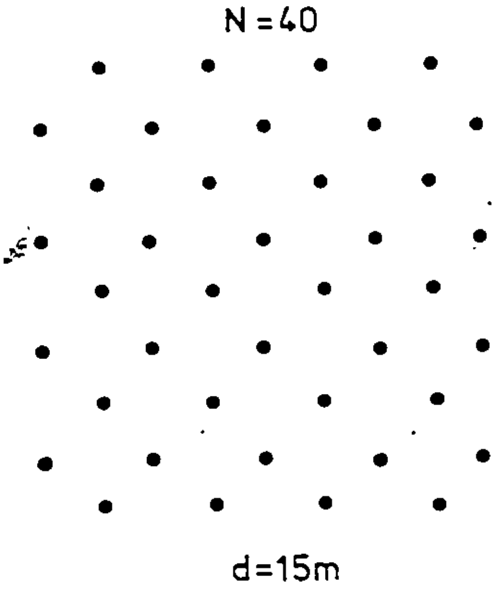
For other marsh-nesting blackbirds, predation pressures are also likely to be the mechanism behind the evolved preference for the marsh habitat. There is evidence to suggest that upland nesting redwings rear fewer young than their marsh-nesting counterparts due to greater predation in the upland habitat (Robertson 1973). Marsh-nesting redwings are dispersed to loosely colonial to colonial when breeding. Yellowheads and tricolored blackbirds (Agelaius tricolor) breed exclusively in marshes where they exhibit a colonial to highly colonial nesting pattern, the tricolor being the most densely colonial of all North American passerines (Orians 1980). Since all three blackbirds rely upon insects as a food source for their young, the adaptive value of coloniality and the degree to which it occurs in blackbirds in general, should be dependent upon the degree and type of predation as well as the location and abundance of insects. Therefore, differences in colony organization between populations and species may be explained by differences in predation pressures and food sources.

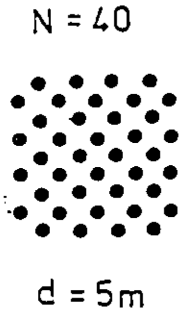
Figure 1. Initiation of egg laying by female yellow-headed blackbirds, as a function of time, for 1983 and 1984.



55
50
45
40
35
30
25
20
15
10
5
0
1983
25
20
15
10
5
0
1984
NUMBER OF NESTS
15
20
25
30
5
10
15
20
25
MAY
JUNE

Figure 2. Placement of nests in experimental colonies of different nest densities. Inter-nest distance in dense and sparse colonies is indicated by d, and sample size by N. The spatial arrangement of 2 sparse and 2 dense colonies in the study marsh, is shown in a box at the bottom of the Figure (S represents sparse and D represents dense colonies).





S D S D

Figure 3. The effect of yellowheads on survival of experimental nests placed along 3 transects through an active colony. TR represents the individual transects. The location of the experimental nests, yellowhead nests, and marsh wren nests are shown. At the bottom of the Figure, the predation pattern on the experimental nests, is depicted as time elapses (day 1 through to 9). Each individual transect is represented by a line and a solid circle indicates that a given experimental nest was destroyed by a predator, on a particular day after the study was initiated (the solid circles are recorded in a cumulative fashion). The lack of a circle indicates that the appropriate experimental nest is undisturbed.

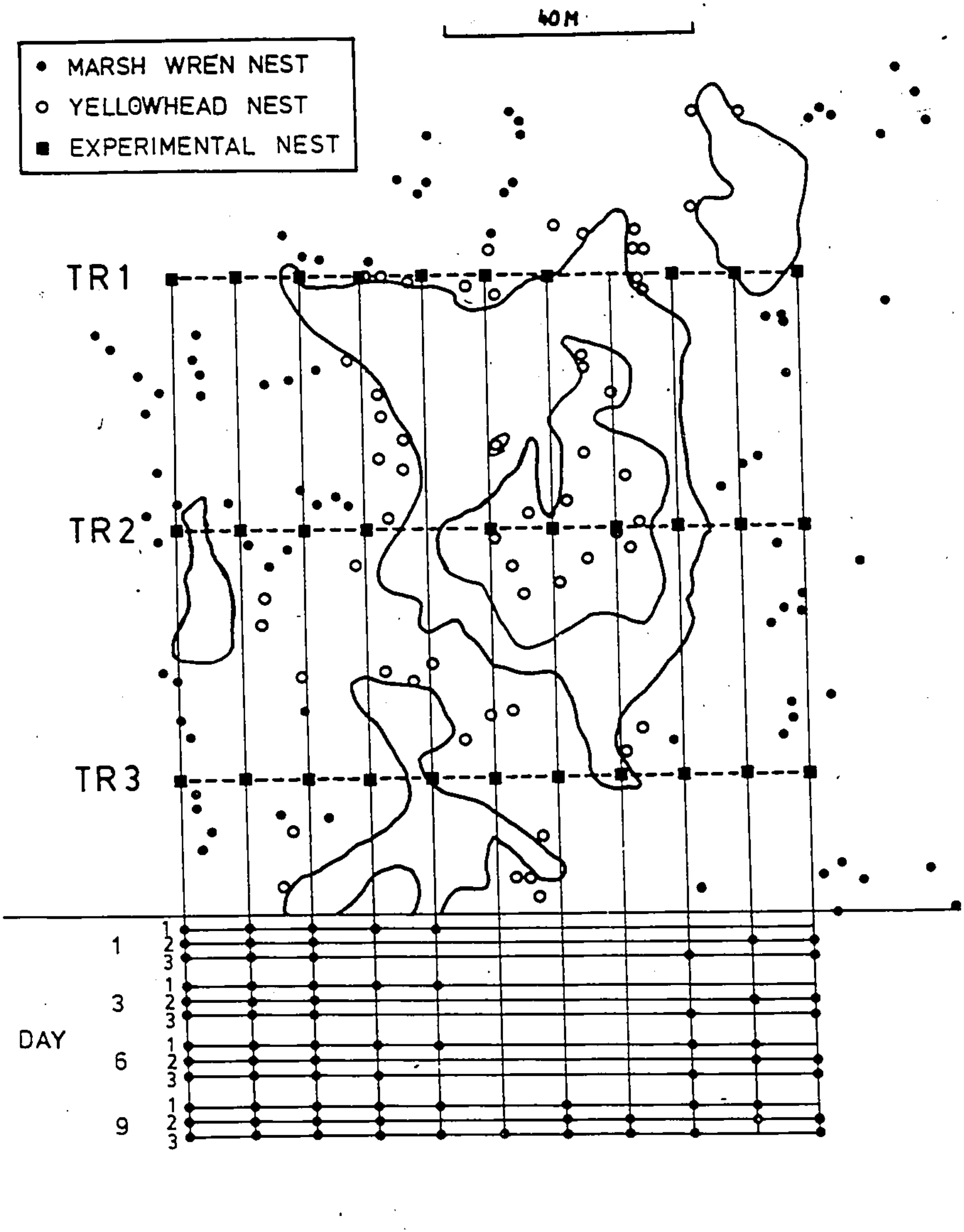

40 M
● MARSH WREN NEST
○ YELLOWHEAD NEST
■ EXPERIMENTAL NEST
TR 1
TR 2
TR 3
DAY
1
3
6
9
1
2
3

Figure 4. Graphical representation of the predicted relationship between distance to the nearest neighbor, and time of settlement, for 3 possible situations describing female yellowhead interactions at time of settlement. Competitive settling females should seek to disperse in space, and therefore the correlation coefficient should be close to -1. For the random settling female, both clumping and dispersion should balance out, and r should approach -0.5. Co-operative settling females should seek to settle contagiously throughout the settling period, and therefore r should approach 0.

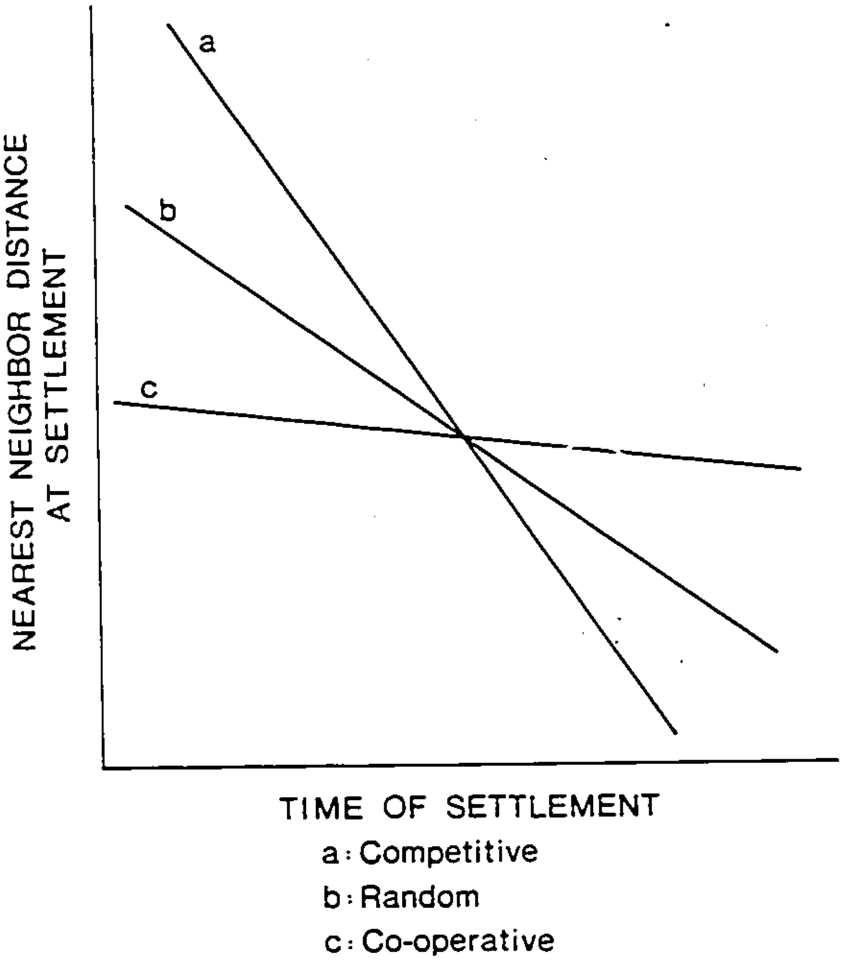

a
b
c
NEAREST NEIGHBOR DISTANCE AT SETTLEMENT
TIME OF SETTLEMENT
a: Competitive
b: Random
c: Co-operative

Table 1. Mean (± SD) water depth, nest height, vegetation height and vegetation density for all active yellowhead nests in 1983 and 1984. A t-test was used to test for differences between years.

	Mean ± SD			
Nest Site Feature	1983 (N=226)	1984 (N=221)	t	p
Water Depth (cm)	38.1 ± 8.0	29.0 ± 6.9	12.9	<0.0001
Nest Height (cm)	98.8 ± 14.6	85.4 ± 12.2	10.5	<0.0001
Vegetation Height (cm)	136.4 ± 17.5	130.8 ± 16.7	3.5	<0.0007
Vegetation Density*	4.9 ± 2.7	6.3 ± 3.1	-4.9	<0.0001

* number of exposed dots on a 50 cm stick with 20 evenly spaced red dots (1 cm diameter) placed on the nest and counted from 2 m away.

Table 2. Mean (± SD) time spent in various activities by yellowhead females in egg and nestling stages. Total observation period per female was 60 minutes.

Nesting Stage	Mean ± SD Time		Mean ± SD Time Foraging (min.)		
of Female (N)	on Nest (min.)	Other (min.)*	In Marsh	On Territory	Off Marsh
Incubation (9)	44.1 ± 9.4	2.5 ± 3.4	0.8 ± 1.8	4.3 ± 7.1	10.6 ± 8.8
Nestling (11)	19.8 ± 14.3	4.2 ± 10.4	6.0 ± 12.6	5.5 ± 5.5	24.4 ± 9.8

* Time spent perched, preening, in sexual chases, mobbing, chasing marsh wrens and interacting with other females.

Table 3. Nesting outcome of all yellowhead nesting attempts in 1983 and 1984.

Nesting Outcome	1983	1984	combined
% Nests Successful	31	51	41
% Nests Depredated	59	44	51
% Nests Abandoned	9	4	7
% Failed For Other Reasons	1	1	1
Total No. Nests	226	221	447

Table 4. Percent (N) yellowhead nests depredated for 4 categories of increasing nearest marsh wren nest distance in 1983 and 1984 (includes only successful and depredated yellowhead nests). The correlation analysis was performed with the original, individual, data points.

	% (N) Nests Depredated When Distance to Nearest Marsh Wren Nest is					
Year	0 to 15m	>15 to 25m	>25 to 35m	>35m	r_s	p(1-tail)
1983	79(29)	73(55)	58(59)	60(60)	0.150	<0.025

	% (N) Nests Depredated When Distance to Nearest Marsh Wren Nest is					
Year	0 to 10m	>10 to 20m	>20 to 30m	>30m	r_s	p(1-tail)
1984	58(50)	54(65)	37(71)	30(23)	0.204	<0.0025

Table 5. Analysis of the spatial pattern of distribution of yellowhead and marsh wren nests built before June 23, 1983, and June 24, 1984, and based on the presence or absence of nests of these species in 10 x 10 m quadrats.

		No. Quadrats When		
		Marsh Wrens		
Year	Yellow-headed Blackbirds	present	absent	total
1983	present	11	142	153
	absent	66	178	244
	total	77	320	387
1984	present	13	130	143
	absent	125	342	467
	total	138	472	610

Note: For 1983: $X^2 = 23.72$, $p < 0.001$.

For 1984: $X^2 = 19.54$, $p < 0.001$.

V

Table 6. Predation on quail eggs placed in artificial nests in two marsh wren territories over a 24-hour study period. Thirty eggs in 15 nests (2 eggs/nest) were distributed in each wren territory.

	Number nests/eggs depredated after			
Wren #	2 hrs	4 hrs	19 hrs	24 hrs
1	10/16	14/26	14/27	15/29
2	10/15	12/18	14/23	15/24

Note: Out of 53 depredated eggs, 39 were punctured.

Table 7. The effect of nest density in an artificial colony on nest survival. In the low density situation, nests were placed 15 m apart, and in the high, 5 m apart.

	% (N) Nests Depredated When Colony Density is			
Day	High (N=80)	Low (N=80)	X^2	p
1	58.8 (47)	72.5 (58)	3.35	> 0.05
3	73.8 (59)	86.3 (69)	3.91	< 0.05
6	76.3 (61)	87.5 (70)	3.41	> 0.05
9	76.3 (61)	87.5 (70)	3.41	> 0.05

Table 8. Egg predation losses of artificial nests in an experimental area where breeding yellowheads were removed and in an area where they were present.

	% (No.) Nests Depredated When Breeding Yellowheads			
Day	Absent (N=160)	Present (N=31)	χ^2	p
1	65.6 (105)	48.4 (15)	3.30	> 0.05
3	80.0 (128)	48.4 (15)	13.79	< 0.001
6	81.9 (131)	58.1 (18)	8.58	< 0.01
9	81.9 (131)	83.9 (26)	0.07	> 0.7

Table 9. The effect of density of active yellowhead nests on the survival of quail eggs in experimental nests. The correlation analysis was performed with the original, individual data points.

	% (Number) Depredated Experimental Nests When Number Active Yellowhead Nests Within 10 m was					
Day	0	1	2	3	r_s	p
1	40 (4)	10 (1)	20 (2)	0 (0)	0.52	< 0.005
3	70 (7)	20 (2)	20 (2)	10 (1)	0.53	< 0.001
6	100 (10)	70 (7)	70 (7)	30 (3)	0.60	< 0.0005
9	100 (10)	90 (9)	80 (8)	70 (7)	0.53	< 0.005

Table 10. The effect of location within a yellowhead colony on yellowhead nest losses due to predation.

	% (No.) Depredated Nests When Location Within a Colony was			
Year	Central	Peripheral	X^2	p
1983	56 (59)	76 (74)	9.54	< 0.005
1984	38 (41)	55 (56)	5.77	< 0.025
Combined	47 (100)	65 (130)	14.09	< 0.001

Table 11. Comparison of 4 yellowhead nest site features between central and peripheral locations in a yellowhead colony by t-test, for 1983 and 1984.

Nest Site Feature	1983				1984			
	Mean ± SD				Mean ± SD			
	Central	Peripheral	t	p	Central	Peripheral	t	p
Vegetation Height (cm)	135.4 ± 16.1	137.5 ± 19.0	0.91	> 0.3	129.5 ± 14.4	132.2 ± 18.8	1.19	> 0.2
Vegetation Density	5.0 ± 2.5	4.8 ± 2.9	-0.64	> 0.5	6.5 ± 2.9	6.0 ± 3.2	-1.18	> 0.2
Nest Height (cm)	97.1 ± 13.7	100.8 ± 15.4	1.91	> 0.05	84.9 ± 12.0	85.9 ± 12.5	0.60	> 0.5
Water Depth (cm)	38.6 ± 7.7	37.6 ± 8.4	-0.91	> 0.3	28.2 ± 7.2	29.8 ± 6.5	1.79	> 0.05
Sample Size	121	105			116	105		

Table 12. Comparison by t-test of central and peripheral yellowhead nests with respect to the distance to the nearest marsh wren nest, distance to the edge of the marsh, date of clutch initiation, stage of depredation, and number of eggs layed.

	1983 Mean ± SD					1984 Mean ± SD				
Variable	Central	Peripheral	t	d.f.	p	Central	Peripheral	t	d.f.	p
Distance to the to the Nearest Marsh Wren Nest**	34.4 ± 10.3	23.0 ± 10.8	-8.15	224	<0.0001	24.6 ± 7.3	12.7 ± 6.8	-12.48	219	<0.0001
Distance to the Edge of the Marsh*	19.1 ± 8.1	4.0 ± 4.3	-17.83	188	<0.0001	14.5 ± 7.7	3.0 ± 4.2	-13.97	181	<0.0001
Date of Clutch Initiation**	25.3 ± 7.6	26.2 ± 7.0	0.87	224	>0.3	25.7 ± 6.2	27.0 ± 6.1	1.50	219	>0.1
Stage of Depredation*	0.5 ± 0.5	0.2 ± 0.4	-4.07	107	<0.0005	0.5 ± 0.5	0.3 + 0.5	-1.33	81	>0.1
Number of Eggs Layed**	3.6 ± 0.6	3.5 ± 0.6	-1.06	178	>0.2	3.6 ± 0.7	3.3 ± 0.7	-2.52	196	<0.02

* with separate estimate of variance

** with pooled estimate of variance

Table 13. The proportion of yellowhead nests built in the center and in the periphery of a yellowhead colony for 4 consecutive time periods.

Year	Date of Nest Initiation	Number (%) of nests built in the Center	Number (%) of nests built in the Periphery	Total
1983	May 15 to 22	43(71.7)	17(28.3)	60
	May 23 to 25	21(36.2)	37(63.8)	58
	May 26 to 29	26(52.0)	24(48.0)	50
	May 30 to June 17	26(49.1)	27(50.9)	53
				221
1984	May 15 to 21	29(74.0)	10(26.0)	39
	May 22 to 24	17(54.0)	14(46.0)	31
	May 25 to 29	23(47.0)	25(53.0)	48
	May 30 to June 9	22(59.0)	15(41.0)	37
				155

Note: For 1983: $X^2=15.27$; d.f.=3; $p<0.005$.

For 1984: $X^2= 6.45$; d.f.=3; $p<0.10$.

Table 14. The effect of location within a yellowhead colony on male yellowhead territory size.

	Mean Territory Size (m^2)±SD				
Year	Central	Peripheral	t	d.f.	p
1983	188 ± 128	294 ± 117	3.55	65	< 0.0005
1984	373 ± 269	486 ± 249	1.76	63	< 0.05
Combined	273 ± 224	394 ± 218	3.15	130	< 0.0025

Table 15. The effect of location in a yellowhead colony on (1) inter-nest distances (m) between yellowhead nests, and (2) yellowhead female density (average number of simultaneously active nests within a 10 m radius of a focal nest).

		Mean ± SD				
	Year	Center	Periphery	t	d.f.	p
Inter-nest Distance	1983	5.1 ± 2.9	6.9 ± 5.5	2.95*	151	< 0.0025
	1984	5.4 ± 3.3	7.1 ± 4.3	3.25*	196	< 0.001
Female Density	1983	3.0 ± 2.1	1.9 ± 1.8	-4.26**	224	< 0.0001
	1984	2.3 ± 1.3	1.2 ± 1.0	-6.88*	214	< 0.0001

* with separate estimate of variance

** with pooled estimate of variance

Table 16. The effect of location within a yellowhead colony on male yellowhead mating success (harem size).

	Mean Harem Size ± SD (N)				
Year	Central	Peripheral	t	d.f.	p
1983	3.3 ± 1.5 (34)	2.9 ± 1.2 (33)	-1.25	65	> 0.1
1984	2.9 ± 1.1 (38)	1.8 ± 1.0 (51)	-4.80	87	< 0.0001
Combined	3.1 ± 1.3 (72)	2.2 ± 1.2 (84)	-4.30	154	< 0.0001

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