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THE EVOLUTION OF PATERNAL CARE PATTERNS AND COLONIALITY IN
YELLOW-HEADED BLACKBIRDS (XANTHOCEPHALUS XANTHOCEPHALUS)

The University of Arizona

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THE EVOLUTION OF PATERNAL CARE PATTERNS AND
COLONIALITY IN YELLOW-HEADED BLACKBIRDS
(XANTHOCEPHALUS XANTHOCEPHALUS).

by

David Francis Gori

A Dissertation Submitted to the Faculty of the
DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY

In Partial Fulfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

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GRADUATE COLLEGE

As members of the Final Examination Committee, we certify that we have read
the dissertation prepared by David Francis Gori

entitled The evolution of paternal care patterns and coloniality in
Yellow-headed Blackbirds (Xanthocephalus xanthocephalus).

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ABSTRACT

Males can influence current reproductive success in one of two ways: by caring for offspring or by seeking additional mates. Models for the evolution of paternal care predict increasing parental investment by males as their ability to contribute to offspring survivorship increases and as the probability of attracting additional mates decreases. I tested the assumptions and predictions of these models for polygynous Yellow-headed Blackbirds (Xanthocephalus xanthocephalus). The results of field observations and experiments indicate that male Yellowheads are capable of assessing the fitness returns associated with parental care and sexual advertisement and will increase parental investment as their ability to enhance offspring fitness increases and the probability of acquiring additional mates decreases. Thus, paternal investment is greater in unproductive marshes, on days when the insect emergence is low, when the arrival rate of unmated females is low, and for males with poor-quality territories.

Current reproductive success also depends on the ability of individuals and their mates to raise young. In theory, males should be capable of assessing the parental competence of mates and adjusting their parental investment with mate quality so as to maximize the fitness return on their investment. To test this hypothesis, fitness-investment curves for nests belonging to competent and incompetent mates were derived using empirical data and, on the basis of the

slopes, preferences for nests predicted. Field observations were consistent with the predictions. Males preferentially cared for young of competent mates and fed them at greater rates than young of incompetent mates; care at the latter nests occurred only when preferred nests were unavailable.

Yellowheads often breed in colonies. In theory, colonies can act as information centers and facilitate the exploitation of spatially unpredictable food resources. I tested this hypothesis for Yellowheads by analyzing the pattern of 1) colony departures and 2) recruitment to an experimental foraging area. The results of the experiment and departure analysis indicate that Yellowhead colonies do act as information centers; birds can locate productive foraging areas more efficiently than in the absence of information by monitoring the success of neighbors and following them on foraging trips.

CHAPTER 1

VARIATION IN PATERNAL CARE IN YELLOW-HEADED BLACKBIRDS: THE ROLE OF MARSH PRODUCTIVITY AND MALE MATING SUCCESS

Introduction

In the last few decades, a considerable effort has been devoted to developing a comprehensive theory for the evolution of parental care (e.g., Orians 1969; Trivers 1972; Williams 1975; Emlen and Oring 1977; Maynard Smith 1977; Ridley 1978; Wittenberger 1979). Two theoretical insights have been critical in directing this effort: first, that males and females may have non-identical reproductive interests and second, that parental care patterns within species result from the interactions between the sexes and between parents and offspring. Models based on these insights have been concerned with identifying i) the optimal strategies for each of the sexes, ii) the environmental and phylogenetic factors that determine how the conflicting interests of the two sexes are resolved, and iii) the constraints each sex imposes on the reproductive alternatives of the other (Wittenberger and Tilson 1980).

Parents of either sex can influence current reproductive success in one of two ways: by caring for existing offspring and enhancing their probabilities of survivorship or by deserting young, finding another mate and breeding again. In most species of birds, the number of offspring produced by a pair depends on the quantity and quality of

parental care and not on female fecundity (Lack 1966). In addition, the delay between fertilization and oviposition gives males the opportunity to desert young before females can. As a result of these two features, the optimal strategy for females is to continue investing in young following oviposition. Desertion by females is favored only when the reproductive success of pairs is limited by fecundity so that by abandoning young, females can devote more energy to egg production (Maynard Smith 1977). This latter condition may occur when the probability of nest failure is high, when the breeding season is sufficiently long to allow double-clutching by females, and in seasonally harsh environments where resources are scarce at the time of egg production but abundant when young are being raised (Jenni 1974; Emlen and Oring 1977). Assuming that females continue to care for young following oviposition, the optimal strategy for males will depend on the relative fitness gains associated with parental care and seeking additional matings. These gains, in turn, will depend on i) the ability of males to contribute to offspring survivorship beyond what the female is already capable of achieving and ii) the probability of attracting additional mates. The latter will be influenced by the temporal availability of unmated females, the dispersion of resources necessary for reproduction and the ability of males to obtain differential access to these resources.

In this paper, I investigate the trade-off between seeking additional mates (sexual advertisement) and parental care for male Yellowheaded Blackbirds (Xanthocephalus xanthocephalus). Specifically,

I ask whether the investment by males in sexual advertisement and parental care is energy-limited and whether a complementarity in investment between the two activities exists such that males that invest more time in parental care spend less time seeking additional mates. These two assumptions are implicit in the models for the evolution of paternal care and are necessary in order for a trade-off in fitness returns to exist. Given that these assumptions hold, I then ask whether variation in the ability of individual males to contribute to offspring fitness and to attract additional females can account for some of the variation in the amount and timing of paternal care between males. Yellowheads breed in marshes that differ in the availability of food and the density of females that settle there. In addition, males are territorial and territories within marshes differ with respect to their attractiveness to females. The quality or attractiveness of a territory is correlated with its structural characteristics including position in the marsh, vegetation density, and the degree of channelling; these characteristics, in turn, are correlated with female nesting success (J. Wittenberger, unpubl. ms; Gori, in prep.). Variation in insect productivity between marshes and territory quality within marshes should affect the fitness returns associated with caring for young and attracting unmated females. If males are capable of assessing these returns and can adjust their behavior so as to maximize reproductive success, then variation in paternal behavior should reflect the underlying variation in fitness returns. Based on these arguments, the following predictions should hold:

1) If investment in current reproduction is energy-limited, experimentally provisioning males with food should reduce the amount of time they spend feeding themselves and result in greater allocation to parental behavior and sexual advertisement.

2) If caring for offspring and attracting additional mates are mutually exclusive activities in time (i.e., cannot be simultaneously pursued by males), males that are not feeding young should invest more time in sexual advertisement than males that are feeding young.

3) Females breeding in productive marshes are more capable of raising young without paternal assistance than females in unproductive ones (providing that the density of females does not increase as fast as the resource base). As a result, the ability of males to contribute to offspring fitness decreases with increasing productivity. At the same time, the probability of attracting additional females may increase with increasing productivity (J. Wittenberger, unpubl. ms). Therefore, males in productive marshes should invest less in parental care than males in unproductive ones.

4) On days when insect emergence is low, the food demands of young are greater and the starvation rate of nestlings is significantly increased. Because of their enhanced ability to contribute to offspring survivorship at these times, males should allocate more energy to parental care on days when the emergence is low.

5) Males in possession of high quality territories attract more females than males with poorer ones. Therefore, the former males should invest less in parental care than the latter males.

5) Males should initiate parental care when the probability of attracting unmated females is low. Since males that have greater than average pairing success early in the season get virtually all of the unmated females arriving later (Gori, unpubl. data), males with very few females should feed young as soon as the primary clutch is old enough to require aid. More successful males should initiate parental care when the arrival rate of unmated females is low.

6) When parental care becomes advantageous, males should preferentially feed the oldest and largest nest on their territory because the fitness return on investment is greater for larger broods (Chapter 2) and because the reproductive value of young increases with age (Fisher 1958).

In this paper, I test these seven predictions and show that i) investment in current reproduction is energy-limited such that increasing the rate of energy intake by males results in more time and energy devoted to parental care and sexual advertisement, ii) there appears to be a trade-off in expected fitness returns between attracting additional mates and caring for young, and iii) males are capable of adjusting the amount and timing of parental behavior in response to variations in these expected returns.

Methods

The Study Area

The research was conducted from 1979 to 1982 on the Columbia National Wildlife Refuge near Othello, Grant Co., Washington. The

topography of the Potholes, as the region is known locally, consists of buttes and basins scoured in Columbia basalt by Pleistocene floods (Bretz 1959). The Columbia basin lies in the rainshadow of the Cascades and receives approximately 20 cm of precipitation annually. Most of the standing water in the area post-dates the advent of local irrigation at the turn of the century. Increasing irrigation run-off and rising ground water levels following completion of the Columbia River Water Project in the 1950's have greatly enlarged existing bodies of water and created numerous others. It is unlikely that many blackbirds were breeding in the area before this increase in standing water.

The upland vegetation is characterized by sagebrush (Artemisia tridentata), bluegrass (Poa sp.), bunchgrass (Agropyron spicatum), and cheatgrass (Bromus tectorum). Greasewoods (Sarcobatus vermiculatus) dominate alkaline pans surrounding the shores of lakes and marshes; cattails (Typha angustiflolia) and bullrush (Scirpus sp.) grow in the shallow aquatic margins of these bodies of water and provide nest sites for Yellowheads.

The Study Organism

Yellow-headed Blackbirds are polygynous, marsh-nesting members of the family Icteridae. They breed throughout the United States and Canada west of the Mississippi River and also in Wisconsin, Illinois, northwest Indiana and southwest Michigan; Yellowheads are locally abundant in productive lakes, marshes, and irrigation ditches. In

the Potholes, breeding begins in late April or early May and continues until late June or early July. Females do all of the nest construction and incubation which takes 1-3 and 12 days respectively. Clutch size is 3.75 ± 0.48 ($\bar{x} \pm S.D.$) eggs/nest ($n = 159$). Once males are established on a territory, they tend to return to the same marsh to breed in subsequent seasons (Gori, unpubl. data; J. Wittenberger, pers. comm.).

Yellowhead males show considerable variation in the amount of parental care directed to young (Ammann 1938; Fautin 1941; Willson 1966); care may take the form of nest-guarding, giving alarm calls, mobbing predators, and feeding young. This study focuses on the feeding of young for several reasons: i) in contrast to other parental activities, such as nest-guarding, foraging for young requires different behaviors and occurs in spatially different locations than advertising for mates. Thus, the two behaviors are mutually exclusive in time which is necessary in order for a trade-off in fitness returns to exist, ii) variation in feeding rates between males appears to be greater than for other forms of paternal care (Gori, pers. obs.), iii) feeding young can occupy a significant portion of a male's time budget, whereas activities such as giving alarm calls and mobbing predators occur infrequently and iv) the direct contribution of food resources to offspring fitness is more easily quantified than other forms of paternal care.

Feeding by males normally begins 5 days after the first egg in the nest hatches (day 6) but may commence a day or two later;

occasionally, males will initiate feeding after young have already fledged (Wilson 1966; Gori, pers. obs.). Since females arrive on territories and initiate nesting throughout the season, nests in all stages of development are available for males to assist. During the breeding season, Yellowheads feed themselves and their young primarily on newly-emerged damselflies and dragonflies. In the study area, males obtain much of this food on their territories while females feed almost exclusively off the territory. Detailed accounts of the breeding cycle and reproductive behavior of Yellowheads can be found in Willson (1966) and Orians (1980).

Observations

The observations reported here were made at four different colonies; three of these, US, Royal, and HD, were located in the drainage area of Hutchinson Lake while the fourth, N. Morgan was located on Morgan Lake. US and Royal colonies were separated by approximately 50 m of open water; since both colonies utilized the same foraging areas and encountered similar levels of insect availability, their observations were pooled in the subsequent analyses. US-Royal was intensively studied from 1979 to 1982; HD was studied in 1981 and N. Morgan in 1982. The number of breeding adults at US-Royal was 126.00 ± 41.02 birds. This figure does not include the 1980 season since breeding that year was terminated prematurely due to ash fall from the Mt. St. Helen's eruption. HD contained 92 breeding adults in 1981; N. Morgan contained 108 breeding adults in 1982.

To facilitate individual identification, I color-banded over 90% of the adult male Yellowheads in the study colonies and mapped all territories. The boundaries were established by observing aggressive encounters and stand-offs between adjacent males early in the season. I also attempted to color-band females but with less success due to their apparent reluctance to enter grain traps. However, by 1982, over 60% of the females in US had been banded. Every 2-3 days, I censused colonies marking all new nests and recording the progress of previously marked ones. Seven or eight days after the first egg in a clutch hatched (day 8 or day 9), I watched the nest for 1 or 2 hours and recorded the time budget of the male and the feeding rate of the female. Whenever possible, I also recorded the feeding rates of surrounding males. On the morning of day 11, I weighed, sexed by weight, and banded nestlings with aluminum Fish and Wildlife Service bands. Some young are capable of leaving the nest at this time although fledging normally occurs later in the day or on the following morning (day 12).

Measurement of Productivity

Marsh productivity was measured using wire-mesh emergence traps similar to those described in Orians (1980). The traps, which were open on bottom, were supported by wooden stakes driven into the substrate. The height was set and maintained so that the bottom of the trap would lie just below the water surface and the top at least 30 cm above; this resulted in an enclosed air space of approximately

0.11 m³. The traps operate in the following manner: emerging aquatic nymphs crawl into them via the cattails and supporting stakes and then metamorphose, in the process losing their gills and developing terrestrial breathing apparatus. Without gills, the newly-emerged teneral are trapped by the surrounding wire mesh and the water below.

Emergence traps were set along the lake margins of the study colonies, 8 traps at US, 8 at Royal, 12 at HD and 14 at N. Morgan. The traps at US, Royal, and HD were emptied each morning by 0600 Pacific Standard Time (PST) and the number of damselflies and dragonflies recorded. Since damselflies emerge during the day and dragonflies during the night and at dawn, damselfly values were assigned to emergence on the previous day while dragonfly values were assigned to the date of collection. The N. Morgan traps were emptied each evening between 1800 and 1900 PST; the number of damselflies and dragonflies recorded were assigned to the date of collection. The mean daily emergence for each colony over the period in which males could potentially care for young was calculated using daily trap averages from May 21 to June 15.

Clutch Reduction Experiment

When male Yellowheads do invest parentally, they typically feed the first nest established on their territory, the primary nest (Willson 1966; Patterson et. al. 1980; J. Wittenberger, pers. comm.). This preference has been attributed to the greater age and therefore, greater reproductive value of young in these nests. To test this

hypothesis, I experimentally reduced the number of young in nests and observed males for any changes in preference. If males are capable of assessing their capacity to contribute to offspring survivorship (Chapter 2) and the reproductive value of nests, they should preferentially feed the oldest, unreduced clutch on the territory. Twenty-four territories in 1981 and 13 territories in 1982 were randomly selected from US, Royal and HD colonies to receive experimental clutch reductions. The reductions were performed either on the first (or primary) nest (single clutch reductions) or on the first two (primary and secondary) nests (double clutch reductions) initiated on the territory. Fifteen territories in 1981 and 8 in 1982 received single clutch reductions while 9 territories in 1981 and 5 in 1982 received double clutch reductions. All remaining territories were unmanipulated and assigned to the control treatment: 32 territories in 1981 and 13 in 1982. Clutch reductions were performed between days 1 and 4 and involved the removal of the last egg(s) or young to hatch. The number of young in experimental nests was reduced to 2 in all cases. Control nests contained 3.62 ± 0.51 young ($n = 161$) at this time. Feeding rates by males and females were recorded when young were 7 or 8 days old; nestlings were banded and weighed on the morning of day 11.

Food Supplementation Experiment

To test whether investment by males in current reproduction was energy-limited, I experimentally increased the availability of food on 13 territories at US-Royal and HD colonies in 1981. To do

this, an artificial feeder provisioned with sunflower seeds was installed on each territory and an abundant supply of seeds maintained there throughout the season. Each of the provisioned males was individually matched with a control male from a neighboring territory of approximately equal quality. In this way, variation in behavior due to differences in the expected mating success of males could be controlled. In addition, the design frequently allowed for simultaneous observation of experimental and control males, thereby controlling for variation in temperature and weather conditions on the date of observation; both of these factors have been shown to affect insect availability and the food demands of young (Willson 1966; Horn 1968; Orians 1980). Experimental and control males were observed whenever nests on their territories were 7 or 8 days old. During observation periods, the time-budgets of males including their feeding rates, the amount of time spent attracting females, the number of calls given, the number of sexual chases, and the amount of time spent foraging on and off the territory were recorded. Comparing the time-budgets of experimental and control males should indicate whether provisioned males invested more in sexual advertisement and parental care than control males. Since only males used the feeders and since sunflower seeds were not fed to young, the fitness return per unit of male investment was unaffected by the experimental treatment.

During the course of the experiment, it became apparent that one of the experimental males did not defend his feeder against

intruders and allowed five different males to feed there regularly. Therefore, in performing the analyses, I initially compared the 13 experimental males with their controls and, if the results of the comparison were non-significant, I included the 5 additional males and their matched controls in order to increase the sample size and obtain greater statistical power. When this was done, the results were unchanged in all but one case.

Results and Discussion

Prediction 1: If current reproduction is energy-limited, then males that are provisioned with supplemental food should spend less time feeding themselves and allocate more energy to sexual advertisement and parental care.

To test this prediction, I performed the feeding experiment described earlier. Experimentally fed males spent significantly more time up on the cattails calling and significantly less time off the territory foraging than control males (Table 1). There was no difference between control and experimental males in the number of sexual chases made or in the amount of time spent down in the cattails foraging. Assuming that leaving the territory has a cost in terms of increasing the risk of cuckoldry (Gori, in prep.), any reduction in foraging time should preferentially occur in the time spent off the territory; the results support this expectation. In addition, experimental males had a significantly greater call rate while up in the cattails and fed young in reduced and unreduced nests at a

Table 1. Time budgets of experimentally fed males and control males. -- Comparisons between experimental and control males were made using Willcoxon matched pairs rank sign tests; means (\pm S.D.), T-values and significance levels (1-tailed) are given below.

	Up In Cattails Advertising (Min/Hr)	# Calls/Min Up In Cattails	Down In Cattails Foraging (Min/Hr)	Off Terr. Foraging (Min/Hr)	# Sexual Chases/Hr	Feeding Rate (# Trips/Hr)
Provisioned Males	22.0 \pm 9.4 (n = 13)	0.72 \pm .61 (n = 13)	12.2 \pm 6.9 (n = 13)	21.8 \pm 10.2 (n = 13)	0.27 \pm 0.37 (n = 13)	4.13 \pm 2.36 (n = 18)
Control Males	13.3 \pm 8.7 T = 7 p < .005	0.44 \pm 0.31 T = 17 p < .025	10.8 \pm 8.2 T = 39 p > .03	35.7 \pm 11.5 T = 6 p < .005	0.28 \pm 0.51 T = 16 p > .4	2.76 \pm 2.45 T = 39 p < .025

significantly greater rate than control males. I interpret these results as follows: provisioning males with food reduced the amount of time they had to spend feeding themselves and increased the total amount of energy available for current reproduction without changing the fitness returns associated with sexual advertisement and parental care. This resulted in an increased investment by males in both activities. Thus, investment in current reproduction appears to be energy-limited for male Yellowheads.

Prediction 2: If parental care and sexual advertisement are mutually exclusive activities in time, males that are not feeding young should spend more time attracting mates than males that are feeding young.

To test this prediction, I compared the time budgets of males that were and were not feeding young for the behavioral categories described previously; time spent off the territory foraging was divided into time spent near the territory (< 50 m away) and far from the territory (\geq 50 m away). The results are summarized in Table 2. In 1981, males that were feeding young (parentals) spent significantly less time down in the cattails foraging and significantly more time off the territory, near, than males that were not feeding young (non-parentals). Associated with this, parental males spent significantly less time up on the cattails calling, gave fewer calls/hr, and were involved in significantly fewer sexual chases/hr than males that were not feeding young. The pattern was similar in 1982. Thus, males that were not raising young spent more time

Table 2. Time budgets of males that fed young (parental) and did not feed young (non-parental) during observation periods. -- Comparisons between parental and non-parental males were made using t-tests; means, t-values, and significance levels (2-tailed) are given below.

	Up In Cattails Advertising (Min/Hr)	# Calls/Hr	Down In Cattails Foraging (Min/Hr)	Off Terr., Near Foraging (Min/Hr)	Off Terr., Far Foraging (Min/Hr)	Sexual Chases (Number/Hr)
Parental Males (n = 77)	11.4 ± 12.5	5.6 ± 8.1	9.3 ± 10.7	14.9 ± 18.1	22.7 ± 20.0	.12 ± .36
Non-Parental Males (n = 47)	19.2 ± 15.0	11.0 ± 15.1	14.1 ± 9.3	5.0 ± 9.8	20.1 ± 21.0	.53 ± 1.20
	t = 3.15	t = 2.52	t = 2.15	t = 3.48	t = 0.67	t = 2.85
	p < .01	p < .05	p < .05	p < .01	p > .5	p < .01

attempting to attract additional females and were involved in more than 4 times the amount of sexual activity as parental males. These results suggest that feeding young reduces the time available for sexual advertisement for male Yellowheads; together with the results for prediction 1, they indicate that a trade-off in fitness returns between parental care and seeking additional mates is likely.

Prediction 3: Males in productive marshes should invest less in parental care than males in unproductive marshes.

This prediction is based on two assumptions: 1) that the ability of males to contribute to offspring survivorship is lower in productive marshes and ii) that males have a greater probability of attracting additional mates in productive marshes than in unproductive ones. In order to test these assumptions, I investigated the relationship between marsh productivity, male pairing success, and the ability of females to raise young without male assistance.

To obtain a measure of insect productivity for the study marshes over the period in which males can potentially care for young, I calculated the mean number of damselflies and dragonflies emerging per trap per day from May 21 to June 15. During this period, young are present in the colony and are completely dependent on their parents for food. The productivity estimates are given in Table 3 and are arranged in order of decreasing damselfly emergence. The mean daily emergence of damselflies was positively correlated with mean daily dragonfly emergence for the marshes and breeding seasons censused (Table 3). However, since newly-emerged dragonflies are available only during the early morning and are less important

Table 3. Daily emergence ($\bar{x} \pm$ S.D.), harem size/male and the number of young fledged from nests not receiving paternal care for each of the study marshes. -- The daily emergence of dragonflies, harem size/male and the fledging success of nests not receiving male parental care were all positively correlated with the daily emergence of damselflies in the marsh; Spearman rank correlation coefficients and significance levels (1-tailed) are given below.

Marsh	Daily Emergence (Damselflies/ Trap/Day)	Daily Emergence (Dragonflies/ Trap/Day)	Harem Size	Fledging Success w/o Paternal Care (# Young/Nest)
N. Morgan 1982	14.58 \pm 6.93 (n = 21)	1.42 \pm 1.13	4.32 \pm 2.28 (n = 20)	3.41 \pm .68 (n = 29)
US-Royal 1979	10.30 \pm 4.41 (n = 24)	0.06 \pm 0.10	4.72 \pm 3.25 (n = 25)	3.08 \pm .78 (n = 29)
US-Royal 1982	8.91 \pm 3.33 (n = 25)	0.10 \pm 0.14	3.90 \pm 1.91 (n = 42)	2.33 \pm .76 (n = 24)
HD 1981	8.01 \pm 2.32 (n = 22)	0.04 \pm 0.04	3.11 \pm 1.52 (n = 22)	2.89 \pm .61 (n = 9)
US-Royal 1981	3.65 \pm 1.38 (n = 21)	0.03 \pm 0.06	3.09 \pm 1.58 (n = 35)	2.22 \pm .58 (n = 27)
		$r_s = 0.90$	$r_s = 0.90$	$r_s = 0.90$
		$p = 0.042$	$p = 0.042$	$p = 0.042$

constituents by weight in the diets of adults and young (Orians 1980), subsequent analyses involving productivity will be restricted to damselfly emergence.

There is significant heterogeneity in the daily emergence values for marshes and years censused indicating statistical differences in the mean productivity of marshes (ANOVA, $F = 19.48$, 112 df, $p < 0.0001$). It is important to note that the actual availability of insects depends on the total number emerging over the entire lake and on the density of breeding birds. Thus, productivity estimates for US-Royal are likely to be conservative since US is situated in a backwater inlet where emergence is lower than in surrounding areas (J. Wittenberger, pers. comm.; Gori, unpubl. data). In addition, twice as many birds bred at US in 1981 and 1982 as did in 1979; consequently, the difference in food availability between 1979 and the other years was probably greater than the values indicate. Despite these qualifications, I assume that the ranking of marshes and years on the basis of productivity remains as indicated in Table 3.

The ability of females to raise young without male assistance was positively correlated with marsh productivity; more young were fledged by females without male help in productive marshes and years than in unproductive ones (Table 3). Similarly, mean harem size/male was positively correlated with marsh productivity; males breeding in productive marshes attracted significantly more females than males in unproductive ones (Table 3). Changes in harem size/male

between years resulted primarily from differential female settlement rather than differential male settlement. At Royal marsh, the number of breeding males remained relatively constant between years (\pm 1-2 males) while the number of breeding females varied with marsh productivity. The same holds for US between 1981 and 1982. Thus, marsh productivity appears to affect the i) density of breeding females in a marsh and hence, their availability to males and ii) the ability of females to fledge young in the absence of paternal care. In unproductive marshes and years, males have a lower probability of attracting unmated females but can potentially contribute more to offspring survivorship.

To test whether males in productive marshes invest less in parental care than males in unproductive ones, I determined the proportion of males feeding nestlings and the proportion feeding nestlings or fledglings for each of the study marshes (Table 4). Monogamously-mated males were excluded from the analysis if the number of young in the nest was reduced to 2 or less by starvation before day 6; the probability that males feed these clutches is significantly lower than for unreduced ones (Chapter 2) and the frequency of starvation-reduced nests varies inversely with marsh productivity (Gori, unpublished data). Inclusion of these data would disproportionately affect values for unproductive marshes and years. The proportion of males that fed nestlings was negatively correlated with marsh productivity, as predicted (Table 4). This relationship is also apparent when comparing US-Royal in productive (1979) and

Table 4. The amount of parental investment by males breeding in the study marshes. -- Marshes are arranged in order of decreasing productivity; see Table 3. Spearman rank correlations were used to investigate the relationship between marsh productivity and male parental investment; correlation coefficients and significance levels (1-tailed) are given below. In general, males in productive marshes invested less in parental care than males in unproductive marshes.

Marsh	Proportion of Males Feeding Nestlings	Proportion of Males Feeding Fledglings	Number of Nests Fed/Male	Proportion of 2 Young Nests Fed	Feeding Rate at Nests With 3-4 Young (Trips/Hr)
N. Morgan 1982	.68 (19)	.84	1.08 \pm .28 (n = 13)	0 (6)	4.42 \pm 3.44 (n = 13)
US-Royal 1979	.71 (21)	.71	1.13 \pm .35 (n = 15)	0 (9)	4.38 \pm 3.19 (n = 15)
US-Royal 1982	.84 (25)	.96	1.33 \pm .49 (n = 12)	.22 (18)	5.47 \pm 4.31 (n = 18)
HD 1981	.82 (17)	.94	1.78 \pm .67 (n = 9)	.31 (16)	6.38 \pm 3.02 (n = 9)
US-ROYAL 1981	.97 (29)	.97	1.70 \pm .57 (n = 20)	.35 (23)	7.00 \pm 4.06 (n = 23)
	$r_s = -.90$ $p = .042$	$r_s = -.80$ $p = .067$	$r_s = -.90$ $p = .042$	$r_s = -.97$ $p < .042$	$r_s = -.90$ $p = .042$

unproductive (1981) years. In 1979, only 71% of the males in US-Royal fed nestlings compared to 97% in 1981 (Fisher exact test, $p = 0.017$). An inverse correlation also exists between marsh productivity and the proportion of males feeding fledglings, although the relationship is only marginally significant (Table 4). For US-Royal, the proportion of males feeding fledglings was significantly lower in 1979 than in 1981 (Fisher exact test, $p = 0.017$). Together these results support the first prediction although the agreement appears to be better for males caring for nestlings than for fledglings. Since the nutritional demands and reproductive value of fledglings are greater than those of nestlings (Fisher 1958; Royama 1966), one might predict that the fitness gains associated with feeding fledglings would be higher. In addition, in all years except 1979, the arrival rate of unmated females was essentially zero by the time young in the primary nest reached the fledgling stage. Therefore, all males (with the possible exception of US-Royal males) would be expected to feed fledglings, thus reducing the differences between marshes and years by the time young leave the nest.

To assess the effect of productivity on parental investment by males that fed nestlings, I compared the number of nests fed by individual males, the proportion of reduced nests fed, and the feeding rates to nests with 3 to 4 young for all marshes and years censused (Table 4). Only control males with harem sizes larger than 2 and that fed at least one nest on their territory were used in calculating the mean number of nests helped/male. Similarly, only

primary and secondary nests were used in determining the proportion of reduced nests fed by males in order to control for the effect of nest rank on the likelihood of male care. As predicted, there was a significant, negative correlation between the mean number of nests fed/male and marsh productivity (Table 4). This trend also holds for US-Royal males between years ($y = - 0.08 x + 2.00$ where x is the mean annual productivity and y is the number of nests fed by individual males, $r^2 = 0.21$, $n = 47$, $p < 0.001$). The proportion of reduced (2 yng) nests fed by males was negatively correlated with marsh productivity; as the availability of food decreased, the proportion of reduced nests helped increased (Table 4). Comparing the extremes in productivity for US-Royal, the proportion of reduced nests fed was significantly lower in 1979 than in 1981 (Fisher exact test, $p = 0.046$). Mean feeding rates by males to nests with 3-4 young were also negatively correlated with marsh productivity (Table 4). This trend is also apparent for US-Royal males between years ($y = - 0.35x + 8.36$ where x is the mean annual productivity and y is the mean feeding rate of individual males, $r^2 = .08$, $n = 56$, $p < 0.02$). Together these results provide additional support for the third prediction. In productive marshes, the total number of nests fed by individual males, the proportion of reduced nests fed and feeding rates by males to unreduced nests were all significantly lower than in unproductive marshes. This result is clearly not due to the differential settlement of males with varying proclivities toward parental care in productive and unproductive marshes since US-Royal

males show a similar pattern between years (individual males return to the same marsh to breed in subsequent years). Rather, males adjust investment in parental care with marsh productivity presumably in response to the underlying variation in fitness gains associated with parental care and sexual advertisement.

Prediction 4: Males should invest more in parental care on days when the insect emergence is low.

To test this prediction, I performed a partial correlation analysis on male feeding rates using damselfly emergence on the day of observation, emergence on the previous day, and harem size (prediction 5) as independent variables. The partial correlation coefficients and significance levels (1-tailed) are summarized in Table 5. As predicted, there was a significant negative correlation between feeding rates by males and insect emergence on the day of observation for both HD and US-Royal colonies in 1981. When daily emergence was low, males fed nestlings at a significantly greater rate. For the other marshes and years censused, feeding rates appeared to be unaffected by daily emergence. Interestingly, there was a significant positive correlation between feeding rates by males and emergence on the preceeding day for US-Royal and HD colonies in 1981 and a marginally significant correlation for US-Royal colony in 1982 (Table 5). Presumably, when food is abundant, males have a more positive energy balance and are capable of feeding young at a higher rate on the following day. This interpretation is consistent with the results of the food supplementation experiment which

Table 5. Partial correlation coefficients for regressions of male feeding rate on harem size, emergence on the day of observation, and emergence on the day before. -- Regressions between male feeding rates and single independent variables were performed while holding constant the remaining two independent variables. Significant correlations are indicated with asterisks; all significance values are based on one-tailed tests.

Marsh	Emergence on Observation Day	Emergence on Day Before Observation	Harem Size
N. Morgan 1982 (n = 14)	.163	-.161	-.007
US-Royal 1979 (n = 27)	.004	-.152	-.425**
US-Royal 1982 (n = 67)	-.093	.173!	-.054
HD 1981 (n = 28)	-.300*	.321*	.130
US-Royal 1981 (n = 39)	-.353**	.282*	.006

! P = .078
 * P < .05
 ** P < .025

show significantly higher feeding rates for males provisioned with supplemental food than for control males (Table 1). Failure to observe daily variation in feeding rates with emergence in other years besides 1981 may have resulted for two reasons. First, the feeding rates of individual males vary a great deal during the day presumably in response to rapid changes in their motivational states (Gori, pers. obs). With a small number of observations on single males, this diurnal variation could have obscured the relationship between emergence and feeding rates in the other years. Second, when productivity is high, daily variations in emergence may have little or no effect on the starvation probabilities of young or on the fitness returns associated with paternal care but, when productivity is low, these daily variations become significant to nestlings and males alike. Significant correlations between male feeding rates and daily emergence for US-Royal and HD in 1981, an unproductive year, and a marginally significant correlation for US-Royal in 1982 are consistent with this latter explanation.

Increased parental investment by males on days when the emergence is low may result from changes in the fitness returns associated with sexual advertisement or parental care. These may arise because the ability of males to contribute to offspring survivorship is relatively greater when the daily emergence is low or because the probability of attracting unmated females is relatively lower at these times. The extent to which the availability of unmated females is affected by daily variations in emergence is

currently unknown although flocks of unmated females, courtship, and copulations have all been observed on days of low emergence. On the other hand, low emergence is often associated with bad weather. During bad weather, the rate of heat loss by young in the nest presumably increases resulting in greater daily energy requirements for nestlings (Willson 1966). In addition, on days when the emergence is low, females make fewer feeding trips to the nest and the starvation rate of young is significantly increased (Willson 1966; Gori, unpubl. data). Both of these observations suggest that the ability of males to contribute to offspring survivorship increases with decreasing daily emergence.

Prediction 5: Parental investment by males should be inversely related to their success in attracting females.

To investigate the effect of mating success on the probability that males provide parental care, I scored the number of "high success" and "low success" males that fed and did not feed nestlings. I operationally defined high success males as those with harem sizes greater than the mean value appropriate for the marsh and year and low success males as those attracting fewer than the mean. The analysis was performed separately for productive (N. Morgan 1982, and US-Royal 1979) and unproductive (US-Royal 1982; US-Royal-HD 1981) marshes. In productive marshes, high success males had a significantly lower probability of caring for young than low success males did (Table 6, Fisher exact test, $p = 0.014$). Fifty percent of the

Table 6. The number of high success and low success males that did and did not feed nestlings in productive marshes. -- High success males had a significantly lower probability of feeding young than low success males (Fisher exact test, $p = 0.014$).

	Fed Nestlings	Did Not Feed Nestlings
High success males	9	9
Low success males	19	3

high success males fed nestlings compared to over 85% of the low success ones. However, in unproductive marshes, high and low success males had an equal probability of caring for young (Table 7, Fisher exact test, $p = 0.371$). In this case, 91% of the high success males fed nestlings compared to 86% for low success males.

As a further test of the prediction, I compared high and low success males that fed young with respect to the mean number of nests fed per male, the duration of care, and their feeding rates to young of unreduced nests. Only males with more than one nest on the territory were included in the determination of mean number of nests fed/male (only those males with no experimental clutch reductions were used in prediction 3); all males were used in the analysis of care duration except US-Royal males in 1979, who were excluded due to a small number of replicate observations on individual nests. Duration of care was calculated by determining the total period individual males were observed feeding nestlings and fledglings. In 1981 and 1982, there was no difference between high success and low success males in the number of nests fed/male (Table 8). Similarly, in both years, high and low success males fed young for a similar period of time (Table 8).

To investigate the effect of male pairing success (harem size) on the feeding rates to nests receiving care, a partial correlation analysis was performed on these variables holding constant the effect of emergence on the day of observation and on the previous day. In 4 out of 5 cases, there was no significant effect

Table 7. The number of high success and low success males that did and did not feed nestlings in unproductive marshes. -- High success and low success males had a similar probability of feeding young (Fisher exact test; $p = 0.371$).

	Fed Nestlings	Did Not Feed Nestlings
High success males	32	3
Low success males	31	5

Table 8. The number of nests fed/male and the duration of parental care by high success and low success males. -- The amount of parental investment by the two groups of males was compared using t-tests; t-values and significance levels (2-tailed) are given below. There was no effect of mating success on the number of nests fed/male or on the duration of care in 1981 and 1982.

	# Nests Fed/Male	Care Duration (Days)
1981 HD and US-Royal		
High Success Males	1.50 \pm .63 (n = 19)	8.68 \pm 3.50
Low Success Males	1.40 \pm .50 (n = 20)	10.10 \pm 3.28
	t = .55 p > .5	t = 1.31 p > .18
1982 US-Royal and N. Morgan		
High Success Males	1.27 \pm .59 (n = 15)	8.56 \pm 6.13 (n = 16)
Low Success Males	1.21 \pm .42 (n = 19)	8.24 \pm 4.83 (n = 21)
	t = .35 p > .5	t = .18 p > .5

harem size on male feeding rates (Table 5). However, in 1979, high success males at US-Royal fed young at a significantly lower rate than low success ones. The variance in harem size at US-Royal in 1979 was significantly higher than in other years or marshes censused (F-tests, all F's > 4.23, all p's < 0.001 except the N. Morgan-US-Royal, 1979, comparison where $F = 2.03$, $0.05 < p < 0.1$). If variation in harem sizes reflects underlying differences in territory quality, the difference in the expected mating success of males would be greater in 1979 than in the other years resulting in a greater difference between males in the expected returns from sexual advertisement and parental care and their investment in both. This, in turn, would increase the probability of observing a relationship between harem size and feeding rates given a considerable level of "noise" in the latter.

In summary, the proportion of males feeding young was significantly lower among high success birds in productive marshes suggesting a reduced probability of paternal care for males with relatively better chances of attracting additional mates. There was no difference in the proportion of high and low success males feeding young in unproductive marshes. Similarly, there were no differences in the mean number of nests fed/male or in the period of time males spent feeding young for high and low success males in 1981 and 1982. Food delivery rates to nests were unaffected by male success in most years except in 1979 when the feeding rates of

US-Royal males were inversely correlated with harem size. Thus, in productive marshes, the mating success of males appeared to affect some aspects of their parental investment.

It is important to note that the variation in mating success between males was not merely a consequence of their different allocations to sexual advertisement but depended, in large part, on differences in territory quality (J. Wittenberger, unpubl. ms.; Gori, in prep.). In addition, the reduced parental care by high success males was not a direct result of their more frequent courtship of females since most advertisement occurred when unmated females were absent from the territory. I suggest that the presence of these females on other territories or around the marsh and the greater probability of attracting them was responsible for the reduced parental care by high success males. Why this effect might be restricted to productive marshes will be discussed under the following prediction.

Prediction 6: Males should initiate parental care when the probability of attracting additional mates is low.

To test the prediction, I calculated the mean calendar date that young in primary nests were 7 days old (focal date) for high success and low success males and then determined the arrival rate of unmated females around this date in order to derive specific predictions for the initiation of paternal care for each of the study marshes. Comparison of the mean observed initiation date for paternal care with the mean focal date gives a relative measure of when care by high and low success males was initiated. To estimate

the arrival rate of unmated females, I determined the number of nests established within a 4 day period prior to the focal date, within 5 days after the focal date, and from this date until the end of the season. Nest establishment was noted at the time when the first egg appeared in the nest, although females were present in the marsh before this since nest construction normally takes 1-3 days. Therefore, I assume that the number of nests initiated 5 days after the focal date reflects the availability of unmated females on or around the focal date and the number of nests initiated 4 days before, the availability of females somewhat before the focal date. Since virtually all of these nests were established on territories belonging to males with greater than average pairing success earlier in the season (Gori, unpubl. data), the arrival rate of unmated females should disproportionately affect the strategies of high success birds. For this reason, I have expressed nest establishment on a per high success male basis in Table 9.

There appears to be a clear distinction between productive and unproductive marshes in the availability of unmated females around the focal date for successful males (Table 9; May 1 = 1). In productive marshes (N. Morgan and US-Royal, 1979), relatively more nests were initiated within 5 days after the focal date for high success males and a greater percentage of the total number of nests were initiated after this date than in unproductive marshes (US-Royal, 1981 and 1982, HD 1981). Furthermore, the arrival rate of females was higher for longer at US-Royal, 1979, than at N.

Table 9. The mean date that young in the primary nests are 7 days old (focal date) for high success (HS) and low success (LS) males and nest establishment before and after the focal date. -- Nest establishment is expressed on a per high success male basis and is used as an estimate for the arrival rate of unmated females. (May 1 = 1) in productive marshes (N. Morgan, 1982, and US-Royal, 1979), the arrival rate of unmated females is still high around the focal date for high success males (see text for further explanation).

Marsh	Focal Date	# Nests Estab- lished/High Succ. Male 4 days before Focal Date	# Nests Estab- lished/High Succ. Male 5 days after Focal Date	# Nests Estab- lished/High Succ. Male after Focal Date	% Total Nests Established after Focal Date
N. Morgan 1982	HS 22.50 ± 2.26 (8)	1.38	1.38	1.75	17
	LS 31.15 ± 6.95 (11)	0.09	0.27	0.38	4
US-Royal 1979	HS 26.55 ± 8.35 (10)	1.80	1.10	3.30	27
	LS 31.19 ± 7.99 (11)	1.00	0	2.20	18
US-Royal 1982	HS 25.42 ± 3.80 (20)	0.45	0.15	0.70	9
	LS 27.57 ± 3.46 (21)	0.24	0.10	0.55	7
US-Royal, HD 1981	HS 24.86 ± 3.18 (21)	0.43	0	0.62	8
	LS 28.58 ± 5.69 (25)	0	0	0.62	8

Morgan: only 3 nests (4%) were initiated after the focal date for low success males at N. Morgan compared to 22 nests (18% at US-Royal, 1979).

Based on these data, I predict that in productive marshes, high success males should begin feeding young after their mean focal date since the expected fitness gains associated with sexual advertisement exceed those for parental care at this time. At N. Morgan, parental care theoretically can increase male fitness by 0.21 fledglings (Table 3) while sexual advertisement can increase fitness by 4.71 fledglings (1.38 nests/high success male (Table 9) x 3.41 fledglings/nest (Table 3)) assuming that sexual advertisement is a prerequisite for mate acquisition. Similarly, at US-Royal 1979, parental care can increase male fitness by 0.54 fledglings (Table 3) compared to 3.39 fledglings for sexual advertisement (1.1 nests/high success male x 3.08 fledglings/nest, Tables 3 and 9). Furthermore, care should be even more delayed at US-Royal, 1979, than at N. Morgan since the arrival rate of females is higher for longer at US-Royal. In contrast, in unproductive marshes, the arrival rate of females was low around the focal date for high success males and therefore, these birds should be feeding young on their focal dates. Low success males in all marshes and years should be feeding young on their focal dates.

The data support all of these predictions. High success males at N. Morgan and US-Royal, 1979, began feeding young significantly later than the mean date at which young in the primary nest

were 7 days old (Table 10). Furthermore, the mean date for initiation of feeding was significantly later for high success males at US-Royal than at N. Morgan (June 13 vs. May 29, Table 10; t-test, $t = 3.33$, 10 df, $p < 0.01$); at US-Royal, the mean rank of the first nest to receive care was 4.33 ± 1.97 compared to a mean rank of 1.00 ± 0.00 for N. Morgan (t-test, $t = 4.56$, 10 df, $p < 0.001$). In addition, only 3 nests were initiated at N. Morgan after May 29 and 2 nests at US-Royal after June 13 indicating that when high success males began feeding young, the arrival rate of unmated females had dropped to essentially zero.

In contrast, high success males at US-Royal, 1982, and US-Royal-HD, 1981, were feeding young on their focal dates (Table 10). Similarly, low success males in all marshes and years were feeding young on their focal dates. Thus, males tend to initiate parental care when the probability of attracting additional mates is low.

Differences in the arrival rates of unmated females in productive and unproductive marshes may also account for why male mating success appeared to affect parental investment in productive marshes but not in unproductive ones. In productive marshes, the arrival of unmated females was still high on the focal date resulting in differences in the expected mating success of high and low success males after the focal date. In contrast, in unproductive marshes, the arrival rate of females was low on the focal date and the expected mating success of all individuals was approximately zero. Theoretically, what is important in determining parental

Table 10. The mean date of initiation of paternal care and the date that young in the primary nests are 7 days old (focal date) for high success (HS) and low success (LS) males. -- Comparisons of the two dates were performed separately for high success and low success males using t-tests; t-values and significance levels (2-tailed) are given for all comparisons.

N. Morgan 1982	HS	22.50 ± 2.26 (8)	29.22 ± 5.85 (7)	t = 3.02, p < .01*
	LS	31.15 ± 6.95 (11)	30.75 ± 5.52 (9)	t = 0.14, p > .5
US-Royal 1979	HS	26.55 ± 8.35 (10)	44.80 ± 10.40 (5)	t = 3.96, p < .01*
	LS	31.19 ± 7.99 (11)	32.10 ± 8.85 (10)	t = 0.25, p > .5
US-Royal 1982	HS	25.42 ± 3.80 (20)	26.38 ± 3.57 (11)	t = 0.69, p > .4
	LS	27.57 ± 3.46 (21)	27.46 ± 3.04 (13)	t = 0.09, p > .9
US-Royal-HD 1981	HS	24.86 ± 3.18 (21)	25.67 ± 3.17 (12)	t = 0.82, p > .4
	LS	28.58 ± 5.69 (25)	28.52 ± 4.50 (17)	t = 0.04, p > .9

investment is an individual's expected mating success, and in productive marshes, this varied between males while in unproductive ones, the expected mating success was equal for all males.

Prediction 7: When parental care becomes advantageous, males should feed the oldest and largest nest on their territory.

To test this prediction, I reduced the number of young in nests (single clutch reduction (SCR) = primary clutch reduced; double clutch reduction (DCR) = primary and secondary clutch reduced; see methods) and then observed whether primary, secondary, or tertiary nests were preferentially fed by control and experimental males. Preferential care for a nest was defined on the basis of the following criteria: i) if the nest received a majority of visits by the male, or ii) if the initiation of care was associated with the termination of investment at another nest. Ninety-three percent of the control males preferentially fed primary nests compared to only 24% of the males in the single clutch reduction treatment (Table 11). The majority of males receiving single clutch reductions (71%) fed secondary nests (Table 11). Similarly, the majority of males receiving double clutch reductions (83%) preferentially fed tertiary nests compared to only 6% of the males in the single clutch reduction treatment and none of the males in the control treatment (Table 11). Thus, males preferentially fed the oldest unreduced nest on their territory suggesting that they are capable of assessing the reproductive value of nests and the relative fitness returns associated with feeding reduced and unreduced clutches (Chapter 2).

Table 11. The number of males that preferentially fed primary, secondary, and tertiary nests for control, single clutch reduction and double clutch reduction treatments, 1981 and 1982 combined. -- The majority of males preferentially fed the oldest, unreduced nest on their territories.

	Control	Single Clutch Reduction	Double Clutch Reduction
1	27	4	0
2	2	12	2
3	0	1	10

Control-SCR $X^2 = 21.55$, $p < 0.001$

Control-DCR $X^2 = 36.13$, $p < 0.001$

SCR-DCR $X^2 = 18.14$, $p < 0.001$

Patterson et al. (1980) report similar results for the single clutch reduction treatment, however, males receiving double clutch reductions in their study preferentially fed reduced primary nests. This difference can be reconciled with the results presented here. In Patterson et al. (1980), tertiary nests had a significantly higher probability of predation than primary nests so that the expected number of young fledged from unreduced tertiary clutches was about equal to the number fledged from reduced primary nests. Preference for the primary nest may have arisen for the following reasons. First, the proportion of parentally incompetent females is higher for tertiary nests than for primary nests and the return on male investment with respect to fledgling weight is greater for nests belonging to competent females (Chapter 2). Second, the overwinter survivorship of young produced in earlier nests may be higher than for young produced later in the breeding season since earlier young may be fledged at a greater weight and have a longer period of time to feed before fall migration (Perrins 1965, 1966). Third, since the between-year variance in predation rates appears to be greater for nests established late in the season than for primary clutches (Gori, unpubl. data), males may increase fitness to a greater extent by caring for reduced nests with a predictable (low variance) probability of predation than by caring for later, unreduced ones with a less predictable (high variance) probability even though the mean fledgling success of the nests are equal (Caraco 1980; Real 1980a, 1980b; Rubenstein 1982). All of these factors would tend to increase the reproductive

value of young in primary nests relative to young in tertiary nests and therefore, explain male preference for reduced primary nests. However, in the present study the probabilities of nest predation for primary and tertiary nests were equal and therefore, the expected number of young fledged from unreduced tertiary nests was significantly greater than for reduced primary nests (Chapter 2). Taken together, the results of the two studies suggest that males may be able to predict the probabilities of nest predation and can incorporate this estimate into their assessments of the expected returns on investment for different nests. Certain marshes have similar predation rates year after year and, within marshes, predation rates are significantly higher later in the season than earlier (Gori, unpubl. data). Both of these factors potentially allow males with breeding experience to assess the predation probabilities on nests.

General Discussion

The results of this study indicate that allocation to current reproduction by male Yellowheads is energy-limited, that investment in parental care and sexual advertisement is mutually exclusive in time and complementary, and that males are able to assess the fitness returns associated with caring for young and attracting additional mates and can adjust the amount and timing of their parental investment so as to maximize reproductive success. Specifically, I have shown that:

1. Males that were provisioned with supplemental food spent more time feeding young and attempting to attract additional mates and also had a significantly greater call rate while advertising than unfed controls. These results suggest that male investment in current reproduction is energy-limited.

2. Males that were not feeding young spent more time attracting mates and less time foraging than males that fed young. In addition, non-parental males gave more calls/hr. and were involved in more than 4 times as many sexual chases as parental males.

3. The average success of males at attracting females (i.e. the density of breeding females) and the ability of these females to fledge hatchlings without male assistance were both positively correlated with marsh productivity. Thus, variation in productivity between marshes and years appears to affect the fitness gains associated with parental care and sexual advertisement; variation in parental investment by males appears to reflect the underlying variation in these pay-offs.

4. The proportion of males caring for nestlings was negatively correlated with the mean marsh productivity of damselflies. For males that fed young, the amount of parental care, as measured by the mean number of nests fed/male, the proportion of reduced nests fed, and the mean feeding rate to nests, was also negatively correlated with marsh productivity. This relationship also appears to hold for individual marshes between productive and unproductive years. Since the majority of males return to marshes year after

year to breed (Gori, unpubl. data; J. Wittenberger, pers. comm.), this latter result indicates that individuals are capable of adjusting their paternal investment with the availability of food and mates.

5. In unproductive marshes, eg. HD and US-Royal, 1981, feeding rates at nests were negatively correlated with the daily emergence of damselflies and positively correlated with emergence on the previous day. Thus, males fed nests at a higher rate when they acquired more energy for themselves on the previous day and when the food demands of young increased. This result is consistent with that of the food supplementation experiment.

6. In productive marshes, males that had greater than average mating success (high success) had a lower probability of feeding nestlings than males with lower than average mating success (low success). Furthermore, high success males fed young at significantly lower rates than low success males did at US-Royal in 1979. In unproductive marshes, there was no difference between males in their feeding rates at nests, the number of nests fed, or in the duration of their parental care.

7. Males initiated parental care when the probability of attracting additional females was low. In unproductive marshes, the arrival rate of unmated females was close to zero by the time primary nests were 7-8 days old and all males were feeding young at this time. In productive marshes, the arrival rate of females was still high on the focal date for high success males and care by these males was delayed; low success birds had a low probability

of attracting these females and were feeding young on their focal dates. In productive marshes, care was initiated by high success males when the arrival rate of new females was approximately zero.

8. In general, males preferentially fed primary nests. When the number of young in these nests was reduced experimentally, males fed the next oldest, unreduced clutch on the territory presumably because the return on investment is greater for unreduced nests and the reproductive value of older young is higher (Chapter 2; Fisher 1958).

Taken together these results provide consistent evidence that males are faced with two alternative strategies for maximizing current reproductive success, investing time and energy in sexual advertisement or in parental care. Investment in both of these strategies appears to be energy-limited in the sense that reducing the amount of time males spend foraging for themselves and increasing their rate of energy acquisition results in an increase in time and energy devoted to current reproduction. In addition, the results show that males are capable of assessing the relative pay-offs associated with these alternative strategies and will increase their investment in parental care when their ability to contribute to offspring survivorship increases and when the probability of acquiring additional mates decreases. Thus, paternal investment is greater in unproductive marshes, on days when the emergence is low, at unreduced nests, when the arrival rate of unmated females is low, and for low success males with poor territories.

A number of other studies report similar results. In European wrens (Troglodytes troglodytes), Armstrong (1955) suggested an association between the occurrence of polygyny, little parental investment by males, and high food availability on the one hand and between monogamy, sizeable paternal investment, and low food availability on the other. Armstrong suggests that in unproductive habitats, paternal care is required to provide enough food for young, while in productive ones, females are capable of raising young without the male's help. Although food abundance may be one factor promoting polygyny, polygynous male wrens still fed young and the problem remains of what factors influenced the amount and timing of their investment. Comparing two populations of Marsh Wrens (Cistothorus palustris), Verner (1964) found that in the productive marshes of eastern Washington, female settlement was less synchronous and harem sizes were larger than in the less productive marshes of western Washington. Associated with this, the latter males fed primary nests as soon as the young hatched while the former began feeding young at the end of the breeding season. The effect of mating success and productivity on the amount of parental investment by males was not investigated.

Similar patterns have also been reported in Bobolinks (Dolichonyx oryzivorus), Red-winged Blackbirds (Agelaius phoeniceus), and meadowlarks (Sturnella sp.). In an Oregon population of Bobolinks, the arrival of females was more synchronized and harem sizes were smaller than those in a Wisconsin population. Associated with

this, males fed both their primary and secondary nests in Oregon (Wittenberger 1978) while secondary nests rarely received assistance in Wisconsin (Martin 1974). Similarly, in Redwings, males breeding in productive marshes in eastern Washington (the Potholes) had larger harems and rarely fed young (Orlans 1980) while males in less productive marshes in Indiana attracted fewer mates and commonly fed nestlings and fledglings (Patterson 1978). For meadowlarks, Lanyon (1957) reported that the frequency of males feeding young "appeared to vary according to the degree of attention devoted to other females" (p. 43); unfortunately, no quantitative data were presented to support this observation.

Comparative results have also been reported in mammals. In hoary marmots (Marmota caligata), males living in isolated colonies spent more time close to infants and directed a greater percentage of their "greetings" to young than did males living in a larger, more interactive colony (Barash 1975). (It is not clear from the data whether the total number of greetings directed at young was greater at isolated colonies). Barash suggests that increased paternal greeting and proximity to young may enhance the social integration of infants and predator avoidance and interprets the greater parental investment by males at isolated colonies as the result of the reduced advantages to defending reproductive interests in the absence of competing males.

The results for Yellowheads and other species provide consistent evidence in support of the models for the evolution of

paternal care. Two factors appear to be of overriding importance in determining the level of parental investment, i) the ability of males to contribute to offspring fitness beyond what the female is capable of achieving alone and ii) the probability that males can attract additional mates. In contrast to previous studies where both of these factors covaried with food availability such that their effects were confounded, the present results indicate that individuals can respond to variations in each of these factors independently.

Summary

Models for the evolution of paternal care assume that males can influence current reproductive success in one of two ways: by caring for young and increasing their chances of survivorship or by deserting young and attempting to attract additional mates. According to the models, parental investment by males will increase as their ability to contribute to offspring survivorship increases and as the probability of attracting unmated females decreases. Using both naturally occurring variation in marsh productivity, male mating success, and nest composition and field experiments, I tested the assumptions and predictions of these models in Yellow-headed Blackbirds. I found that the assumed trade-off between sexual advertisement and parental care was apparently justified for Yellow-heads because these activities were mutually exclusive in time, energy-limited, and showed a complementarity in investment such that males that fed young (parentals) spent less time advertising

for mates than non-parental males. Furthermore, I found that male Yellowheads were capable of assessing the fitness returns associated with parental care and sexual advertisement and increased their parental investment when their ability to contribute to offspring survivorship increased and when the probability of acquiring additional mates decreased. Thus, parental investment by males was greater in unproductive marshes, on days when the emergence was low, at unreduced nests, when the arrival rate of unmated females was low, and for males with lower than average mating success.

CHAPTER 2

ADJUSTMENT OF MALE PARENTAL INVESTMENT WITH MATE QUALITY AND NUMBER OF YOUNG IN POLYGYNOUS YELLOW-HEADED BLACKBIRDS

Introduction

In many species with parental care, the number and quality of offspring an individual produces depends not only on its own competence as a parent but also on the abilities of its mate. Parental ability is not constant among individuals but may vary with age, rank, experience, mate familiarity, physical condition and genetic quality (Coulson 1966; Lack 1968; Burley and Moran 1979; Burley 1981). Because of the contribution of parental care to Darwinian fitness, individuals should be under strong selective pressure to evaluate the parental abilities of mates and potential mates and to adjust their own investment in young in accordance with these assessments so as to maximize reproductive success.

Numerous authors have recognized the theoretical importance of selecting mates with superior parental abilities (Trivers 1972; Williams 1975; Burley 1977; Maynard Smith 1978). However, the empirical evidence for mate selection on this basis or on the basis of correlated proximate cues is limited. In Kittiwake Gulls and pigeons, individuals of both sexes have been shown to pair selectively with older, more experienced birds; age and breeding experience in both species are positively correlated with fledging success

(Coulson 1966; Burley and Moran 1979; Burley 1981). In Common Terns, male courtship feeding is significantly correlated with the rate at which males later feed young (Nisbet 1973) and in Redwinged Blackbirds, courtship time is significantly correlated with male breeding experience and subsequent feeding effort (Yasukawa 1981; Searcy and Yasukawa 1981). In neither of the latter two studies, however, was there clear evidence that females used these cues in mate selection.

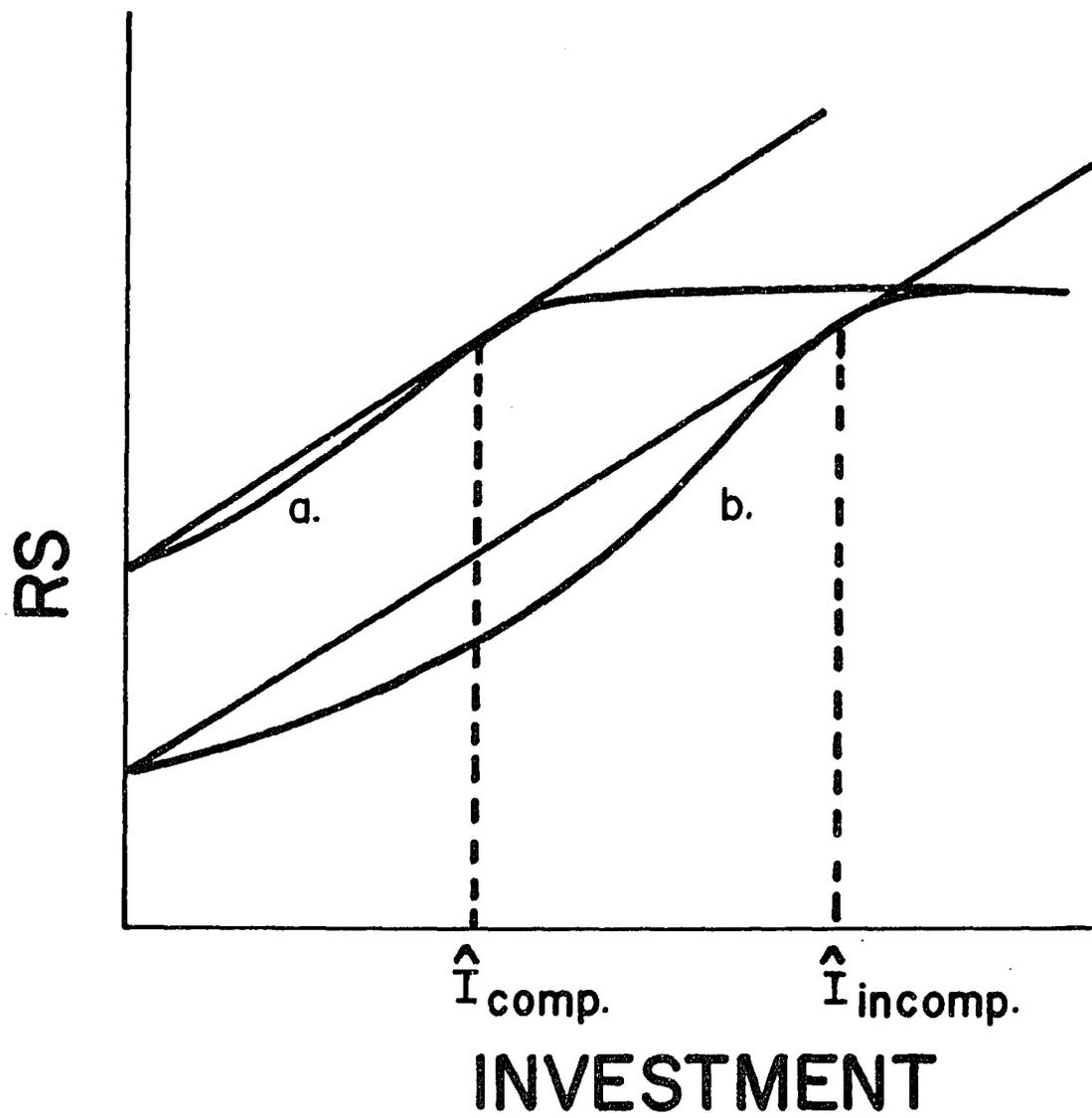
Given that mate selection occurs, little attention has been devoted to the corollary question of how individual investment should vary with mate quality. How should an individual adjust its investment in response to a mate who shows a reduced capacity to raise young? If the probabilities of finding a better mate and successfully breeding that season are high, desertion may be favored (Trivers 1972; Maynard Smith 1977; Dawkins and Carlisle 1976). Otherwise, an individual may maximize reproductive success by remaining with that mate at least for the duration of the season and adjusting the amount of parental care given to young. In theory, this adjustment can involve either an increase or decrease in investment depending on an individual's potential for investment, on the expected return from that investment, and on the number of mates it may obtain during the breeding season. The following argument is presented to clarify the effect of these variables on the adjustment decision.

Assume that reproductive success is an increasing function of parental investment and that above a certain point additional investment yields progressively smaller returns in reproductive

success: that is, the function has a negative second derivative over the range of large individual investments (Figure 1). Following Trivers (1972), parental investment is defined as an expenditure of energy or other limited resources on current young which increases their survivorship at the expense of a parent's ability to invest in future offspring. When fitness for a breeding season depends on the fate of a single mate or nest, the investment that maximizes reproductive success, \hat{I} , is simply the point of tangency between the curve and a line of maximum slope running through the y-intercept. Having a parentally incompetent mate in effect shifts an individual's curve to the right resulting in a greater predicted \hat{I} (Figure 1). Therefore, for females and monogamously-mated males, investment in young should increase when mated with parentally incompetent individuals.

In contrast to the previous situation, fitness for a polygynous male during a breeding season does not depend on the performance of single mates or nests. Males have a choice of where to direct aid, and they should prefer to help mates that give them the greatest return on their investment. As with monogamously-mated individuals, the rate of return per investment will depend on the slope of the fitness function; a greater slope corresponds to a greater return per unit of investment. Therefore, males can maximize reproductive success by helping either capable or incapable mates depending on which has the greater slope over the region of intended investment. The amount of time a male devotes to parental care will depend on a number of factors including i) the degree to

Figure 1. A hypothetical relationship between reproductive success (RS) and parental investment for females and monogamously-mated males with parentally competent (a) and incompetent (b) mates. -- The investment which maximizes RS, \hat{i} , occurs at the intersection of the curve with the tangent line of maximum slope passing through the y-intercept. An incompetent mate in effect shifts an individual's curve to the right resulting in a larger \hat{i} .



which fitness can be enhanced by raising young compared to attracting additional mates and the amount of time males devote to pursuing the latter activity (Chapter 1) and ii) the precise trade-off between current investment and future reproduction.

In this paper, I present evidence that male Yellow-headed Blackbirds (Xanthocephalus xanthocephalus) are capable of distinguishing the parental capabilities of their mates and can adjust the level of their parental investment with mate quality and the number of young in nests in a manner consistent with theory. Since the adjustment for polygynous males depends on the underlying fitness functions, I derive these empirically for competent and incompetent mates and then use these functions to predict male preference. The predicted pattern of investment is then tested using field observations of male Yellow-heads.

Methods

The Study Area

The research was conducted in 1981 and 1982 in the Hutchinson Lake drainage area, Columbia National Wildlife Refuge, Grant Co., Washington. The refuge is located in the Columbia Basin desert which lies in rainshadow of the Cascade Mountains and receives approximately 20 cm. of precipitation annually. The regional topography is characterized by buttes and basins scoured in the Columbia basalt by a series of large-scale Pleistocene floods (Bretz 1959). Low-lying areas were virtually dry until the advent of local irrigation at the

turn of the century. With the completion of the Columbia River Water Project in the early 1950's, existing bodies of water were greatly enlarged and numerous others created by extensive irrigation runoff and rising ground water levels. It is unlikely that blackbirds were breeding in any significant numbers in the area before the existence of standing water.

The upland vegetation is characterized by sagebrush (Artemesia tridentata), bluegrass (Poa sp.), bunchgrass (Agropyron spicatum), and cheatgrass (Bromus tectorum). Greasewoods (Sarcobatus vermiculatus) dominate the alkaline pans surrounding the shores of lakes and marshes; cattails (Typha angustifolia) and bullrushes (Scirpus sp.) grow in the shallow aquatic margins of these bodies of water and provide nest sites for blackbirds.

The Study Organism

Yellow-headed blackbirds are polygynous, marsh-nesting members of the family Icteridae. They breed throughout the United States and Canada west of the Mississippi River and are locally abundant in productive lakes, marshes and irrigation ditches (Orians 1966, 1980). In the study area, males may attract from 0 to 15 mates; mean harem size was 3.09 ± 1.51 (S.D.) females/male ($n = 57$) in 1981 and 3.90 ± 1.91 females/male ($n = 42$) in 1982. Females arrive asynchronously onto territories to breed so that young are available for males to raise throughout the breeding season. Yellow-head males show considerable variation in the amount of parental care directed to young, especially in the rate at which they feed

nestlings and fledglings. The analyses presented in this paper are restricted to this component of paternal care. Feeding by males normally begins 5 days after hatching of the first egg in the nest (day 6; day 1 corresponds to the hatching date of the first egg) but may commence a day or two later. Occasionally, males will begin feeding even after young have already fledged. Because of the delay in the initiation of paternal care, the number of young in nests on day 6 should be positively correlated with the parental competence of females.

During the breeding season, adult Yellowheads feed themselves and their young primarily on emergent damselflies and dragonflies. In the study area, males obtain this food both on and off their territories while females with young feed almost exclusively off the territory. Yellowheads begin nesting in late April, early May and continue until late June. Detailed accounts of the breeding cycle can be found in Willson (1966) and Orians (1980).

Observational and Experimental Methods

The observations reported here were made on 3 colonies in the Hutchinson Lake drainage area. I color-banded over 90% of the adult male Yellowheads in these colonies and mapped all territories. Boundaries were established by observing territory disputes and stand-offs between adjacent males early in the season. I also attempted to color-band females but with less success due to their apparent reluctance to enter grain traps. By 1982, however, over 60% of the females in one of the colonies had been banded. Every 2 to 3 days,

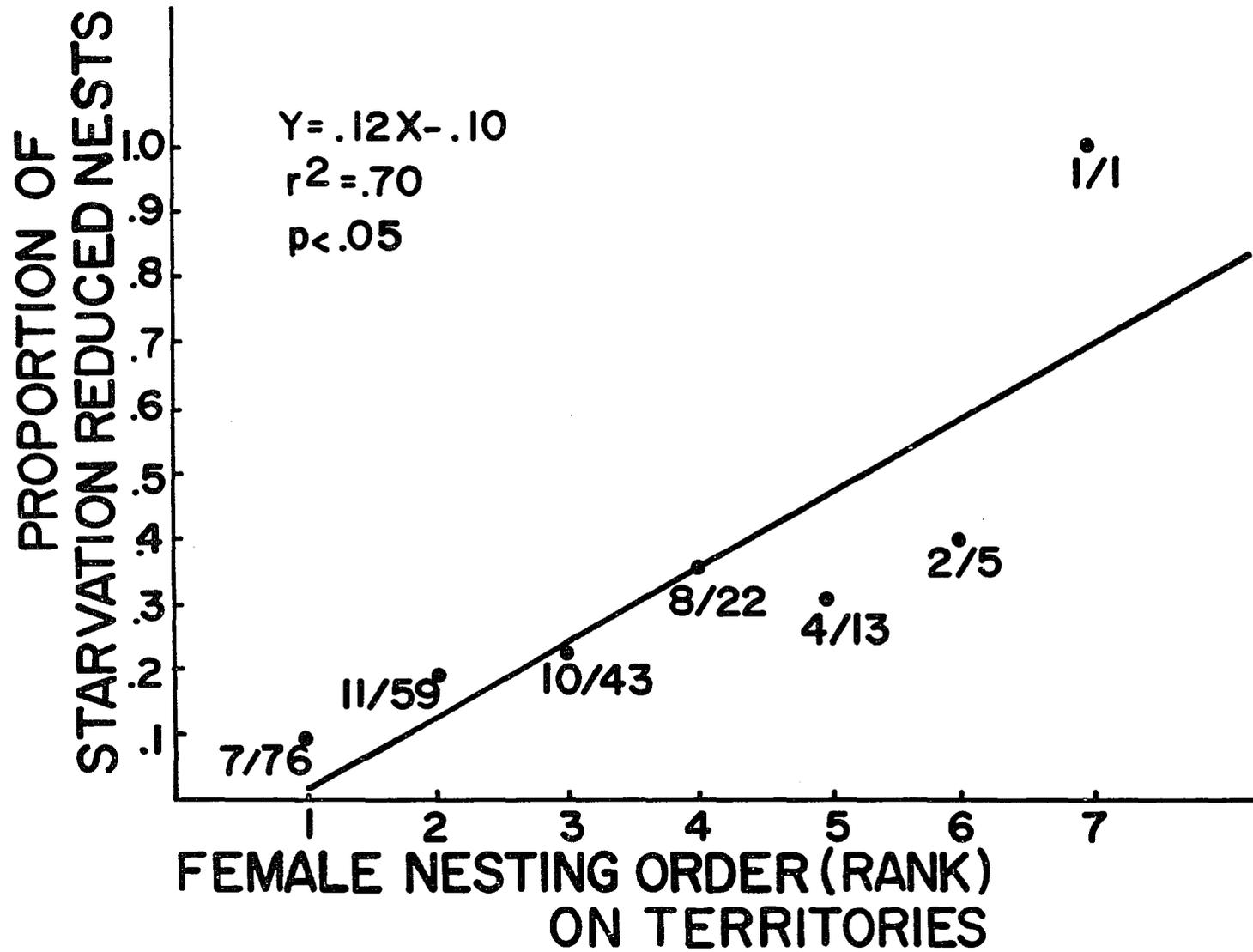
I censused colonies, marking all new nests and recording the progress of previously marked ones. Seven or eight days after the first egg in a clutch hatched (day 8 or day 9), I watched the nest for 1 or 2 hours and recorded the time budget of the male and the feeding rate of the female. Most of the nests in the 3 colonies were observed at least once; observations were made between 0900 and 1300 and between 1400 and 1600 hours Pacific Standard Time. On the morning of day 11, I weighed, sexed by weight, and banded nestlings with aluminum Fish and Wildlife Service bands. Some young are capable of leaving the nest at this time, although fledging normally occurs later in the day or on the following morning (day 12). Male offspring leave the nest at a substantially greater weight than females. This weight difference first appears several days after hatching and at fledging, male and female weight distributions are completely non-overlapping (Willson 1966, Gori unpublished data).

Females show considerable variation in parental ability. Normally, they hatch 3 to 4 young and at least 3 young are still alive until day 6. I considered females in this group to be parentally competent. In some cases, however, 3 to 4 young hatch but only 2 young survive to day 6. I operationally defined these females as poor parents, assuming that starvation resulting from parental incompetence was the primary cause of clutch reduction in these cases. Predation on nests is common, but it normally involves removal of all young from nests (Orians 1980; Patterson et al. 1980). In addition, my 1979 data on nestling growth rates indicate that

disappearance of single individuals from complete nests is preceded first by the cessation of weight gain then by rapid weight loss (Gori, unpublished data). I assume that these conditions are a likely prelude to starvation. Unfortunately, dead young are removed from nests by females making it difficult to test this assumption although in rare cases when they are left, these are the same individuals in which weight loss was rapid.

In order to decouple the correlation between the number of young in nests and mate quality and investigate the effect of these factors separately on male investment, twenty-four territories in 1981 and 13 territories in 1982 were randomly selected to receive experimental clutch reductions. The reductions were performed on either the first (primary) or the first two nests (primary and secondary) initiated on the territory and involved the removal of the last egg(s) or the last young to hatch. The number of young was reduced to two in all cases. The reductions were performed anywhere from day 1 to day 5 with a mean day of 2.65 ± 1.54 ($n = 46$). The majority of females receiving these reductions were competent parents (see Figure 2 and text for further explanation) but, following the experimental treatment, had the same number of young as incompetent females. By comparing male behavior at experimental and starvation-reduced nests, the response of males to competent and incompetent mates could be determined while controlling for differences in the number of young/nest. Similarly, comparing experimental and

Figure 2. The relationship between the proportion of starvation-reduced nests and female nesting order on territories. -- Later nesting females are more likely to have starvation-reduced nests than earlier nesting ones. The number of starvation-reduced nests/total number of nests is given for each rank category.



unreduced (control) nests of similar rank (i.e. primary nests) would indicate how the number of young affects male investment while controlling for differences in mate quality.

Two measures of male investment were used in the analysis, i) whether or not nestlings were fed during observation periods and ii) the actual feeding rate. Male feeding rates were significantly correlated with another measure of investment, the time spent foraging for young ($y = 3.18x + 12.90$, where x is the number of feeding trips/hr. and y is the number of minutes spent foraging for young, $r^2 = 0.46$, 157 df, $p < 0.01$). I assume here that all foraging bouts culminating in the feeding of young were devoted to gathering food for the nestlings. Many foraging bouts do not result in a trip to the nest but are followed by other activities such as calling and attracting additional females. When males engage in these activities after foraging, their bills do not contain food.

Results and Discussion

Parental Competency

To establish that females with starvation-reduced clutches were less capable parents than control and experimental females, I compared the three groups with respect to the number of young fledged/nest, the fledgling weight of male and female offspring, and the rate of food delivery to the nest (Table 12). In order to control for possible differences in the amount and effectiveness of male investment between groups, only nests receiving no paternal

Table 12. Reproductive success and feeding rates for experimental, starvation-reduced, and control females that raise young without male care. -- Fledging weights for experimental and starvation-reduced nests were calculated using nests producing 2 young; for control nests, separate weight averages are given for nests fledging 2 and 3 young. Comparisons between experimental and starvation-reduced females and experimental and control females were made using t-tests; significance levels (two-tailed) for these comparisons are indicated where appropriate (see text for the results of additional comparisons).

	Starvation-Reduced	Experimental	Control
# Yng Alive on Day 6	1.95 ± .22 (n = 40)	1.98 ± .14 (n = 48)	3.34 ± .48*** (n = 161)
Female Feeding Rate on Day 8	6.64 ± 3.68 (n = 22)	9.20 ± 3.44* (n = 20)	10.17 ± .48 (n = 42)
# Yng Fledged/Nest	1.59 ± .50 (n = 27)	1.97 ± .19*** (n = 29)	2.53 ± .63*** (n = 71)
Fledging Wt., 2 Yng Nests Males	53.78 ± 5.93 (n = 14)	55.56 ± 7.63 (n = 29)	57.17 ± 5.33 (n = 24)
Fledging Wt., 2 Yng Nests Females	36.57 ± 5.10 (n = 18)	38.78 ± 1.82* (n = 27)	37.62 ± 3.75 (n = 34)
Fledging Wt., 3 Yng Nests Males			54.54 ± 5.72 (n = 37)
Fledging Wt., 3 Yng Nests Females			34.63 ± 4.95 (n = 74)

*P < 0.05

***P < 0.001

care were used in the analysis. In addition, only reduced nests with 2 young at the time of nest observation (day 8 or 9) were considered. Experimental females fledged an average of 1.97 ± 0.19 young/nest without male aid, significantly more than females in the starvation-reduced group who fledged 1.59 ± 0.50 young/nest (t-test, $t = 3.80$, 54 df, $p < 0.001$). The fledging weight of female young was significantly greater for experimental nests than for starvation-reduces ones but there was no difference in the fledging weight of males between treatments (Table 12; females, $t = 2.07$, 43 df, $p < 0.05$; males, $t = 0.77$, 41 df, $p > 0.40$). Consistent with these results, experimental females delivered food to their nests at a significantly greater rate than starvation-reduced females (Table 12; t-test, $t = 2.32$, 40 df, $p < 0.05$).

Control (unreduced) females fledged an average of 2.53 ± 0.63 young/nest without male care, significantly more than experimental or starvation-reduced females (Table 12; control vs. experimental, $t = 4.72$, 98 df, $p < 0.001$; control vs. starvation-reduced, $t = 6.95$, 96 df, $p < 0.001$). The mean fledging weight of males from control nests with 2 young was significantly greater than the weight of males leaving starvation-reduced nests (Table 12; t-test, $t = 1.81$, 36 df, $p < 0.05$, one-tailed); female young were fledged at similar weights ($t = 0.85$, 50 df, $p > 0.3$). There was no difference in the mean weight of male and female young leaving experimental and control nests with 2 young (Table 12); t-test, males, $t = 0.87$, 51 df, $p > 0.4$; females, $t = 1.47$, 59 df, $p > 0.1$). Control females delivered

food to young at a significantly greater rate than starvation-reduced females (Table 12; t-test, $t = 3.13$, 62 df, $p < 0.01$) but at a similar rate to experimental females (t-test, $t = 0.84$, 60 df, $p > 0.4$). In summary, these results suggest that starvation-reduced females were less competent parents than experimental and control females and that experimental females were capable of raising more young than they did following clutch reductions.

The lower fledging success and smaller size of female young from starvation-reduced nests is not a result of these nests containing more young than experimentals until day 6. On the average, experimental reductions were performed on day 2.65 ± 1.54 ($n = 46$) while starvation-reduced nests contained 2 young by day 4.4 ± 0.87 ($n = 43$), a difference of less than 2 days. Unreduced (control) nests contained significantly more young on day 6 than both starvation-reduced and experimental nests (Table 12; t-tests, control vs. starvation-reduced, $t = 17.83$, 199 df, $p < 0.001$; control vs. experimental, $t = 19.36$, 207 df, $p \ll 0.001$) and yet fledged more, not less, young than reduced nests. In addition, control nests fledging 2 young contained 3 or more young until day 8.78 ± 0.89 , a significantly longer period of time than starvation-reduced nests (t-test, $t = 16.28$, 55 df, $p \ll 0.001$), and yet fledged male young at a significantly greater weight.

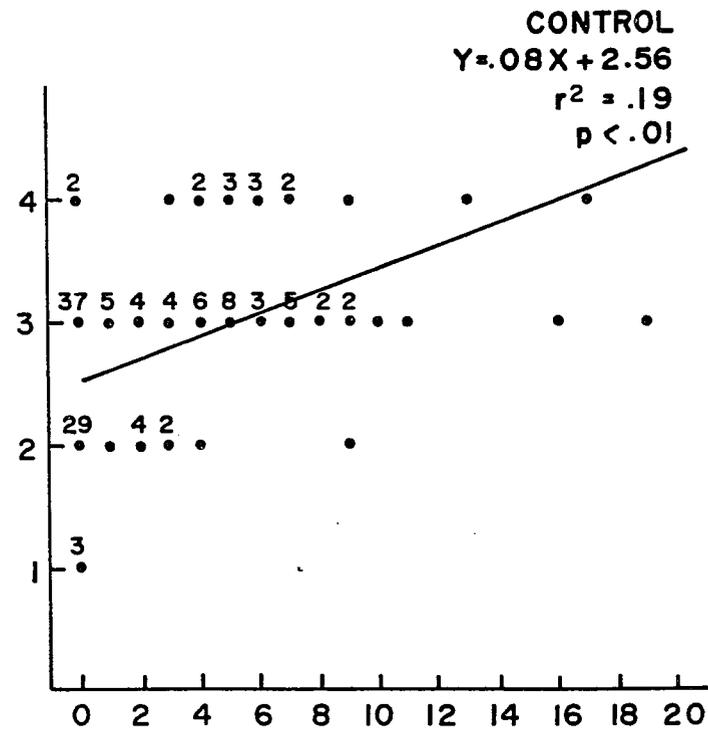
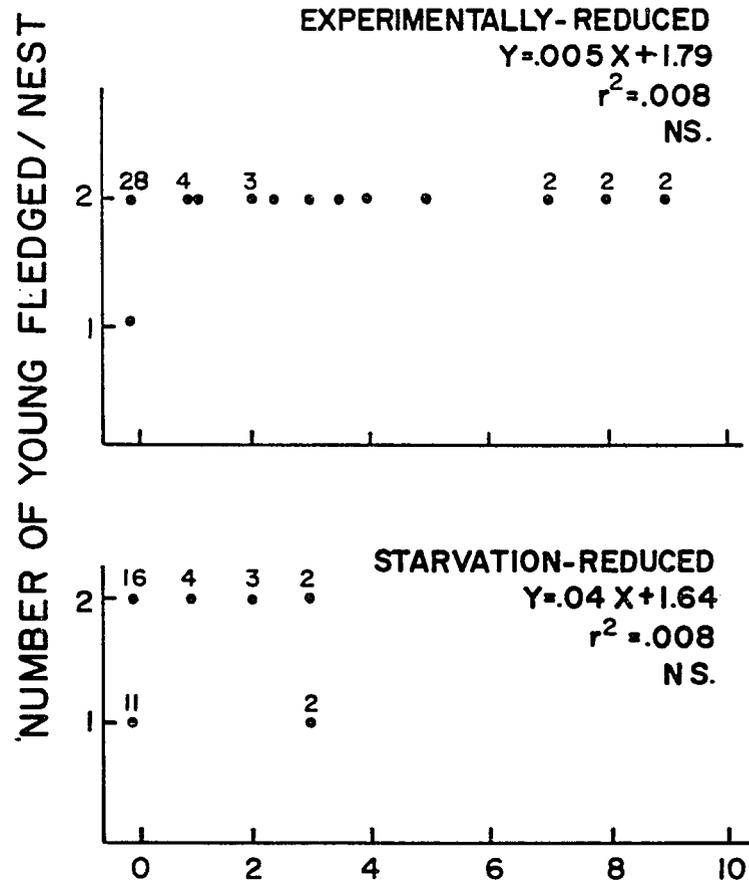
In order to investigate seasonal trends in the occurrence of starvation-reduced nests, I determined the number of these occurring as a function of their order of initiation on territories (nest

rank). Territories receiving experimental reductions were excluded from the analysis. The proportion of starvation-reduced nests among all clutches increased linearly with female nesting order on territories with later nesting females more likely to have starvation-reduced nests than earlier nesting ones (Figure 2). This trend cannot be explained by the seasonal availability of food since odanate emergence increases throughout the breeding season and is several orders of magnitude greater later in the season than earlier (Orions 1980; Gori, unpublished data). A more likely explanation is that a greater proportion of later nesting females are poor or inexperienced parents. These results also indicate that approximately 11% of the females in the experimental group are poor parents.

Fitness Functions

In order to predict how polygynous males should behave toward parentally competent and incompetent mates, I constructed fitness-investment functions for experimental, starvation-reduced and control nests. I used two measures of fitness, the number of young fledged/nest and fledgling weight, and plotted each against male feeding rate. Nests receiving no male aid were assigned values of zero for male investment. Figure 3 shows the relationship between number of young fledged/nest and male investment for experimentally reduced, starvation-reduced, and control nests. For unreduced nests, there is a positive correlation between male feeding rate and fledging success indicating an increase in fitness for males investing in

Figure 3. The relationship between male investment and fledging success for experimental, starvation-reduced, and control nests. -- The number of young fledged/nest increases linearly with male feeding rate for control nests; there is no apparent effect of male investment on fledging success for experimental and starvation-reduced nests.

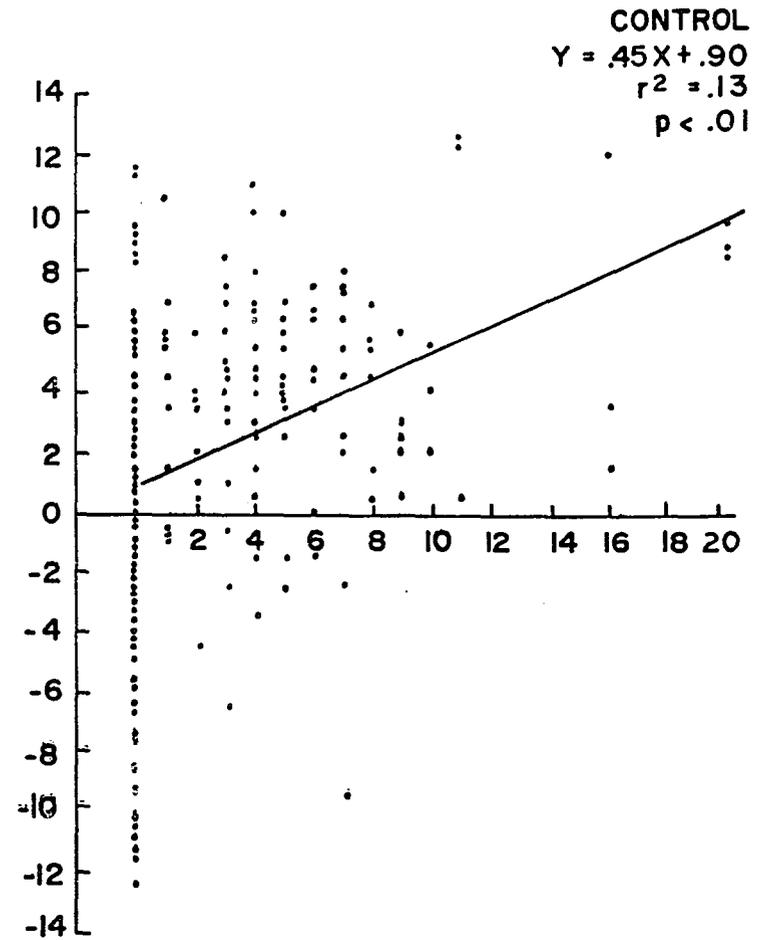
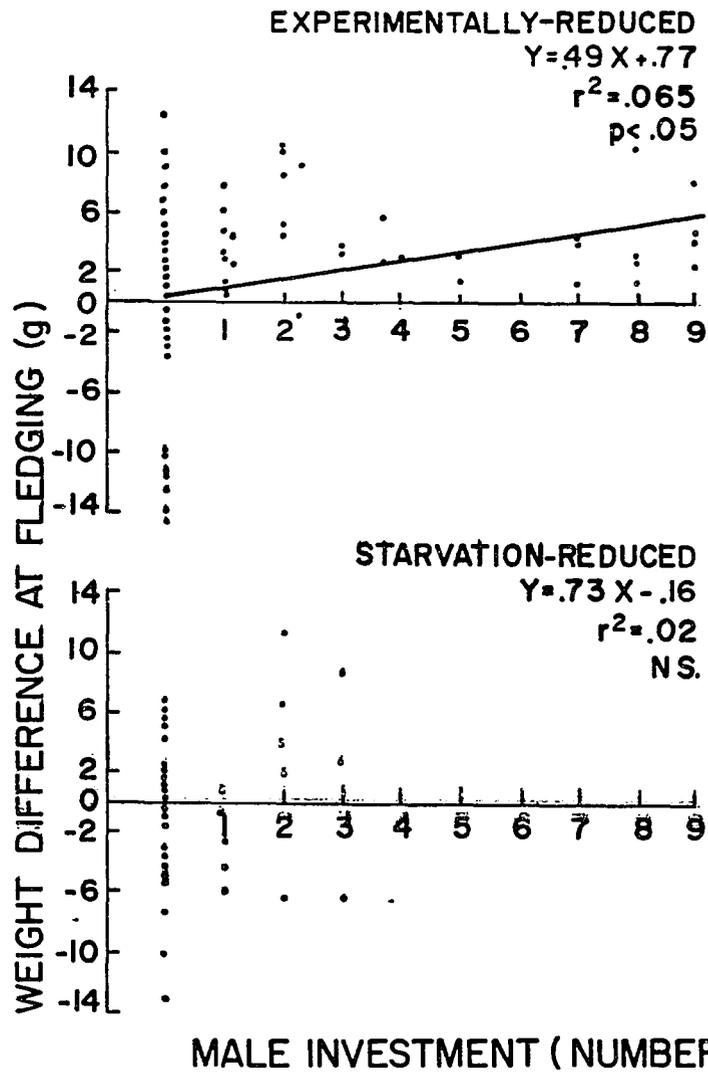


MALE INVESTMENT (NUMBER OF TRIPS/HOUR)

these nests (Figure 3). In contrast, there is no significant relationship between the two variables for either experimental or starvation-reduced nests (Figure 3). With respect to this measure of fitness, males should help competent females with 3 to 4 young but avoid clutches with 2 young since there is no observable return on their investment when caring for these nests.

In the analysis of fledgling weight, I used only experimental and starvation-reduced nests producing 2 young and control nests fledging 3 young. Fledgling weights were normalized according to sex and year to control for differences in the weights of male and female young and variation in marsh productivity between years. To do this, I calculated sex-specific weight averages for 1981 and 1982 using only nests receiving no male aid and analyzing the three treatments separately. Then, for each nest, I determined the difference between an individual's fledgling weight and the calculated mean appropriate for its sex, year, and treatment and plotted the deviations against male feeding rate. If male investment favorably affects the fledgling weight of young, these deviations should tend to be positive and increase with increasing male investment. Figure 4 shows the relationship between fledgling weight and male investment for experimentally reduced, starvation-reduced, and control nests. There is a significant positive correlation between fledgling weight difference and male investment for experimental and control nests but no apparent relationship for starvation-reduced nests (Figure 4). Thus, paternal care increases the fledgling weight of young belonging to

Figure 4. The relationship between male investment and the fledging weight of young from experimental, starvation-reduced, and control nests. -- In the figure, the difference between an individual's fledging weight and the mean weight appropriate for its sex and year were plotted against the male's feeding rate. Mean weights for male and female young were calculated from nests receiving no paternal care and were similar to values given in Table 12. Only experimental and starvation-reduced nests with 2 young and control nests with 3 young were used in the analysis (see text for further explanation). The fledging weight of young increased linearly with male investment for control and experimental nests but was unaffected by male care for starvation-reduced nests.



competent females but has no effect on the fledging weight of young of incompetent ones. On the basis of these and the previous results for fledging success, I predict that males should prefer to raise the young of capable mates because of the greater return on their investment from these nests. Nests with more than 2 young should be preferred, but if these are unavailable or too young to require aid, males should care for experimental nests. The amount of care given to experimental nests should be less, since with competent mates, less investment is required by males to fledge 2 young.

Why did males feed at starvation-reduced nests if there was no demonstrable effect on offspring fitness resulting from the investment? One possibility is that males occasionally assess the parental capabilities of mates inaccurately and feed at starvation-reduced nests assuming they belong to competent females. Alternatively, a weak, positive relationship between male investment and offspring fitness may exist for certain starvation-reduced nests but the inclusion of extremely incompetent females in the analysis may have obscured our observation of the relationship. The latter possibility is at least reasonable since parental competence presumably lies on a continuum such that there may be little difference between relatively incompetent experimental females and competent starvation-reduced ones.

If male investment at starvation-reduced nests does increase offspring fitness, then males should care for the young in these

nests only when more preferred nests are unavailable. Since the proportion of competent mates is lower later in the season (Figure 2), I predict that males should be more likely to help incompetent females later in the season than earlier. Furthermore, the amount of care given to young in starvation-reduced nests should be lower than for experimental nests since the return on male investment is presumably less at the former nests.

Test of Predictions

To see if males preferentially cared for nests with more than 2 young, I scored whether or not unreduced and experimental nests were fed by males. Only primary nests were used in this analysis in order to minimize the number of parentally incompetent individuals among experimental females (Figure 2). Males showed a strong preference for helping nests with 3 to 4 young (Table 13); ninety-two percent of these nests were fed by males compared to 45% for experimental nests. To test whether the level of male investment varied with the number of young, I calculated mean male feeding rates for unreduced and experimental nests receiving male aid. Again, only primary nests were used in the analysis. Males fed unreduced nests at a rate of 5.85 ± 4.36 trips/hr. while experimental nests were fed at a significantly lower rate of 2.75 ± 2.15 trips/hr. (t-test, $t = 2.15$, 41 df, $p < 0.05$). As predicted, males were more likely to care for nests with more than 2 young and furthermore, fed these

Table 13. The number of experimental (2 young) and control (3 to 4 young) nests helped and not helped by males. -- The analysis is restricted to primary nests in order to minimize the number of incompetent females among experimentals. Males show a strong preference for raising nests of competent mates with more than 2 young (Fisher exact test; $p = 0.00002$).

	Helped	Not Helped
Experimental Nests with 2 Young	14	17
Control Nests with 3 to 4 Young	35	3

nests at a higher rate than they did nests with 2 young. Patterson et al. (1980) observed a similar preference for unreduced nests by male Yellowheads.

To see if investment at experimental nests occurred when control (unreduced) nests were unavailable, I scored whether or not males fed at experimental nests when unreduced nests with young older than 5 days old were present or absent on the territory. Males showed a significantly greater probability of feeding young in experimental nests when control nests of sufficient age were absent from the territory than when they were present (Table 14). In fact, experimental nests were never fed when unreduced nests with young older than 5 days were also available for males to feed. Furthermore, seventy-one percent of the males caring for primary experimental nests either stopped feeding at these nests or fed at a lower rate when care was initiated at secondary nests with more young (Gori, unpublished data). Both of these lines of evidence suggest that investment at experimental nests occurred when more preferred unreduced nests were unavailable or too young to require aid.

To test for male preference among 2 young nests, I scored whether or not experimental and starvation-reduced nests were helped by males. Only starvation-reduced clutches belonging to primary and secondary nesting females were used in the analysis to control for the variation in the likelihood of male aid with female rank. Males showed a strong preference for helping at experimental nests (Table 15). Forty percent of these nests were fed by males compared

Table 14. The number of experimentally reduced nests helped and not helped by males when control nests with young older than 5 days were present or absent on the territory. -- Investment at experimental nests occurs when control nests old enough to require aid are unavailable to males (Fisher exact test, $p = 0.003$).

	Helped	Not Helped
Experimental Nests with Control Nests Absent	19	19
Experimental Nests with Control Nests Present	0	10

Table 15. The number of experimental and starvation-reduced nests helped and not helped by males. -- Only primary and secondary nests were used in the analysis to control for variation in the likelihood of male care with nest rank. Males show a strong preference for raising experimental nests (Fisher exact test, $p = 0.031$).

	Helped	Not Helped
Experimental Nests with 2 Young	19	29
Starvation-Reduced Nests with 2 Young	2	15

to 12% for starvation-reduced nests despite the fact that all clutches contained 2 young at the time of observation.

To test whether the level of male investment varied with female parental quality, I calculated the mean male feeding rate for experimental and starvation-reduced nests receiving male aid. All reduced nests with 2 young, irrespective of female rank, were used in the analysis. Males fed at experimental nests an average of 4.05 ± 2.99 times/hr. while starvation-reduced nests were fed at a significantly lower rate of 2.0 ± 0.89 trips/hr. (t-test, $t = 2.20$, 28 df, $p < 0.05$). As predicted, males were more likely to help at reduced nests belonging to competent females and fed these nests at a higher rate than they did the nests of incompetent mates.

As suggested in Figure 2, most starvation-reduced nests belonged to later nesting females (i.e. tertiary, quaternary, etc.) while experimental nests were restricted to primary and secondary females. The mean rank for experimental nests was 1.3 ± 0.4 compared to a mean rank of 2.7 ± 1.2 for starvation-reduced nests (t-test, $t = 4.93$, 29 df, $p < 0.001$). As an alternative explanation, the reduction in male investment at starvation-reduced clutches may have been due to differences in female rank rather than to parental capability. To test this possibility, I performed a linear regression using nest rank as the independent variable and male feeding rate as the dependent variable. The slope of the regression line was statistically indistinguishable from zero suggesting no

relationship between the two variables ($y = 0.18x + 5.41$, 62 df, $r^2 = 0.006$, $p > 0.4$). Rank differences, therefore, cannot account for the variation in male investment between treatments. Reduced investment at starvation-reduced nests may also have resulted if incompetent females were more likely to be mated to parentally incompetent males. To test this possibility, I compared feeding rates at nests with 3 to 4 young for males helping starvation-reduced nests and for those helping experimental nests. The mean feeding rate at unreduced clutches was 5.62 ± 3.12 trips/hr. for males helping experimental nests compared to 6.76 ± 5.76 trips/hr. for males helping starvation-reduced nests. These rates do not differ statistically indicating that males helping at starvation-reduced clutches were as competent at feeding 3 to 4 young as males helping at experimental nests (t-test, $t = 0.64$, 28 df, $p > 0.5$). One reasonable interpretation of these data is that males reduced investment at starvation-reduced nests because of the lower return on their investment at these nests.

To see if investment at starvation-reduced nests occurred when more preferred nests were unavailable, I scored whether or not males fed at starvation-reduced nests as a function of whether control and experimental nests with young older than 5 days old were present or absent on the territory. The analysis was restricted to nests initiated before May 17 since males very rarely fed at nests established after this date (Gori, unpublished data). Males had a significantly greater probability of feeding young from

starvation-reduced nests when more preferred nests requiring aid were unavailable (Table 16). In 9 out of the 11 cases that males fed at starvation-reduced nests, more preferred nests of sufficient age were absent from territories when care was initiated.

To test whether males were more likely to care for the nests of incompetent mates later in the season, I scored whether or not males helped at primary, secondary, tertiary, and quaternary starvation-reduced nests. As predicted, males had a significantly greater probability of caring for starvation-reduced nests of later nesting females on territories than earlier nesting ones (Table 17). This preference is presumably due to the lower probability of obtaining capable mates later in the season and therefore, the reduced availability of these nests on territories. With fewer preferred nests available, the probability that males fed young in starvation-reduced nests increased (Table 16).

General Discussion

An individual's competence as a parent may depend on a number of factors including age, prior breeding experience, rank, physical condition, mate familiarity, and genetic quality (eg. Coulson 1966; Lack 1968; Burley 1981; Clutton-Brock et al. 1982). Variation in these factors may be considerable, resulting in significant differences in parental ability between individuals. Ideally, the recognition of individuals as good or bad parents should occur prior to mating and should serve as an important criterion in mate

Table 16. The number of starvation-reduced nests helped and not helped by males when more preferred nests (control or experimental) with young older than 5 days were present or absent on the territory. -- Investment at starvation-reduced nests occurs when control and experimental nests old enough to require aid are unavailable to males (Fisher exact test, $p = 0.002$).

	Helped	Not Helped
Starvation-Reduced Nests with More Preferred Nests Present	2	15
Starvation-Reduced Nests with More Preferred Nests Absent	9	4

Table 17. The number of starvation-reduced nests helped and not helped by males as a function of nest rank on the territory. -- Tertiary and quaternary nests of incompetent females have a greater probability of receiving male care than primary and secondary nest belonging to incompetent females (Fisher exact test, $p = 0.073$).

	Helped	Not Helped
1° and 2° Nests	2	15
3° and 4° Nests	7	11

selection. This requires the use of proximate cues during courtship that are reliable predictors of future parental behavior. Cues based on general vigor or physical condition are likely to be used by many species in assessing parental competence during courtship since they are rarely subject to false advertisement. Good physical condition and parental quality both require the maintenance of a positive energy balance and this results only if individuals can obtain food efficiently. Age and breeding experience will also be important when age (or rank) provides increased access to critical resources or when breeding success is strongly affected by prior experience. Natural selection should consistently favor individuals that use proximate cues that are maximally resistant to deception.

Despite the theoretical advantages to assortatively mating on the basis of parental competence, errors in selection, physical accidents, or the limited availability of good mates may result in disparate parental abilities between mates. Therefore, parents should continue to evaluate the capabilities of mates and adjust their investment in accordance with current assessments. Females and monogamously-mated males that have parentally incompetent mates should either desert or compensate by increasing the level of investment in young. Except in extreme cases, desertion should be an unprofitable strategy because it requires males to abandon their territories and both sexes to locate superior, unmated individuals. For species with relatively synchronized breeding seasons and a 1:1 adult sex ratio, the probability of finding unmated individuals

once breeding has commenced will be low. Thus, in most situations, monogamously-mated individuals will maximize reproductive success by increasing investment in the young of incompetent mates rather than by pursuing a strategy of desertion.

There is little evidence that monogamously-mated individuals actually do adjust the level of parental care with mate quality. Some bird species show a negative correlation between the feeding rates of individuals within a pair over time suggesting that the ability to monitor and compensate for increases and decreases in the investment of mates exists (Martindale 1980). Martindale (1980) reports a single case in Gila Woodpeckers of increased male feeding following disappearance of the female. Viewing this as an extreme case of parental incompetence on the part of the female, male behavior was in qualitative agreement with the predictions of the model. Similar increases in parental care following the disappearance of mates have also been reported in monogamous eastern bluebirds (Gowaty 1983) and cardinals (Richmond 1978).

Unlike females and their monogamously-mated counterparts, polygynous males have a choice of where to direct their investment. Theory predicts that male preference for aiding at the nests of competent and incompetent females will depend on which yields the greater fitness returns. To determine this, I constructed fitness curves for males helping unreduced, experimental and starvation-reduced nests using two measures of fitness, the number of young fledged/nest and fledgling weight. In Great Tits, fledging weight

is positively correlated with post-fledging survivorship with larger young being more likely to survive through the winter than smaller young (Perrins 1965). Similar data for Yellowheads and related Icterids are presently unavailable, but if the same applies in these species, then fledgling weight is a reasonable measure of fitness. From the slopes of the fitness curves, I predicted that males should prefer caring at the nests of competent mates especially those with more than 2 young. This preference for competent mates may be further enhanced if parental capability has an underlying genetic component which is inherited by young. If nests with 3 to 4 young are unavailable or too young to require aid, males should care for nests with 2 young, preferentially investing in those belonging to competent females. The amount of care given to reduced nests should be lower. In the case of experimental nests, less care is required by males with competent mates to raise 2 young to maximum or near maximum fitness than is required for 3 to 4 young. In the case of starvation-reduced nests, the return on investment is lower for nests belonging to incompetent females and greater allocation by males to sexual advertisement and future reproduction may be favored in these cases (Chapter 1). Furthermore, because the probability of obtaining capable mates declines as the season progresses, males should be more likely to aid at starvation-reduced nests later in the season than earlier. All of these predictions are supported by field observations of male Yellowheads. Males show a strong preference for nests with more than 2 young and will feed these nests

at a significantly greater rate than experimental nests. If nests with 3 to 4 young are unavailable or too young to require aid, males will care for reduced nests, preferentially investing in those of experimental females and feeding these at a higher rate than starvation-reduced nests. Furthermore, the probability that males help incompetent females is significantly greater later in the season than earlier. Thus, patterns of male parental care in polygynous Yellow-headed blackbirds are consistent with those predicted from theory. Male Yellowheads clearly can distinguish the number of young in nests and parentally competent mates from less competent ones and will differentially invest at these nests so as to maximize their individual fitness.

The ability of males to distinguish these quantities is presumably beneficial because despite the overall correlation between the number of young in nests on day 6 and female parental competence, there may still be considerable variation in the ability of females to fledge these young. This variation may arise for the following reasons. First, parental competence is likely to show continuous variation while the number of young in nests is discrete. Second, extremes in weather conditions and insect emergence may affect the survivorship of young in nests independently of the ability of females to raise young. Third, the food demands of young are not constant throughout the nestling period but significantly increase after day 6 (Gori, unpublished data). Because of these factors, females of varying degrees of parental competence will

have the same number of young in their nests on day 6. Therefore, males that are capable of distinguishing both the number of young in nests and the ability of females to raise these young will show a greater return on their parental investment than males that make only one or neither of these assessments. The specific cues used by males to assess parental competence are unknown although, potentially, the food delivery rate of the female, how well-fed the young look, or the intensity of food begging calls may provide information on the ability of the female to feed the young.

Parental competence in Yellowheads may be largely a function of age and breeding experience. The proportion of starvation-reduced nests was positively correlated with female nesting order on territories. This result is consistent with previous studies on Yellowheads and other species which show greater nesting success for individuals that breed early in the season (Paynter 1949; Richdale 1957, 1963; Kluijver 1951; Coulson and White 1956, 1958; Davis 1957; Snow 1958; Perrins 1965, 1966, 1970; Potts 1966; Nelson 1966; Coulson 1966; Lack 1966, 1968; Goddard and Board 1967; Haartman 1967; O'Donald 1972; Martin 1974; Davis 1976; Crawford 1977). In these studies, early breeders tend to be older, more experienced, and in better physical condition than late breeders and for this reason, are presumably more competent as parents. Consistent with this interpretation, the chest and throat plumage of later-nesting female Yellowheads appeared to be duller than that of early-nesting females (Gori, pers. observ.); plumage brightness in Yellowheads

and closely related Red-winged Blackbirds has been shown to be greater for older females than for yearlings (Crawford 1977). Thus, starvation-reduced nests probably belonged to yearling females that were breeding in marshes for first time. Their inexperience in locating productive feeding areas and foraging for young may account for the increased mortality of young in their nests.

Summary

In species with parental care, an individual's reproductive success will depend, in part, on its own abilities as a parent and on those of its mate. In theory, individuals should be capable of assessing the parental competence of mates and of adjusting their parental investment in young with mate quality so as to maximize the fitness return on their investment. To test this hypothesis for polygynous male Yellow-headed Blackbirds, I empirically derived fitness-investment functions for nests belonging to competent and incompetent mates. On the basis of the slopes of these functions, I predicted that 1) males should prefer to raise young belonging to competent females over those belonging to incompetent ones and should feed the young of competent mates at a higher rate than those of incompetent mates, 2) males should prefer to help at nests of competent females with 3-4 young over those with 2 young and should feed at nests with 2 young at lower rate than nests with more young and 3) males should invest at less preferred nests only when more preferred ones are unavailable or too young to require aid. All of

these predictions were supported by field observations. Male Yellowheads appear to be capable of assessing the parental competence of mates and the number of young in nests and can adjust the level of their parent investment at nests with both of these factors so as to maximize the fitness return on their investment.

CHAPTER 3

YELLOW-HEADED BLACKBIRD COLONIES AS INFORMATION CENTERS: EVIDENCE FOR INFORMATION EXCHANGE

Introduction

For several decades, investigators have suggested that sociality in birds and mammals has evolved as a strategy to facilitate the exploitation of food resources (eg. Fisher 1954; Crook 1965, 1970; Lack 1968; Emlen 1971; Emlen and Demong 1975; Murton 1971a, 1971b; Ward 1965; Zahavi 1971a, 1971b; Ward and Zahavi 1973; Krebs 1974; Erwin 1978; Evans 1982). In birds, this hypothesis has been proposed to account for winter flocking behavior (Cody 1971; Murton 1971a, b; Murton et al. 1971; Krebs et al. 1972; Krebs 1973; Pulliam 1973; Caraco 1979), communal roosts (Ward and Zahavi 1973; Weatherhead 1983), and colonial breeding (Horn 1968; Ward and Zahavi 1973; Erwin 1978; Evans 1982). A number of studies have demonstrated that foraging in flocks enhances the ability of individuals to locate food (Murton 1971a, 1971b; Krebs et al. 1972; Krebs 1973; Caraco 1979; Rohwer and Ewald 1981). However, there is no convincing evidence that breeding colonies or communal roosts provide similar benefits (Hoogland and Sherman 1976; Pratt 1980; Bayer 1981, 1982). This paper presents experimental evidence that coloniality in Yellow-headed Blackbirds (Xanthocephalus xanthocephalus) aids in

the location and exploitation of food resources in the breeding season.

In 1973, Ward and Zahavi discussed the hypothesis that breeding colonies act as information centers. According to the hypothesis, if food resources are concentrated in ephemeral, spatially unpredictable patches, individuals can locate food more efficiently by taking advantage of the searching experience of other individuals. Birds that are unsuccessful at finding food can locate productive feeding areas by following successful individuals on foraging trips. In this way, the need for individuals to sample the environment for themselves is alleviated and the costs associated with locating food resources are greatly reduced. Thus, individuals can benefit by breeding in colonies through the increased opportunities of observing other birds and of following successful individuals to productive foraging areas when the spatial distribution of food shifts.

There is good evidence that birds can acquire information on the location of food when direct visual contact with foraging individuals is established. In seabirds (Rand 1954; Sealy 1973; Hoffman et al. 1981; Gochfeld and Burger 1982), herons (Krebs 1974; Kushlan 1977; Caldwell 1981) and weaver finches (Ward 1965), solitary individuals are attracted to groups of foraging individuals that congregate where food is abundant (i.e. local enhancement, Thorpe 1956). The specific cue is apparently the sight of other birds and not the presence of resources per se since individuals are attracted to models placed in areas in the absence of food

(Krebs 1974; Kushlan 1977). In pigeons (Murton 1971a, 1971b), chickadees (Krebs 1973), and tits (Krebs et al. 1972), birds in winter flocks are capable of imitating the search behaviors of successful food finders.

Additional kinds of information are potentially available to colonial breeding birds. These include observing the arrival and departure directions of colony members or monitoring the success of birds returning to the colony and following the more successful individuals to their foraging areas. Ward and Zahavi (1973) explicitly considered the latter type of information in their discussion (Bayer 1982), although the hypothesis clearly applies to any information acquired at the colony in the absence of visual contact with foraging individuals.

The evidence in support of the information center hypothesis is anecdotal and indirect. Ward (1965) and Siegfried (1971) report that when birds leave the colony in the morning, some individuals fly a short distance and then wait for "more purposeful" birds to depart before following them. Horn (1968) observed that Brewer's Blackbirds were very efficient at finding concentrations of recently emerged damselflies and suggested that this was the result of individuals following other birds to food. In support of this interpretation, he reports several cases of presumed following. In Oilbirds (Snow 1961), White Pelicans (Brown and Urban 1969), Cliff Swallows (Emlen 1952) and Bank Swallows (Emlen 1971; Emlen and Demong 1975), departures from the colony are reported to be highly

synchronous and foraging flocks are often observed away from the colony. The apparent non-randomness of departures and the existence of foraging flocks is taken as evidence for information exchange at the colony. Krebs (1974) statistically analyzed the departure times of Great Blue Herons and found that the distribution of inter-departure intervals differed significantly from a random distribution with many more short departure intervals observed than expected. Furthermore, birds from the same sub-area within the colony tended to be more synchronous in their departures and more similar in their flight directions than predicted on a colony-wide basis. Krebs interpreted these patterns as being the result of birds monitoring the success of neighbors and following more successful individuals to their foraging areas. In contrast, Pratt (1980) and Bayer (1981) found no evidence for synchronous departures or similar departure directions taken by neighbors in other Great Blue Heron colonies.

The previous studies are inconclusive for several reasons. First, casual observations of birds leaving the colony in apparent groups does not preclude the possibility that individuals are departing independently of one another. A certain number of "simultaneous" departures are expected by chance alone. In order to establish whether departures are statistically independent, the observed distribution of departures must be compared to an appropriate random model as done by Krebs (1974). Second, "clumped" departures may be the result of extrinsic environmental and social factors and not information exchange per se. Such factors include tidal cycle,

time of day, nesting synchrony, a limited number of economical flight routes, and advantages associated with flock recruitment at the colony. For example, in Great Blue Herons and other ardeids, the intensity of foraging is related to tidal cycle (Krebs 1974; Bayer 1981). If individuals are forced into synchrony at the beginning of each low tide period when foraging is most intense and if average trip duration remains approximately constant, then departures will remain in synchrony for the entire day. Furthermore, if the degree of nesting synchrony for sub-areas within the colony is greater than the overall colony synchrony (Hoogland and Sherman 1976; Gochfeld 1980), similar parental demands among neighbors may result in a greater departure synchrony for sub-areas within the colony. Time of day may influence prey abundance (Ashmole 1971; Brown 1980), predation rates (Palmer 1962; Manuwal 1979), and thermal development (Brown and Urban 1969; Clark 1979), all of which may synchronize the activities of foraging individuals. If there are a limited number of economical flight routes from the colony, birds may depart in similar directions but forage in different areas; all of the above studies considered only departure directions in their analyses. If group foraging is advantageous, synchronous departures may result from flock recruitment at the colony. Recruitment in this manner would enhance efficient flock formation on the feeding grounds and may facilitate the location of other foraging flocks; again, these group departures may have little to do with information exchange.

To test the information center hypothesis, it is necessary to show i) that food resources are distributed in ephemeral, spatially unpredictable patches which are sufficiently rich (and stable) to support more than a single individual and ii) that naive or unsuccessful individuals with information from the colony can locate productive feeding areas more efficiently than otherwise similar birds without access to this information. To date, no study has satisfactorily demonstrated the second point despite the fact that this prediction is critical to testing the hypothesis.

In this paper, I report the results of an attempt to test the information center hypothesis in colonially breeding Yellow-headed Blackbirds. Specifically, I will show i) that foraging areas used by Yellowheads are spatially and temporally unpredictable and that once located, food is sufficiently abundant within these areas to support a number of foraging individuals and ii) that the pattern of colony departures is statistically non-random and consistent with several predictions of the information center hypothesis. I then report the results of a simple feeding experiment which was designed to demonstrate information exchange directly. Finally, I discuss the probable informational cues used by Yellowheads at the colony.

Methods

The Study Area

The research was conducted from 1979 to 1982 on the Columbia National Wildlife Refuge near Othello, Grant Co., Washington. The

topography of the Potholes, as the area is known locally, consists of buttes and basins scoured in Columbia basalt by Pleistocene floods (Bretz 1959). The Columbia basin lies in the rainshadow of the Cascades and receives approximately 20 cm. of precipitation annually. Most of the standing water in the area post-dates the advent of local irrigation at the turn of the century. Irrigation run-off and rising ground water levels following completion of the Columbia River Water Project in the 1950's have greatly enlarged existing bodies of water and created numerous others. It is unlikely that blackbirds were breeding in the area before the existence of standing water.

The upland vegetation is characterized by sagebrush (Artemisia tridentata), bluegrass (Poa sp.), bunchgrass (Agropyron spicatum), and cheatgrass (Bromus tectorum). Greasewoods (Sarcobatus vermiculatus) dominate alkaline pans surrounding the shores of lakes and marshes; cattails (Typha angustifolia) and bullrush (Scirpus sp.) grow in the shallow aquatic margins of these bodies of water and provide nest sites for Yellowheads.

The Study Organism

Yellow-headed blackbirds are polygynous, marsh-nesting members of the family Icteridae. They breed throughout the United States and Canada, west of the Mississippi River, and in Wisconsin, Illinois, northwest Indiana, and southwest Michigan; Yellowheads are locally abundant in productive lakes, marshes, and irrigation ditches (Orians 1980). Colonies vary in size depending on

availability of nesting habitat, insect productivity, and predator densities (Orians 1980; Wittenberger, unpubl. ms; Gori, unpubl. data). In the study area, individual territorial males may attract anywhere from 0 to 15 females; mean harem size was 4.72 ± 3.25 ($\bar{x} \pm S.D.$) females/male in 1979 (N = 25), 3.10 ± 1.51 females/male in 1981 (N = 57), and 3.90 ± 1.91 females/male in 1982 (N = 42). In the Potholes, Yellowheads begin nesting in late April or early May and continue breeding until late June or early July. Females arrive onto territories to breed throughout this period so that the degree of nesting synchrony is similar throughout the colony. Detailed accounts of the breeding cycle and reproductive behavior of Yellowheads can be found in Willson (1966) and Orians (1980).

During the breeding season, Yellowheads feed themselves and their young primarily on newly emerged damselflies and dragonflies (teneral). In the study area, males obtain much of this food on their territories while females feed almost exclusively off the territory. Emergence of the tenerals from aquatic nymphs varies both spatially and temporally and dense aggregations of adults and tenerals may occur as a result of local temperature and wind patterns (Willson 1966; Horn 1968; Orians 1980).

Observations and Experiment

The observations reported here were made at two Yellowhead colonies, US and HD, in the Hutchinson Lake Drainage area. US was studied from 1979 to 1982 and HD in 1980 and 1981. The mean number

of adult birds breeding in US during this period was 126.00 ± 41.02 birds. This figure does not include the 1980 season when virtually all breeding attempts failed due to ash fall from the Mt. Saint Helen's eruption. HD colony contained 61 breeding adults prior to the eruption in 1980 and 92 adult birds in 1981.

I color-banded over 90% of the adult male Yellowheads in these colonies and mapped all territories. The boundaries were established by observing territory disputes and stand-offs between adjacent males early in the season. I also attempted to color band females but with less success due to their apparent reluctance to enter grain traps. By 1982, however, over 60% of the females in US had been banded. Every 2 to 3 days, I censused colonies, marking all new nests and recording the progress of previously marked ones.

At different times during the 1979, 1980, and 1981 seasons, I recorded bird departures from US and HD colonies. Most of the observation periods began early in the morning between 0500 and 0700 Pacific Standard Time (PST) although several were initiated later in the day; period lengths ranged from 1 to 2.5 hours. In 1979 and 1980, during each observation period, I recorded the time of every departure and the flight direction taken. In 1981, a field assistant and I recorded all this information as well as the identity of the departing bird and, whenever possible, the final destination. These data were used to test predictions concerning the independence of Yellowhead colony departures.

Throughout the 1981 season, I censused foraging areas used by HD colony and recorded Yellowhead group sizes. I operationally defined flocks to include two or more individuals foraging within 6 m of one another; birds separated by greater distances were considered to be feeding alone.

To test directly for information exchange at the colony, I performed a feeding experiment in 1982. The intent was to establish an artificial foraging area that was superior to other areas being used by the colony, and then to observe the pattern and rate of recruitment to this site for evidence of information exchange. Piles of sunflower seeds and plastic containers filled with mealworms were placed together on the shore of a small pond in a pasture 600 m north of US. The pond was situated in a small basin bordered on three sides by steep ridges. Because of these ridges, the feeding site could not be seen by birds at US and was visible to birds flying north only after crossing them. The site could not be seen by birds flying in other directions.

Two weeks before the experiment was initiated, piles of sunflower seeds were placed around the shores of the pond in order to introduce birds to the site. Yellowheads discovered the seed piles sometime during the first day and continued to feed in the area until I removed all provisioned food 2 days later. Although adult birds will take sunflower seeds for themselves, young are fed exclusively on insects (Gori, pers. obs.).

On days the experiment was performed, for a one-hour period before food was set out, a field assistant and I recorded i) the direction of all long-distance departures from US, ii) the identity and departure times of all birds flying toward the experimental foraging area (north) and iii) the trip durations of randomly selected birds. From the information in ii), I calculated the rate of new birds flying in the direction of the site before food provisionment (pre-provisionment recruitment rate) by comparing the identity of birds recorded during the second 30 minute period with those recorded during the first.

Following the one-hour observation period, the experimental foraging area was provisioned with seeds and worms and an observer stationed approximately 40 m away from the site. Initially, all arrivals and departures from the foraging area and, whenever possible, band combinations were recorded on a continuously running tape recorder. As the number of birds using the site increased, arrivals could be noted only as time permitted; a complete record of arrival times was obtained for the first replicate. Departures from the feeding area were relayed by 2-way radio to a second observer stationed at the colony. In this way, the movement of birds from the feeding site to the colony could be followed and the individuals identified by observing which nest or territory they returned to. This information was relayed back to the observer at the experimental site and simultaneously recorded on the tape. The precise timing of events was later reconstructed and transcribed by playing

back the tape with a stopwatch. From these data, I calculated a mean recruitment rate of new birds to the site by comparing the identities of birds arriving during successive 30 minute periods with those recorded as feeding there or flying in the direction of the site previously.

The experiment was performed on 4 separate mornings, June 1, 4, 7, and 12 at approximately 0530 PST. Each replicate was allowed to run for 1 1/2 hours or until the mealworms were depleted; all experiments ran for at least 1 hour. The feeding site was moved to a different area along the shore of the pond for each replicate.

On intervening mornings from 0600 to 0730 PST, I observed randomly selected birds for 30 minute periods and recorded the duration of their foraging trips. Comparing trip durations for birds feeding at the site with those for birds feeding in other areas will indicate the relative quality of the experimental foraging area compared to other areas used by the colony; I assume that shorter trip durations reflect better foraging areas.

Results and Discussion

The Resource

In order for the colony to have any value as an information center, food resources must be patchily distributed, spatially and temporally unpredictable, and locally abundant so that individuals can benefit from the food-finding of others. The relative utilization of foraging areas by HD colony members on several mornings in

May 1981 is summarized in Table 18. Different foraging areas were preferentially utilized on different days suggesting both spatial and temporal unpredictability in the distribution of food for Yellowheads. This pattern of differential utilization presumably reflects diurnal variation in temperature, local wind conditions, and insect emergence all of which affect the temporal and spatial distribution of blackbird food resources (Willson 1966; Horn 1968; Orians 1980); the pattern is not the result of local resource depletion within foraging areas since emergent insects are renewed on a daily basis. It is unlikely that Yellowheads can anticipate shifts in the resource distribution without directly sampling the environment or obtaining information from knowledgeable colony members.

The average group size within HD colony foraging areas early in the morning was 3.37 ± 3.28 birds/flock ($N = 57$). This figure includes observations of solitary foragers which represent less than 35% of the total number of sightings made during census periods. The prevalence and average size of foraging flocks suggest that food is abundant enough within patches to support more than a single individual. Thus, Yellowhead food resources appear to fulfill the requirements of the information center hypothesis.

Predictions from the Information Center Hypothesis

If Yellowheads are locating productive foraging areas by following colony members to them, several predictions regarding the

Table 18. The number of departures by HD colony members to foraging areas over several mornings in 1981. -- Different foraging areas were preferentially utilized by the colony on different days ($\chi^2 = 132.02$, 12 df, $p \ll .001$).

Date	Foraging Areas				
	S.E. Grassland	E. Grassland	W. Pasture	S.W. Pasture	N. Pasture
May 15, 1981	8	3	18	23	4
May 16, 1981	0	1	1	35	22
May 18, 1981	0	29	42	23	2
May 19, 1981	0	12	10	14	7

timing and direction of departure flights from the colony can be made.

1) There should be a tendency for birds to leave the colony in groups and for colony departures to be statistically clumped in time.

2) Birds leaving the colony together (≤ 15 sec apart) should be more likely to fly in the same direction than birds departing at greater intervals.

3) Assuming that most information comes from neighbors because of their proximity, birds leaving the colony together should be disproportionately drawn from the same sub-area within the colony.

4) Because of the time they spend on nests, incubating females should have less information on the location of good foraging areas than females that are feeding young. Therefore, incubating females should be more likely to follow colony members than females with young and furthermore, should prefer to follow the latter females because of their greater knowledge of currently productive foraging areas and because their foraging success can be assessed more accurately. (Females with young return to the colony with food in their bills while incubating females do not; the amount of food brought back to the colony may be used by birds to estimate foraging success).

Results that are consistent with these predictions provide support for the information center hypothesis. However, since a number of other environmental and social factors can also give rise

to the above patterns (except prediction 4; see Introduction), a stronger test of the hypothesis would be to demonstrate information exchange at the colony directly. To do this, I performed the experiment described earlier. Since the experimental site could not be seen from the colony or by birds flying in directions other than directly over it, the recruitment of new birds could occur in two ways: i) birds may fly in the direction of the site in the absence of information from colony members and locate it by observing provisioned food or other birds feeding there, i.e. local enhancement or ii) individuals with information may follow knowledgeable colony members directly to it. If birds are locating the site via the latter, then

5) The recruitment rate of new birds to the site should exceed the pre-provisionment rate of new birds flying in the direction of the site.

6) The arrival of birds to the experimental foraging area should be statistically clumped in time.

7) If most information comes from neighbors, recruitment should disproportionately involve birds from the same or adjacent territories as the initial site discoverers.

Clumping of Departures

To test the first prediction, I determined inter-departure intervals for all successive departures recorded during the 1979, 1980, and 1981 observation periods and compared the distribution

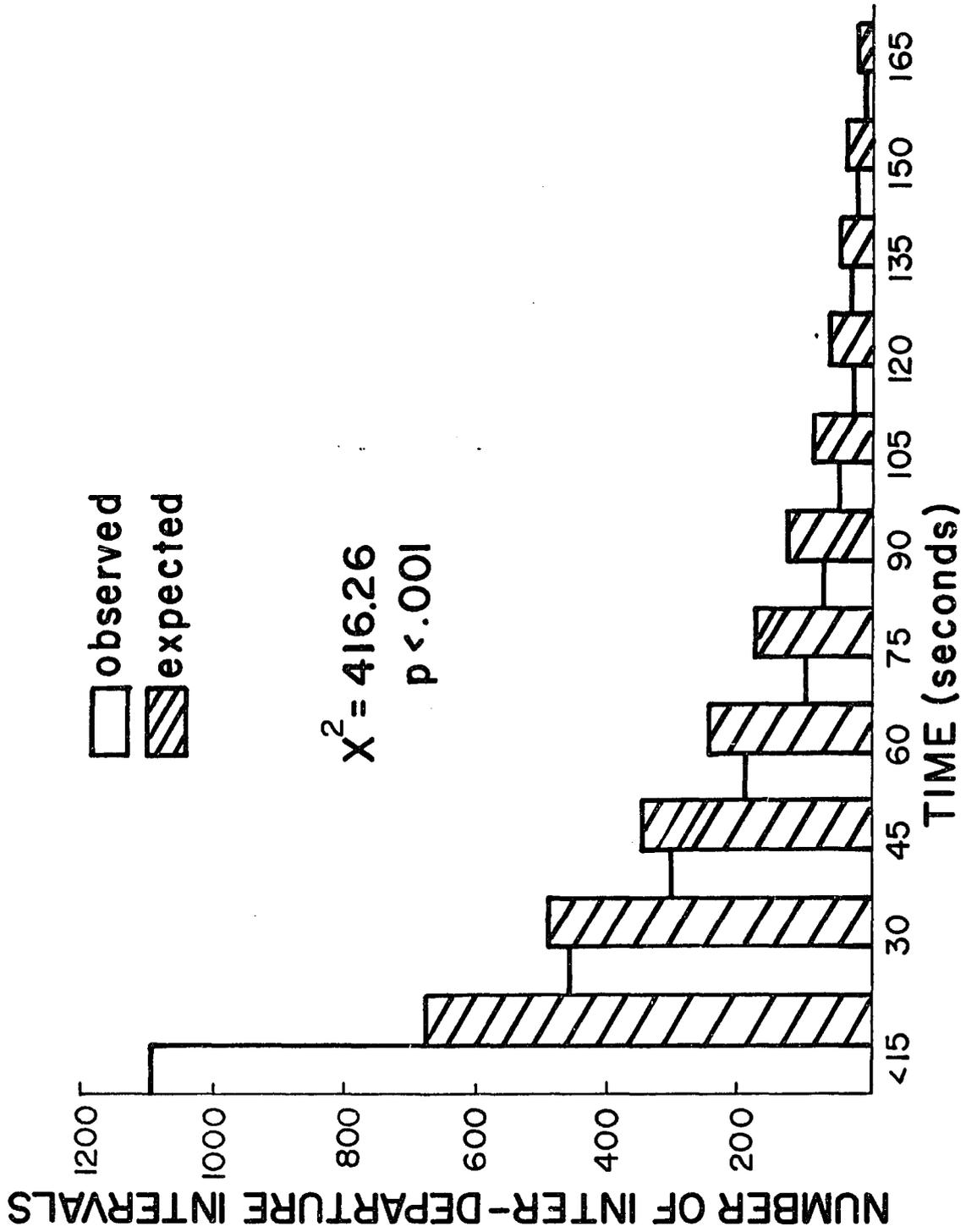
of these intervals to a negative exponential model, assuming as a null hypothesis that departures are random and independent of one another. The expected distribution was obtained using the following equation:

$$N'_t = N_o e^{-P_o t}$$

where N_o is the total number of departure intervals, N'_t is the number of intervals longer than t , the interval number, and $P_o = 1/t_o$ where $t_o = \frac{\sum_{t=0}^n N_t(t + 0.5)}{N_o}$. N_t is the observed number of departure intervals occurring during interval t (Andrzejewski and Wierzbowska 1961; Krebs 1974). To facilitate comparison, I separated departure intervals into 15 sec units, i.e. ≤ 15 sec apart, 16-30 sec apart, 31-45 sec apart, etc. Since birds are visible from the colony for at least 15 seconds following their departure, successive departures falling within the shortest interval potentially involve individuals that are following one another. Seventy-four percent of the departures falling within the first interval occurred ≤ 5 sec apart.

The observed and expected distribution of departure intervals for the combined 1979, 1980, and 1981 observations are shown in Figure 5. The observed distribution differed statistically from the expected one with many more departures ≤ 15 sec apart than expected (Figure 5). For single observation periods, observed and expected distributions differed statistically in 17 out of 22 cases; again, an excess of short departure intervals was observed. If

Figure 5. The observed and expected distribution of time intervals between successive departures of Yellowheads from colonies in 1979, 1980, and 1981 combined. -- The expected distribution (shaded) was generated using a negative exponential model; see text for further explanation. There were significantly more departures ≤ 15 sec apart than expected suggesting that departures from the colony were not random but highly clumped ($\chi^2 = 416.26$, 11 df, $p \ll 0.001$).



non-significant periods are pooled by year, a similar pattern is evident even for these data (1979, $\chi^2 = 40.14$, 11 df, $p < 0.005$; 1980, $\chi^2 = 18.10$, 9 df, $p < 0.05$). These results indicate that departures from the colony are not random but highly clumped.

Similarity of Direction

To test whether individuals leaving the colony together have similar departure directions, I scored the number of times an individual flew off in the same or in a different direction as the preceding individual and compared the scores for pairs leaving the colony together (≤ 15 sec apart) with those for pairs leaving at greater than 15 sec intervals (solitary departures). The 1980 observations were not included in the analysis since departure directions were infrequently recorded during these periods. In both 1979 and 1981, birds departing together were more than twice as likely to fly in the same direction as successive solitary departures (Table 19). These results suggest that clumped departures are not independent of one another.

Do Neighbors Leave Together?

To test the third prediction, I analyzed the 1981 data dividing departures into two groups; following and solitary. Following departures were defined as successive departures less than 15 seconds apart and in the same direction while solitary departures were defined as successive departures more than 15 seconds

Table 19. The number of successive departures that were in the same or in different directions for departures occurring < 15 sec apart and those occurring at greater intervals. -- In 1979 and 1980, departures \leq 15 sec apart had a greater probability of being in the same direction than departures occurring > 15 sec apart (1979, $X^2 = 193.94$, 1 df, $p \ll 0.001$; 1981, $X^2 = 37.57$, 1 df, $p \ll 0.001$).

	Departures in the Same Direction		Departures in Different Directions	
	1979	1981	1979	1981
Successive Departures < 15 Sec Apart	438	67	407	23
Successive Departures > 15 Sec Apart	201	34	774	76

apart or in a different direction. I then scored following and solitary departures as to whether they were made by neighbors or non-neighbors and compared the totals for the two groups using a 2 x 2 contingency table. Birds involved in successive departures were defined as neighbors if they came from the same or adjacent territories. Adjacent territories included all adjoining territories sharing a common boundary. Pairs from non-adjacent territories were defined as non-neighbors. Birds that followed colony members had a significantly greater probability of being from the same or adjacent territory as the preceding individual than did birds that departed solitarily (Table 20). Thus, clumped departures disproportionately involve neighbors suggesting that birds are more likely to acquire information at the colony from nearby individuals.

Are Incubating Females Followers?

To test the fourth prediction, that incubating females are more likely to be followers than females that are feeding young, I compared the number of following and solitary departures made by each group of females. Only the May 18 and May 19, 1981 observation periods were considered since prior to this no females were feeding young. As predicted, incubating females had a significantly greater probability of following colony members than did females with young (Table 21). Thirty-seven percent of the departures made by incubating females were following departures compared to only 22% by females with young. To test whether incubating females

Table 20. The number of following and solitary departures made by neighbors and non-neighbors. -- For comparison, the percentage of each departure type made by neighbors is given in parentheses. Birds that followed colony members had a greater probability of being from the same or adjacent territory as the preceding individual than birds that departed solitary ($X^2 = 22.58$, 1 df, $p \ll 0.001$).

	Pairs from the Same or Adjacent Territories; Neighbors	Pairs Not from the Same or Adjacent Territories; Non-Neighbors
Following Departures	55 (87%)	8
Solitary Departures	101 (54%)	87

Table 21. The number of following and solitary departures made by incubating females and females with young.-- (See text for an explanation of terms). For comparison, the percentage of following departures for each group of females is given in parentheses. Incubating females were more likely to be followers than females with young ($X^2 = 3.91$, 1 df, $p < 0.05$).

	Incubating Female	Female with Young
Following Departure; Departure < 15 Sec after and in the Same Direction	18 (37%)	22 (22%)
Solitary Departure; Departure > 15 Sec after or in a Different Direction	31	80

preferentially follow females feeding young, I determined the proportion of all departures made by incubating and feeding females and used these proportions to generate the expected number of times females would follow incubating and feeding females if birds followed colony members at random. Incubating females followed females with young a significantly greater number of times than expected (Table 22). In contrast, females that are feeding young showed no apparent preference or avoidance for females of either type (Table 22). In summary, incubating females are more likely to be followers than females with young and furthermore, show a preference for following the latter females presumably because females that are feeding young have a greater knowledge of currently productive foraging areas and their foraging success can be assessed more accurately.

Experimental Confirmation

If the experimental site is a superior foraging area, then the duration of feeding trips for birds using the site should be shorter than the trips made by birds feeding in other areas. Trip durations for birds using the experimental site were calculated from tape transcripts while the durations of trips elsewhere were obtained from observations made during the pre-provisionment periods and on days between the experimental replicates. No significant differences were detected between trip durations recorded during pre-provisionment periods and those obtained on other days, therefore these data were pooled in subsequent analyses. Trip durations for

Table 22. The observed and expected number of times incubating females and females with young followed other females of each type. -- The proportion of all departures made by each group of females was used to generate the expected values. Incubating females showed a significant preference for following females that were feeding young (G-test with continuity correction, $G = 4.68$, $p < 0.05$); females with young showed no preference for following females of either type ($G = 1.27$, $p > 0.3$).

	Followed Females Feeding Young	Followed Incubating Females
Incubating Females		
Observed	13	1
Expected	8.96	5.04
Females with Young		
Observed	11	11
Expected	14.08	7.92

birds feeding at the experimental site (2.62 ± 1.82 minutes) were on the average 4 times shorter than for birds feeding elsewhere (10.78 ± 9.20 minutes; t-test, $t = 11.05$, 223 df, $p \ll 0.001$). In addition, recruited birds returned to the colony with their bills packed with mealworms while birds feeding in other areas carried smaller loads (Gori, pers. obs.). These results suggest that food capture rates were much greater at the experimental foraging area than in other areas used concurrently by the colony.

Is there any evidence that information concerning this superior foraging area was transferred to naive colony members by knowledgeable ones? The mean recruitment rate of birds to the site (16.93 ± 5.20 new birds/30 min, $n = 4$) was higher than the mean pre-provisionment rate of new birds flying in the direction of the site (2.75 ± 1.26 new birds/30 min). The difference between these rates is highly significant despite the small number of replicates (Mann-Whitney U-test, $U = 16$, $p < 0.003$). The rapid recruitment of Yellowheads to the experimental foraging area indicates that birds must be obtaining information from knowledgeable colony members and using it to locate provisioned food. When the experiment was performed, over 93% of the females in the colony were feeding young. As a result, virtually all of the female recruitment to the site involved birds with young and not incubating females.

To test whether the arrivals of birds to the site were clumped, I determined inter-arrival intervals for all successive visitations to the experimental site and compared the distribution

of these intervals to a negative exponential distribution (see equation presented earlier). Only data from the first replicate were used since a complete record of arrivals were made in that case; during the other replicates, most arrivals went unrecorded because I concentrated on observing departures and noted arrivals only as time permitted. The observed distribution of arrival intervals differed statistically from the random distribution in showing many more arrivals less than 5 seconds apart than expected (Figure 6). This result, along with the pattern of clumped departures from the colony shown earlier, suggests that Yellowheads are locating the experimental foraging area by closely following other birds.

To test whether recruitment disproportionately involves neighbors, new arrivals were scored as to whether they were neighbors or non-neighbors of the first five birds to discover the site (focal birds). As before, neighbors were considered to be from the same or adjacent territories as focal birds and non-neighbors to be from non-focal, non-adjacent territories. Individuals not recruited to the site were similarly scored. The identity of the focal birds differed in the four replicates. In all replicates, recruits had a significantly greater probability of being from the same or adjacent territory as the initial site discoverers than non-recruits did (Table 23). This pattern of recruitment, along with the disproportionate involvement of neighbors in clumped departures shown earlier, suggests that Yellowheads are acquiring information primarily from neighbors.

Figure 6. The observed and expected distribution of time intervals between successive arrivals of Yellowheads to the experimental foraging area in replicate 1. -- The expected distribution (shaded) was generated using a negative exponential model; see text for further explanation. Significantly more arrivals occurred ≤ 15 sec apart than expected suggesting that naive Yellowheads are following knowledgeable colony members to the site ($\chi^2 = 102.68$, 11 df, $p \ll 0.001$).

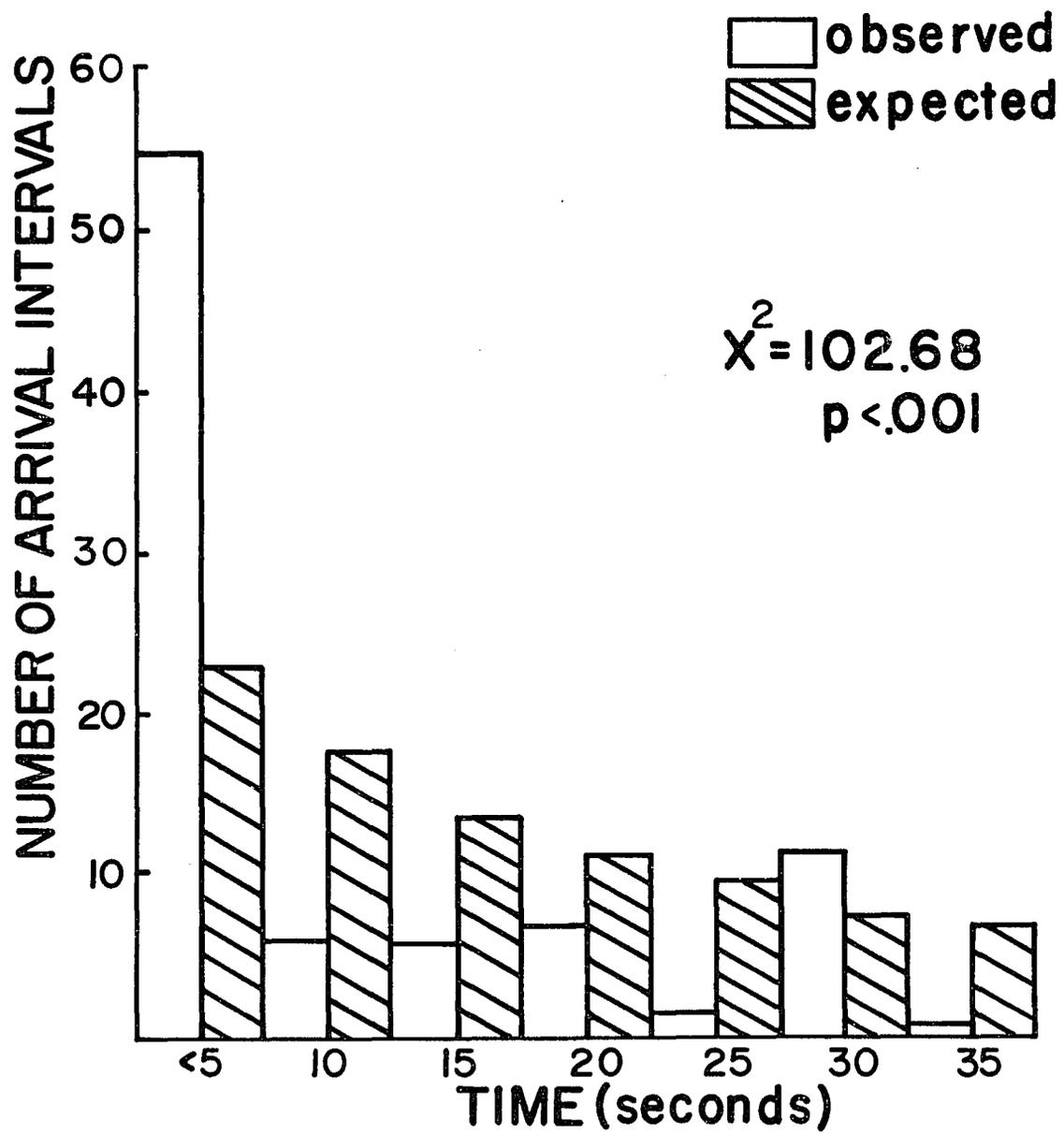


Table 23. The number of birds recruited and not recruited to the experimental foraging area in replicate 1 that were neighbors or non-neighbors of the first 5 birds to discover the site. -- For comparison, the percentage of neighbors among recruits and non-recruits are given in parentheses. Recruits had a greater probability of being neighbors of initial site discoverers than non-recruits ($X^2 = 21.69$, 1 df, $p \ll .001$). The pattern was similar for the other 3 replicates (replicate 2, $X^2 = 32.94$, 1 df, $p \ll 0.001$; replicate 3, $X^2 = 11.16$, 1 df, $p \ll 0.001$; replicate 4, $X^2 = 25.34$, 1 df, $p \ll 0.001$).

	From Focal or Adjacent Territories; Neighbors		From Non-Adjacent Territories; Non-Neighbors
Recruited Birds	33	(87%)	5
Non-recruited Birds	48	(43%)	63

General Discussion

The results obtained in the colony departure analysis and from the experiment support the hypothesis that colonial breeding in Yellowheads facilitates the exploitation of patchily distributed, unpredictable food resources. The important results can be summarized as follows:

1) Foraging areas used by the colony shift from one day to the next and, within foraging areas, most birds feed in flocks early in the morning. These results suggest that the distribution of food resources is spatially and temporally unpredictable and that within patches, food is sufficiently abundant to support a number of individuals.

2) Departures from the colony are statistically clumped. Birds that are involved in clumped departures are more likely to leave the colony in the same direction and to be neighbors than birds involved in successive solitary departures.

3) Incubating females are more likely to be followers than females that are feeding young and furthermore, show a preference for following females with young, presumably because these latter birds possess a better knowledge of where currently productive foraging areas are located and their foraging success can be assessed more accurately.

4) The recruitment rate of new birds to the experimental feeding area was significantly greater than the pre-provisionment rate of new birds flying in the direction of the site. This result

indicates that information on the location and quality of the site was exchanged at the colony.

5) Neighbors of the first birds to discover the experimental site were more likely to be subsequently recruited than non-neighbors suggesting that information exchange occurs primarily between neighbors. Furthermore, the arrival times of birds to the site were statistically clumped suggesting that naive birds were following colony members to the site. Both of these results are consistent with the results obtained in the departure analysis.

Taken together, these results indicate that Yellowhead colonies can act as information centers that facilitate the exploitation of food resources as discussed by Ward and Zahavi (1973).

Informational Cues Used by Yellowheads

What are the specific cues that birds might use as information? Two types of information are potentially available at the colony: i) birds may observe the arrival or departure directions of colony members and follow individuals leaving in a direction frequently taken by other birds or ii) birds may monitor the success of returning colony members directly, then follow successful individuals to their foraging areas. The pattern of bird recruitment to the experimental foraging area suggests that Yellowheads are using the latter. If birds are observing only arrival and departure directions, neighbors and non-neighbors should have an equal probability of recruitment since long-distance arrivals and departures

visible to all birds in the colony. (A human observer standing beside US at eye-level with the tops of cattails can see all long-distance arrivals and departures from the colony. I assume that Yellowheads are similarly capable and have frequently observed individuals, including incubating females, perched on the tops of cattails before following other birds from the colony). On the other hand, if Yellowheads directly monitor the foraging success of neighbors, then recruits to the experimental foraging areas should be disproportionately drawn from the same or adjacent territories as birds initially discovering the site. The experimental results showed that neighbors of initial site discoverers were clearly favored as recruits (Table 23). The use of arrival or departure directions as the sole informational cue is inadequate in explaining this recruitment pattern; the pattern is consistent with birds monitoring the foraging success of neighbors.

Monitoring the success of neighbors can occur in two ways: i) birds may directly communicate their foraging success through specific vocalizations or behaviors or ii) individuals may parasitize this information, for example, by assessing the size of food loads brought back to the colony, "purposefulness" of behavior (sensu Ward and Zahavi 1973), or the time individuals spend away from nests. The balance between the costs and benefits associated with directly communicating foraging success will determine whether birds advertise or attempt to hide their success from colony members.

Food discoverers may benefit from recruiting colony members through increased prey capture rates or reduced predation risks associated with larger foraging groups (Murton 1971a, 1971b; Murton et al. 1971; Pulliam 1973; Caraco 1979; Rohwer and Ewald 1981). However, recruitment may result in a more rapid depletion of resources within a foraging area and, therefore, higher search costs for food-discoverers as a result of having to locate new foraging areas more frequently. In Yellowheads, returning birds enter the colony flying close to the ground presumably making it difficult for other individuals to see them or the size of their food loads. These arrivals are invariably silent, although in other situations, birds are capable of calling with food in their bills (Gori, pers. obs.). In contrast, departure flights occur at significantly greater heights and females often initiate these with a characteristic vocalization as they leave the nest. These observations suggest that the costs associated with rapid resource depletion may be more significant for Yellowheads than the gains associated with larger foraging groups. As a result, returning birds attempt to hide their foraging success from colony members.

Despite the disadvantage to food-discoverers the ability to use the colony as an information center presumably evolves because all birds, at times, are unsuccessful at finding food and on these occasions they benefit enough from information exchange to compensate for the costs when successful. Given the latter costs, why don't

all birds remain at the colony and wait for superior foraging areas to be discovered? There are several reasons for why such a strategy may be disadvantageous. First, the average benefits to information exchange are frequency-dependent. As the number of birds that stay at the colony increases, the amount of information brought back by foragers and the probability that productive foraging areas are discovered both decrease. Second, assessments of foraging success on the basis of load size or time spent away from the nest may not always be accurate and birds may do better by foraging without information than by following colony members. The exception to this is individuals that are naive to the location of feeding areas or who were previously unsuccessful at foraging. Third, monitoring the success of colony members has a cost in the form of calories forfeited by not foraging. For females feeding young, this cost may be quite high since starvation of nestlings and fledglings is common (Fautin 1941; Willson 1966; Orians 1980; Gori, Chapter 1). As a result, most birds do not benefit by waiting too long at the colony for superior foraging areas to be discovered. This restricts the number of birds that monitor colony members and, therefore, limits the cost successful birds incur due to information exchange.

Colonial Breeding as a Foraging Strategy and the Evolution of Coloniality

The evidence presented here indicates that Yellowheads benefit from breeding in colonies by being able to locate productive

foraging areas more efficiently. I would now like to address the question of whether the information center hypothesis provides an adequate explanation for the evolution of coloniality in Yellowheads? As previously mentioned, males are territorial defending areas of emergent vegetation which females use as nest sites and, in most populations, as foraging areas. Territory size may vary from 15 m^2 to 7500 m^2 and, for this reason, Yellowheads have been described as being solitary to colonial (Lack 1968). Dense aggregations of breeding adults tend to occur in marshes where insect emergence is high, the incidence of predation is low, and when a significant proportion of the food is obtained off the territory (Orians 1980; J. Wittenberger, unpub. data; Gori, unpubl. data). When males are removed or disappear from their territories, they are quickly replaced by new males that were not previously territory holders in the marsh (Orians 1980; Rutberg and Rohwer 1980; Gori, pers. obs.). These observations suggest that a proportion of the available adult males fail to obtain territories in a breeding season and that high-quality nesting habitat is limited in these populations. Furthermore, females are presumably better off by mating polygynously with territorial males than by mating with non-territorial males if these individuals were to establish territories in less-suitable (i.e. upland) areas (Orians 1969; Wittenberger 1976). Thus, coloniality in Yellowheads has probably evolved as a result of the limited availability of suitable nesting habitat relative to the food supply and, therefore, is not primarily a strategy for food exploitation. Group living,

however, has costs and benefits and natural selection should consistently favor behaviors that increase the benefits and reduce the costs of sociality. The ability of Yellowheads to use the colony as an information center is one way in which the benefits of sociality are increased in this species.

Summary

One of the possible advantages that has been suggested for coloniality is that it facilitates the exploitation of ephemeral, unpredictable food resources. According to this hypothesis, colonies act as information centers and members benefit from the foraging experience (information) of other birds by reducing the search costs associated with locating new foraging areas. I tested whether breeding colonies of Yellow-headed Blackbirds were acting 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 information exchange. The departure analysis showed the following: 1) the colony tended to use different foraging areas on different days suggesting that the distribution of food resources was spatially and temporally unpredictable, 2) departures from the colony tended to be highly clumped in time, 3) birds leaving the colony together (≤ 15 sec apart) had a significantly greater probability of flying off in the same direction than birds leaving at > 15 sec intervals, 4) neighbors were more likely

to leave the colony together than non-neighbors, and 5) incubating females were more likely to follow other birds from the colony than females that were feeding young; in addition, the former females preferentially followed the latter. Consistent with these results, the feeding experiment showed the following: 1) the observed recruitment rate of birds to the experimental foraging area was significantly greater than the expected rate assuming no information exchange, 2) arrivals to the site were highly clumped in time and 3) neighbors of the initial birds to discover the site had a higher probability of subsequent recruitment than non-neighbors. Together these results indicate that Yellowhead colonies can act as information centers; naive or unsuccessful foragers can locate productive feeding areas more efficiently than would otherwise be possible in the absence of information exchange by monitoring the success of colony members, especially neighbors, and following them on foraging trips.

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