National Library of Canada
Bibliothèque nationale du Canada

Canadian Theses Service
Service des thèses canadiennes

Ottawa, Canada
K1A 0N4

NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30, and subsequent amendments.

AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30, et ses amendements subséquents.

ISBN 0-315-55624-2

THE UNIVERSITY OF ALBERTA

THE MAINTENANCE OF MONOGAMY IN BLACK-BILLED MAGPIES AND TREE SWALLOWS

by

PETER O. DUNN

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL 1989

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR	PETER O. DUNN
TITLE OF THESIS	THE MAINTENANCE OF MONOGAMY IN BLACK-BILLE MAGPIES AND TREE SWALLOWS
DEGREE FOR WHICH THESIS WAS PRESENTED	DOCTOR OF PHILOSOPHY
YEAR THIS DEGREE GRANTED	LL 1989

Permission is hereby granted to THE UNIVERSITY OF ALBERTA LIBRARY reproduce single copies of this thesis and to lend or sell such copies for privat scholarly or scientific research purposes only.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

(SIGNED) Peter O.

PERMANENT ADDRESS:

51 Hill Rd.
W. Redding, Connecticut 06
USA

DATED 31 August 1989

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled THE MAINTENANCE OF MONOGAMY IN BLACK-BILLED MAGPIES AND TREE SWALLOWS submitted by PETER O. DUNN in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

Supervisor

John R. Spence

External Examiner

Date 28 August 1989

Abstract

Monogamy is the most common mating system in birds. In contrast, most other vertebrates are polygynous. Several factors are thought to maintain monogamy in most bird populations: 1) no offspring can be raised without male parental care, 2) female reproductive success is usually greater when monogamous than when mated to an already-mated male, or 3) already-mated females prevent other females from settling and breeding with their mates. This study examined these hypotheses in black-billed magpies (Pica pica) and tree swallows (Tachycineta bicolor) in central Alberta, Canada. Based on relative levels of male parental care, I expected that a need for male parental care (hypo. 1) would be more likely to explain monogamy in magpies than swallows.

Male removal experiments indicated that a need for male parental care (hypo. 1) was probably a sufficient explanation for monogamy in magpies (all nests of unaided females failed to produce offspring), while it was not a sufficient explanation for monogamy in swallows (unaided females incurred no significant reduction in reproductive success or survival when compared with control females). Both the male removal experiment and natural cases of polygyny suggested that polygyny would not be disadvantageous to female swallows (hypo. 2 rejected).

Tree swallows appear to be monogamous because, in general, food abundance and nest sites are limiting. Only in areas of high food abundance does it appear that male parental care is not necessary, and intrasexual competition for nest-sites prevents most males from gaining a territory large enough (and with more than one nest-site) to permit two females to breed without one female excluding the other. Female exclusion of other potential mates is probably not maintained by a need to prevent loss of male parental care (hypo. 3), because already-mated females incur no loss of reproductive success when a secondary female breeds on her territory. Already-mated females probably attempt to exclude other females to prevent nest usurpation or egg-dumping. The results of this study indicate the need to consider the effect of variation in food abundance and female-female interactions on avian mating behavior.

Acknowledgments

I thank S. Braun, M. Dhindsa, R. Ebel, J. Faragini, D. Hutchinson, P. Johnston, V. Kerr, P. Komers, S. Lord, C. McCallum, K. Norden, R. Osterwaldt, D. Padilla, M. Quinn, J. Roberts, P. Stubbs, L. Wakelyn and S. Westover for assistance in the field. I thank especially C. McCallum for her help with the production of the thesis. D. Boag, R. Ebel, W. Hochachka, G. Holroyd, D. Hussell and C. Scharf provided logistical advice and assisted in the initial development of the study. I especially thank D. Boag and C. Scharf for initiating the research on magpies in the City of Edmonton, D. Hussell for supplying the insect nets and the Beaverhill Bird Observatory for its cooperation and assistance. I would also like to thank the Golf Course Supervisor, Parks and Recreation Department and By-Law Enforcement Department of the City of Edmonton for their cooperation during my study of magpies. Biosciences Animal Services maintained the magpies in captivity. Chapter II was reviewed by G. Baeyens, S. Beissenger, D. Buitron, M. Dhindsa, W. Hochachka, K. Martin, J. Schieck and P. Weatherhead. Chapter III was reviewed by G. Holroyd, D. Hussell, D. Jones and R. Robertson.

I would like to thank my supervisory committee for their constructive ideas and reviews throughout this study Drs. D. Boag, S. Hannon, G. Holroyd, and J. Spence. In addition, I benefited from the reviews of my examining committee members Drs. P. Gowaty and C. Strobeck. I appreciate greatly their attention to detail and concern for the quality of my study.

I wish to thank my supervisor, Dr. Susan Hannon, for her many ideas and encourageme tont throughout my research. She helped me learn to think more critically and her comments during the writing of this thesis improved the final version immensely.

Finally, I wish to thank my friends who made my stay in Edmonton both enjoyable and enlightening, especially L. Breton, A. Desrochers, J. Desrosiers, G. Dobush, W. Jansen, P. Marino, N. McFadden, D. Padilla, J. Schieck, S. Schweiger, J. Swenson, L. Wakelyn and S. Zohar. I thank especially Leslie Wakelyn for her extraordinary patience and kindness.

Financial support for this study was provided by the National Science and Engineering Research Council of Canada through a grant to S. Hannon, the Wilson

Dunn and the Recreation, Parks and Wildlife Foundation of Alberta through grants to the Beaverhill Bird Observatory.

Table of Contents

List of Tables

List of Tables cont.

List of figures

Figure Page

List of figures cont.

I. GENERAL INTRODUCTION

Monogamy is the most common mating system in birds (Lack 1968, Oring 1982 Møller 1982). In contrast, most other vertebrates are polygynous. Polygyny is thought to be the most advantageous breeding tactic for males because the reproductive success of females is limited by the production of relatively costly eggs, while male reproductive success is limited only by the number of mates acquired (since sperm is cheap to produce; Trivers 1985). The rarity of polygyny in birds makes them an interesting class for understanding the constraints on male mating behavior and, thereby, sexual selection. Over the last two decades various explanations have been proposed for the formation of monogamous pair bonds in birds. but until recently very few rigorous tests have been made of these hypotheses.

Lack (1968) proposed that birds were monogamous because male parental care was necessary to feed and raise a full brood of young (male parental care hypothesis). Others such as Verner (1964), Verner and Willson (1966) and Orians (1969) thought that resources needed for breeding by females (e.g., food and nest-sites) were rarely sufficient to compensate females that chose polygyny for the potential costs involved (polygyny threshold hypothesis). Chosing polygyny may result in a loss of male parental care, more nest predators or a decrease in food availability. The male parental care and polygyny threshold hypotheses have been the leading explanations for monogamy in birds for over 15 years (Wittenberger and Tilson 1980, Greenlaw and Post 1985). However, several recent studies of typically polygynous (Lightbody and Weatherhead 1988, Searcy 1988, Milks and Picman unpubl. data, Wootton et al. 1987) and monogamous (Smith et al. 1982, Gowaty 1983, Greenlaw and Post 1985) birds have suggested that these two hypotheses cannot explain completely the mating behavior of several species of birds, including some species used to develop the polygyny threshold hypothesis. The results of these studies indicate that monogamy in birds may be more complicated than suspected previously (Wittenberger and Tilson 1980).

This study examined several hypotheses for the maintenance of monogamy in black-billed magpies (Pica pica) and tree swallows (Tachycineta bicolor). These two species were chosen for study because they have different life history tactics and potentially different factors maintaining monogamy in their populations. Black-billed magpies are monogamous corvids with long-term pair-bonds and relatively small sexual differences in the cost of parental care (although males do not incubate, they do provide females with most of their food during incubation). Compared with magpies, tree swallows have shorter life-spans, potentially shorter pair-bonds (annual vs. perennial), greater frequency of polygyny (a few potential cases in magpies vs. 5-8% of male swallows) and presumably lower costs associated with male parental care (male swallows only guard the nest-box and feed the young, they neither incubate eggs nor feed the female). Male magpies appear to invest relatively more than male swallows in parental care; therefore, I expected that a need for male parental care would be more likely to maintain monogamy in magpies than swallows.

Besides an examination of male parental care, a second objective of this study was to determine if the polygyny threshold model applied to tree swallows. This hypothesis could only be tested in tree swallows because polygyny in magpies is very rare. Prior to this study, Quinney (1983) suggested that tree swallows were generally monogamous because monogamy was usually more advantageous to the reproductive success of females than polygyny (polygyny threshold hypothesis supported). However, Simmons (1985) pointed out that Quinney (1983) was unable to fully test the predictions of the polygyny threshold hypothesis and, therefore, Quinney's conclusion was premature. To help resolve this question, I tested the polygyny threshold model using both descriptive and experimental techniques.

ORGANIZATION OF THE THESIS

In this thesis I report the results of tests of three leading hypotheses for the maintenance of monogamy in birds (Wittenberger and Tilson 1980): 1) male parental care hypothesis, 2) polygyny threshold hypothesis and 3) female aggression hypothesis. The male parental care hypothesis is examined in magpies and swallows in Chapters II and III, respectively. Chapter IV examines the potential role of female aggression in limiting polygyny in tree swallows. In Chapter V I examine the polygyny threshold model as an explanation for monogamy in tree swallows. Finally, in the general discussion I summarize why I think black-billed magpies and tree swallows are monogamous, and I review my results in relation to alternative hypotheses for the maintenance of monogamy in birds. The remainder of this chapter explains the terminology used and reviews the three hypotheses above.

DEFINITIONS

For this study, I define monogamy as a prolonged association and generally exclusive mating relationship between one male and one female during a given breeding season (Wittenberger and Tilson 1980, Murray 1984). Copulations outside monogamous pair-bonds (extra pair-bond copulations) have been reported via parentage studies (e.g., Gowaty and Karlin 1984) and have been suggested or observed in the species I studied (Buitron 1983, Lombardo 1986, pers. obs.). This behavior could bias estimates of reproductive success in apparently monogamous species (Gowaty 1985). In the absence of a means of assigning parentage (e.g., DNA fingerprinting; Burke and Bruford 1987), I have had to assume that the estimated reproductive success of birds is correlated with their gametic success. Nevertheless, several of the conclusions of this study are based on the behavior of females prior to breeding and are, therefore, not directly affected by this bias. I have also tried to reduce any potential bias in the estimation of reproductive success by basing several of my conclusions on random samples of females that incurred the simulated effects of polygyny. (i.e., females whose mates were removed). I assumed that any bias between monogamous and polygynous females in terms of the frequency of extra pair-bond copulations was reduced by taking random samples from the monogamous subpopulation.

Primary and secondary females were the first and second females to settle on a territory. A monogamous female refers only to a single female on a given territory, while females mated to polygynous males can be either primary or secondary females. In some interspecific comparisons, I have termed species "typically monogamous" if less than 10% of a population's males engaged in polygny. This is a higher level of polygyny than Verner and Wilson (1969) accepted for separating mongamous and polygynous species. Their 5% level was chosen to separate random cases of polygyny from polygyny as a result of female choice (Carey and Nolan 1979); however, I find it difficult to consider tree swallows "typically polygynous" when just 5-8% of males are polygynous. Admittedly, these values are arbitrary. It is best probably to consider the mating behavior of animals along a gradient from monogamy to polygyny. However, the use of "typically monogamous" provides a convenient indication of the relative frequency of a species' or population's apparent mating behavior.

I use the term "male parental care" to describe the cost of acquiring and defending a territory and mate and assisting the female with raising offspring. Some of my experiments use male removals; in these cases my use of the term "male parental care" only refers to male assitance that would have been made following the time of male removal (e.g., male assistance with feeding young if males were removed after hatch).

Another term with frequently different meanings is "territory quality". Except where noted, I will use this term as a short-hand way to describe the quality of the breeding situation as a whole (i.e., including food abundance, male behavior, vegetation structure etc.). This was the original sense of the term in the polygyny threshold model (Orians 1969). A high quality territory is one in which females can raise more offspring in a given year, all other things being equal. It is important to note here that the measure of territory quality used must be independent of reproductive success; otherwise the operational definition of territory quality will be circular. In my study of tree swallows, the independent measure of "territory" quality (actually, the quality of the area) was insect abundance.

REVIEW OF HYPOTHESES

Monogamy can evolve when it is advantageous to both sexes (mutual monogamy) or when it is preferable for one sex only and this sex can impose monogamy on the other (one-sided monogamy; Wittenberger 1979, Wickler and Seibt 1983). In all cases of monogamy, neither sex can monopolize the reproductive behavior of more than one member of the opposite sex (Emlen and Oring 1977). The ecological and behavioral factors that promote monogamy have been summarized by Emlen and Oring (1977), Kleiman (1977), Wittenberger and Tilson (1980), Oring (1982) and Peck and Feldman (1988). Below I review three of the leading hypotheses for the maintenance of monogamy in birds (Wittenberger and Tilson 1980, Greenlaw and Post 1985). It is important to note that several of the factors described below may be operating simultaneously. These interactions, and alternative hypotheses, are considered in the body of the thesis.

1. Male parental care

In some species, male parental care may be essential for the successful production of offspring because both parents must continually attend eggs or young or the nutritional requirements of the young necessitate feeding by both parents. This hypothesis predicts that monogamy will be advantageous to both the male and the female (Wittenberger and Tilson 1980). Mandatory male parental care may be the major cause of "obligate" monogamy in birds which live in harsh environments, have high predation rates or have determinant clutches of one egg (Oring 1982).

The male parental care hypothesis will be falsified if one can demonstrate that male parental care is not necessary to produce some offspring that recruit into the breeding population (Wittenberger and Tilson 1980; see below). At least 16 studies have tested this hypothesis by comparing the fledging success of paired and unaided (males removed experimentally) females (Fig. II-1). Almost all of these studies found that unaided females produced some fledglings; this suggests that male parental care is not necessary. However, it is difficult to find evidence to support the male parental care hypothesis because this hypothesis is not exclusive (it is only a subset of the polygyny threshold hypothesis below) and there is no simple, objective criterion for deciding whether or not a need for male parental care is sufficient to maintain monogamy.

If unaided females <u>never</u> produce any offspring and secondary females receive no male parental care, then males should always be monogamous because secondary females would contribute nothing to the male's fitness in addition to the reproductive success of his primary mate. Male removal studies examine the situation in which secondary females receive no male parental care. They do not examine the possibility that by spliting his parental care between two females, a polygynous male may increase his fitness relative to monogamous males. However, this possibility only has to be examined if unaided females cannot produce any offspring (see Chapter II). If unaided females produce some offspring, then strict monogamy is probably less advantageous to males than polygyny in which the male gives all of his parental care to the primary female.

2. Polygyny threshold is not exceeded

Monogamy should be maintained in a territorial species if breeding with an unmated male on a lower quality territory is more advantageous than pairing with an already-mated male on a higher quality territory (Fig. I-1; Orians 1969, Garson et al. 1981, Wittenberger and Tilson 1980). In other words, the quality of breeding opportunities is not sufficient to make bigamy advantageous to females. In a given area, the polygyny threshold is the minimum difference in the quality of breeding situations that will allow secondary females on high-quality territories to raise as many offspring as monogamous females on poorer quality territories (Fig. I-1). Under this hypothesis, male parental care is not necessary for producing <u>some</u> offspring (unlike hypothesis no. 1) and monogamy is more advantageous to females than males. The polygyny threshold hypothesis may be evaluated as an explanation for monogamy by determining if occasional cases of polygyny (in typically monogamous species) conform to the assumptions and predictions of the model. For example, if females do not choose among territories because their pairing status (monogamous or secondary) has no effect on reproductive success, then one would have to reject this model as an explanation for monogamy.

<u>Assumptions</u>

The polygyny threshold hypothesis assumes (Garson et al. 1981):

1) Females maximize their annual reproductive success, rather than long-term survival and reproductive success. Modifications of the polygyny threshold hypothesis that incorporate long-term reproductive success are described in Pleszczynska and Hansell (1980) and Weatherhead and Robertson (1979).

2) Females choose freely where they breed. That is, they make a choice based on correct knowledge of the quality of all breeding situations, and they are not influenced by the behavior of already-mated females (i.e., female aggression does not limit settlement; see hypothesis no. 3 below).

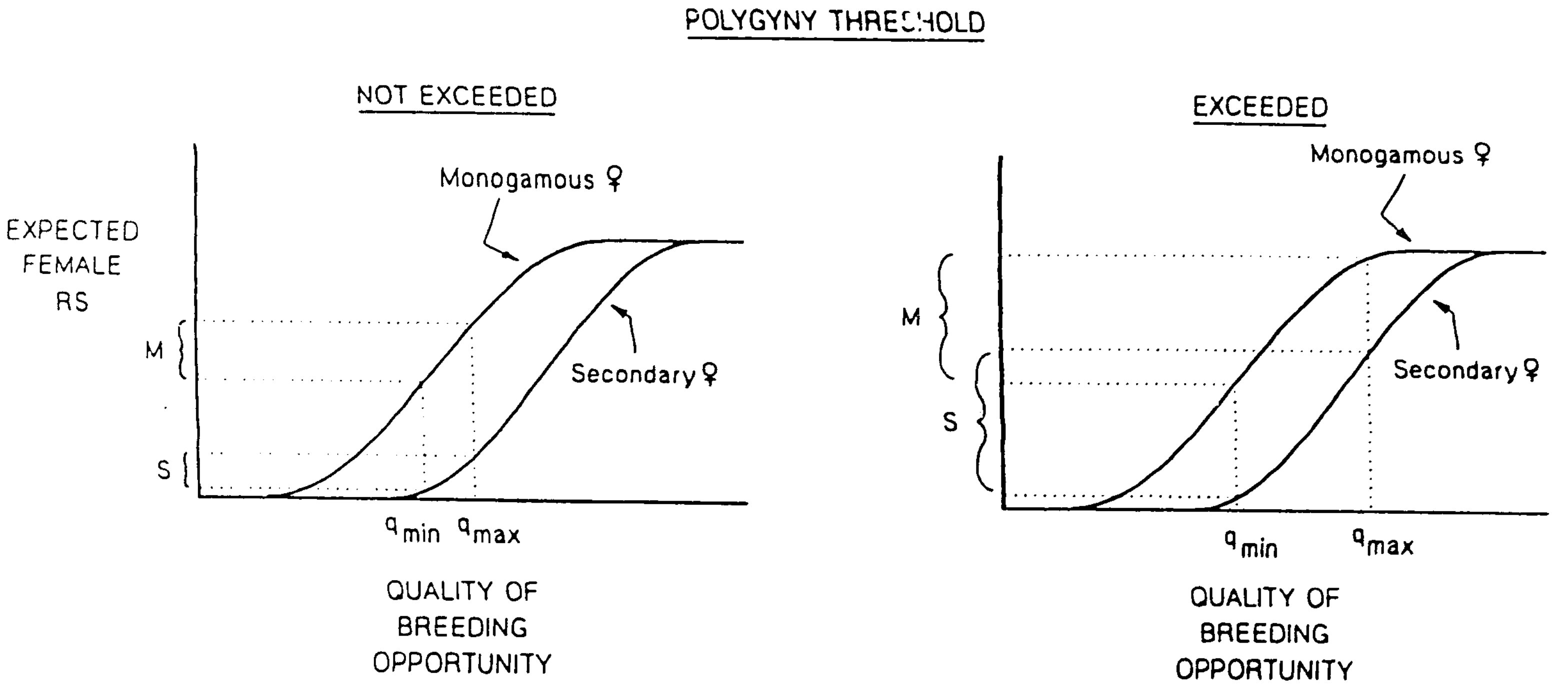


Fig. I-1. The polygyny threshold model with the polygyny threshold not exceeded (monogamy favored by all females) and exceeded (polygyny favored by some females). Quality of the breeding opportunity varies from q max to q min. Note that the difference in territory quality is greater on the right where the polygyny threshold is exceeded. Expected female reproductive success for monogamous (M) and secondary (S) females is shown for the best (q max) and worst (q min) breeding opportunities. Note that there is no overlap between the expected reproductiva success of monogamous and secondary females where the polygyny threshold is not exceeded. However, when the polygyny threshold is exceeded, secondary females on high quality territories (qmax) can expect greater reproductive success than monogamous females on lower quality territories (q min).

3) Females are able to assess the mating status of males. This assumption may be violated in species where the male has widely separated territories or the territories are in dense vegetation (e.g., polyterritorial species; Alatalo and Lundberg 1984).

4) Compared with monogamous females on the same quality territories, primary and secondary females incur a cost. This cost occurs because sharing a territory results in lower male parental care per female, increased predation risk or lower food availability.

Predictions

Several quantitative predictions can be made from the polygyny threshold hypothesis (Altmann et al. 1977, Garson et al. 1981, Lightbody and Weatherhead 1988; Table I-1).

1) The polygyny threshold model predicts that the quality of the breeding situation should be correlated positively with male mating status (no. of mates), because males that offer the highest quality breeding situations attract the most mates. Therefore, experimentally increasing territory quality should increase the frequency of polygyny.

2) When polygyny occurs in normally monogamous species:

> i) Secondary females on high quality territories should raise as many offspring as monogamous females on lower quality territories when they settle at the same time. This occurs because at any given time females attempt to maximize their expected fitness when they choose a breeding situation, whether the male on the territory is unmated or already-mated (Fig. I-2).
>
> ii) Settlement date should be earlier on territories of polygynous than monogamous males. This assumes that territory quality does not change over the settlement period. Females should settle first on the best quality breeding situations and only these territories will be sufficiently high in quality to compensate polygynous females for the cost of polygyny. Note in Fig. I-2 that males on territories 3, 4 and

Table I-1. Tests of the polygyny threshold model in birds. Y=prediction supported; N=prediction not supported; ?=equivocal results.

		Predictions			
Species	Source	1 Territory quality positively correlated with male mating status (E=experimental test)	2i Reproductive success of secondary females equal to or greater than that of concurrently settling monogamous females	2ii Female settlement earlier on territories of polygynous than monogamous males	2iii Positive correlation between settlement order of primary and secondary females
Polygynous					
Dickcissel	Zimmerman (1966)	Y			
	Harmeson (1974)	Y			
Red-winged blackbird	Holm (1973)	Y		Y	
	Weatherhead and Robertson (1977)	Y			
	Ewald and Rohwer (1982)	Y (E)			
	Orians (1980)		N	Y	
Lark bunting	Pleszczynska and Hansell (1980)	Y (E)	Y	Y	
Bobolink	Martin (1974)	Y			
	Wittenberger (1980)	Y			
	Wootton et al. (1986)	Y			
Marsh wren	Verner (1964)	Y			
	Verner and Engelson (1970)	Y			
	Leonard and Picman (1988)	N			
Northern harrier	Simmons et al. (1986)	Y			
	Altenberg et al. (1982)		N?		
Great reed warbler	Catchpole et al (1985)		N		

Table 1-1 (cont.). Tests of the polygyny threshold model in birds. Y=prediction supported; N=prediction not supported; ?=equivocal results.

Species	Source	Predictions			
		1 Territory quality positively correlated with male mating status (E=experimental test)	2i Reproductive success of secondary females equal to or greater than that of concurrently settling monogamous females	2ii Female settlement earlier on territories of polygynous than monogamous males	2iii Positive correlation between settlement order of primary and secondary females
Yellow-headed blackbird	Lightbody and Weatherhead (1988)	N	Y		N
	Orians (1980)			Y	
	Willson (1966)	Y			
Eastern meadowlark	Knapton (1988)	N	Y	N	N
Western meadowlark	Dickinson et al. (1987)		Y	Y	
Monogamous					
Blackpoll warbler	Eliason (1986)	N	Y		
Indigo bunting	Cary and Nolan (1979)	Y	Y	Y	
Tree swallow	Quinney (1983, 1986)	Y?	Y?		
	This study	N	Y	N	N
Pied flycatcher	Alatalo et al. (1981, 1982)	N?	N		
Blue tit	Dhondt (1987)		N		
Variable mating behaviour					
Dunnock	Davies and Lundberg (1984)	Y(E)			
	Davies and Houston (1986)		N		

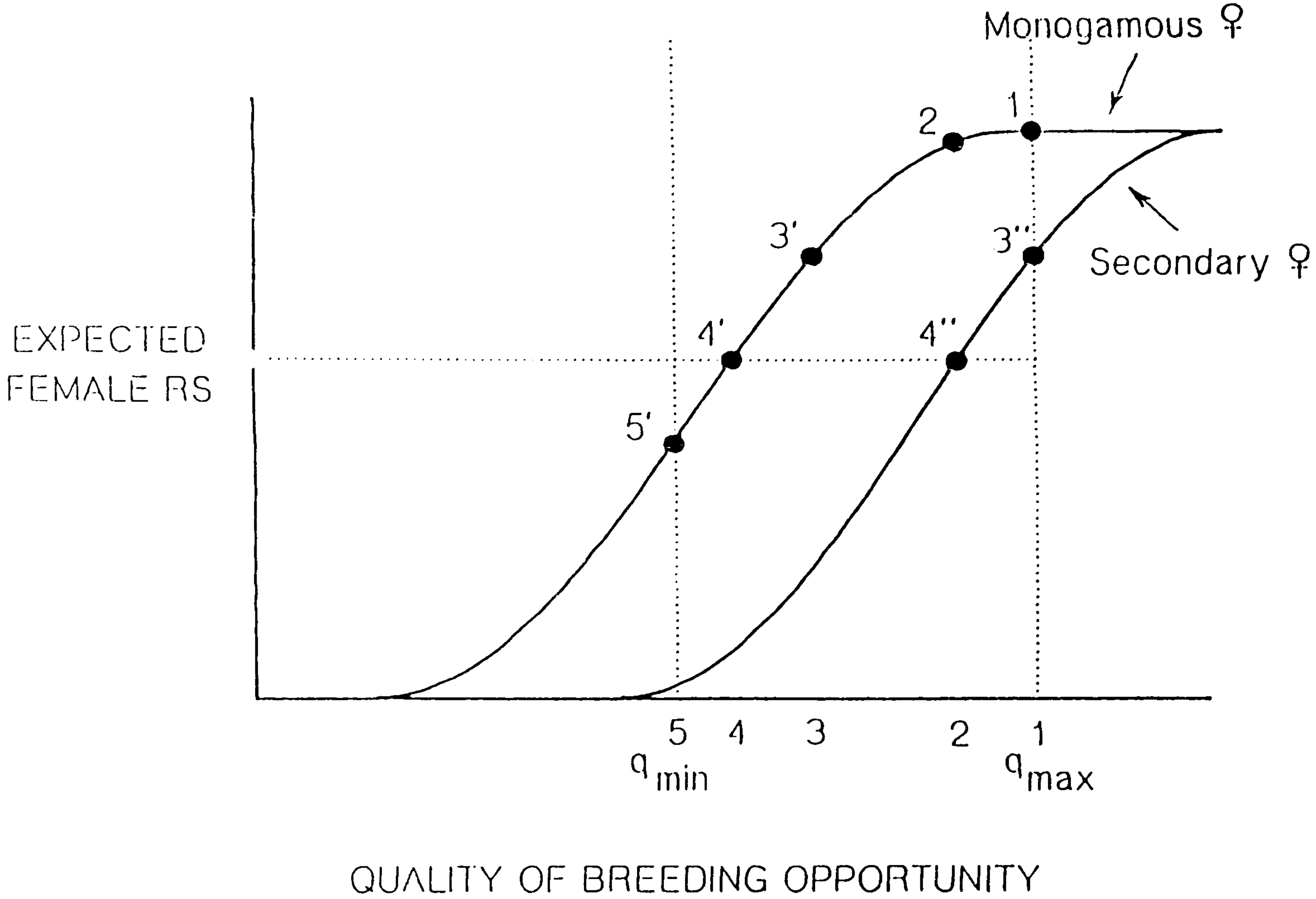


Fig. I-2. The polygyny threshold model adapted from Orians (1969) and Garson et al. (1981). **The hypothetical settling order is shown for 7 females on 5 territories (numbered on the abscissa). Note that because female 4' (on territory 4) and female 4" (on territory 2) can expect the same reproductive success, a female could settle on either territory first and expect the same reproductive success whether she was monogamous on territory 4 or polygynous on territory 2.**

5 are monogamous, while males on territories 1 and 2 are polygynous.

iii) The order of territories settled by primary females will be correlated positively with the order chosen by secondary females. This correlation is expected because each territory will have gone through two sets of comparisons of quality (in cases of bigamy), and the rank order of territory quality should be the same for both primary and secondary females (note that this comparison must only be made on territories with the same number of mates per male; Fig. I-2).

Wittenberger and Tilson (1980) predicted that this hypothesis would explain most cases of monogamy in noncolonial, altricial birds with multipurpose territories. In these species resource availability may not differ enough among territories to exceed the polygyny threshold. The male parental care hypothesis may be thought of as a special case of the polygyny threshold hypothesis, in which the quality of the breeding opportunity is so low that both parents are an absolute necessity for raising offspring (because of low resource availability or high predation rates, etc.; Gowaty 1981). I have separated these two hypotheses to distinguish cases where monogamy is advantageous to both sexes from cases where it may be advantageous only for females (Wittenberger and Tilson 1980).

There have been very few complete tests of the predictions of the polygyny threshold hypothesis in typically monogamous birds (Table I-1). Several descriptive studies have found differences in the quality of territories held by monogamous and polygynous males, but this does not provide support for just the polygyny threshold model (e.g., this is also likely to occur under the female aggression hypothesis [Ch. 3]), nor do these results preclude the possibility of spurious correlations (especially when researchers measure many variables). A polygyny threshold based on vegetation structure or food has only been tested experimentally with lark buntings (<u>Calamospiza melanocorys</u>, Pleszczynska and Hansell 1980), dunnocks (<u>Prunella modularis</u>, Davies and Lundberg 1986) and red-winged blackbirds (<u>Agelaius phoenicus</u>, Ewald and Rowher 1982; Table I-1). Others have examined the role of male territory size on the frequency of polygyny using male removal experiments (Hannon 1984, Smith et al. 1982) or testosterone treatments (Wingfield 1984) that resulted in larger male territories. In these studies, males with larger territories became polygynous. Therefore, territory size may be correlated with a polygyny threshold in some species. However, if females base their choice of breeding situation on territory size, then there should be a correlation between female reproductive success and territory size (for a given number of females/territory). However, this correlation was not examined in the above studies, apart from yellow-headed blackbirds (Lightbody and Weatherhead 1988) for which no correlation was found.

3. Aggression by females maintains monogamy

Even if polygyny is advantageous to some females, birds might still remain monogamous if already-mated females behave aggressively toward potential secondary females and prevent them from settling and breeding with their mates. Monogamous females would presumably be aggressive toward potential secondary females if these females increased competition or predation or decreased the amount of male parental care received by the primary female (Yasukawa and Searcy 1982). Several studies suggest that female aggression limits the number of mates gained by males, but few studies have rigorously tested this hypothesis. The female aggression hypothesis predicts: 1) the settlement of secondary females imposes a reproductive cost on already-mated females, 2) prior to settlement of the secondary female, primary females were less aggressive toward intruders than monogamous females, 3) after settlement of the secondary female, primary females should continue to be aggressive toward the secondary female to reduce the costs of sharing a territory (by either forcing the secondary female out or reducing the amount of resources she uses) and 4) if female aggression limits the settlement of secondary females, then secondary females should settle later than monogamous females, most likely when monogamous females become less aggressive (e.g., after laying).

LITERATURE CITED

ALATALO, R. V., A. CARLSON, A. LUNDBERG, & S. ULFSTRAND. 1981. The conflict between male polygyny and female monogamy: the case of the pied flycatcher, Ficedula hypoleuca. Am. Nat. 117: 738-753.

ALATALO, R. V., & A. LUNDBERG. 1984. Polyterritorial polygyny in the pied flycatcher Ficedula hypoleuca - evidence for the deception hypothesis. Ann. Zool. Fennici 21: 217-228.

ALATALO, R. V., A. LUNDBERG, & K. STAHLBRANDT. 1982. Why do pied flycatcher females mate with already-mated males? Anim. Behav. 30: 585-593.

ALTMANN, S. A., S. S. WAGNER, & S. LENINGTON. 1977. Two models for the evolution of polygyny. Behav. Ecol. Sociobiol. 2: 397-410.

ALTENBERG, W., S. DAAN, J. STARKENBURG, & M. ZIJLSTRA. 1982. Polygamy in the marsh harrier, Circus aeruginosus: individual variation in hunting performance and number of mates. Behav. 79: 272-312.

CATCHPOLE, C., B. LEISLER, & H. WINKLER. 1985. Polygyny in the great reed warbler, Acrocephalus arundinaceus: a possible case of deception. Behav. Ecol. Sociobiol. 16: 285-291.

CAREY, M., & V. NOLAN. 1979. Population dynamics of indigo buntings and the evolution of avian polygyny. Evol. 33: 1180-1192.

DAVIES, N. B., & A. I. HOUSTON. 1986. Reproductive success of dunnocks, Prunella modularis, in a variable mating system. II. Conflicts of interest among breeding adults. J. Anim. Ecol. 55: 139-154.

DAVIES, N. B., & A. LUNDBERG. 1984. Food distribution and a variable mating system in the dunnock, Prunella modularis. J. Anim. Ecol. 53: 895-912.

DAWKINS, R., & T. R. CARLISLE. 1976. Parental investment, mate desertion and a fallacy. Nature 262: 131-133.

DICKINSON, T. E., J. B. FALLS, & J. KOPACHENA. 1987. Effects of female pairing status and timing of breeding on nesting productivity in western meadowlarks (Sturnella neglecta). Can. J. Zool. 65: 3093-3101.

ELIASON, B. C. 1986. Female site fidelity and polygyny in the blackpoll warbler (Dendroica striata). Auk 103: 782-790.

EMLEN, S. T., & L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223.

EWALD, P. W., & S. ROHWER. 1982. Effects of supplemental feeding on timing of breeding, clutch size and polygyny in red-winged blackbirds, Agelaius phoeniceus. J. Anim. Ecol. 51: 429-450.

GARSON, P. J., W. K. PLESZCZYNSKA, & C. H. HOLM. 1981. The "polygyny threshold" model: a reassessment. Can. J. Zool. 59:902-910.

GOWATY, P. A. 1981. An extension of the Orians-Verner-Willson model to acccunt for mating systems besides polygyny. Am. Nat. 118: 851-859.

GOWATY, P. A. 1983. Male parental care and apparent monogamy among eastern

GOWATY, P. A. 1985. Multiple parentage and apparent monogamy in birds. Pp. 11-21 *in* Avian Monogamy (P. A. Gowaty and D. W. Mock, eds.). Washington, D. C., American Ornithol. Union, Ornithol. Monogr. no. 37.

GOWATY, P. A. & A. A. KARLIN. 1984. Multiple maternity and paternity in single broods of apparently monogamous eastern bluebirds (*Sialia sialis*). Behav. Ecol. Sociobiol. 15: 91-95.

GREENLAW, J. S., & W. POST. 1985. Evolution of monogamy in seaside sparrows, *Ammodramus maritimus*: tests of hypotheses. Anim. Behav. 33:373-383.

HANNON, S. J. 1984. Factors limiting polygyny in the willow ptarmigan. Anim. Behav. 32:153-161.

HARMESON, J. P. 1974. Breeding ecology of the dickcissel. Auk 91: 348-359.

HOLM, C. H. 1973. Breeding sex ratios, territoriality, and reproductive success in the red-winged blackbird (*Agelaius phoeniceus*). Ecology 54: 356-365.

KLEIMAN, D. G. 1977. Monogamy in mammals. Q. Rev. Biol. 52: 39-69.

LACK, D. 1968. Ecological adaptations for breeding in birds. London, Methuen.

LEONARD, M. L., & J. PICMAN. 1987. Mate choice by marsh wrens: the influence of male and territory quality. Anim. Behav. 36: 517-528.

LENINGTON, S. 1980. Female choice and polygyny in red-winged blackbirds. Anim. Behav. 28: 347-361.

LIGHTBODY, J. P., & P. J. WEATHERHEAD. 1988. Female settling patterns and polygyny: tests of a neutral-mate-choice hypothesis. Am. Nat. 132: 20-33.

LOMBARDO, M. P. 1986. Extrapair copulation in the tree swallow. Wilson Bull. 98: 150-152.

MARTIN, S. G. 1974. Adaptations for polygynous breeding in the bobolink, *Dolichonyx oryzivorous*. Am. Zool. 14: 109-119.

MAYNARD SMITH, J. 1977. Parental investment: a prospective analysis. Anim. Behav. 25: 1-9.

MØLLER, A. P. 1986. Mating systems among European passerines: a review. Ibis 128: 234-250.

MURRAY, B. G. Jr. 1984. A demographic theory on the evolution of mating systems as exemplified by birds. Evol. Biol. 18: 71-140.

ORIANS, G. H. 1969. On the evolution of mating systems in birds and mammals. Am. Nat. 103:589-603.

ORIANS, G. H. 1980. Some adaptations of marsh-nesting blackbirds. Monog. Pop. Biol. no. 14. Princeton, Princeton Univ. Press.

ORING, L. W. 1982. Avian mating systems. Pp. 1-92 *in* Avian biology, vol. VI (D. S. Farner and J. R. King, Eds.). New York, Academic Press.

PECK, J. R., & M. W. FELDMAN. 1988. Kin selection and the evolution of monogamy. Science 240: 1672-1674.

PLESZCZYNSKA, W. K. 1978. Microgeographic prediction of polygyny in the lark bunting. Science 201: 935-937.

PLESZCZYNSKA, W., K., & R. I. HANSELL. 1980. Polygyny and decision theory: testing of a model in lark buntings (Calamospiza melanocorys). Am. Nat. 116: 821-830.

QUINNEY, T. E. 1983. Tree swallows cross a polygyny threshold. Auk 100:750-754.

QUINNEY, T. E. 1986. Polygyny in tree swallows. Auk 103: 442-443.

SEARCY, W. A. 1988. Do red-winged blackbirds limit their own breeding densities? Ecology 69: 85-95.

SIMMONS, R. 1985. Did tree swallows cross a polygyny threshold? Auk 102: 210-211.

SIMMONS, R., R. B. MACWHIRTER, P. BARNARD, & G. L. HANSEN. 1986. The influence of microtines on polygyny, productivity, age, and provisioning of breeding northern harriers: a 5-year study. Can. J. Zool. 64: 2447-2456.

SMITH, J. N. M., Y. T. YOM-TOV, & R. MOSES. 1982. Polygyny, male parental care, and sex ratio in song sparrows: an experimental study. Auk 99:555-564.

TRIVERS, R. 1985. Social evolution. Menlo Park, Calif. Benjamin-Cummings Publ.

VERNER, J. 1964. Evolution of polygamy in the long-billed marsh wren. Evol. 18: 252-261.

VERNER, J., & G. H. ENGELSEN. 1970. Territories, multiple nest building and polygyny in the long-billed marsh wren. Auk 87: 557-567.

WEATHERHEAD, P. J., & R. J. ROBERTSON. 1977. Harem size, territory quality and reproductive success in the red-winged blackbird (Agelaius phoeniceus). Can. J. Zool. 55: 1261-1267.

WEATHERHEAD, P. J., & R. J. ROBERTSON. 1979. Offspring quality and the polygyny threshold: "the sexy son hypothesis". Am. Nat. 113: 201-208.

WICKLER, W., & U. SEIBT. 1983. Monogamy: an ambiguous concept. Pp. 33-52 in (P. Bateson Ed.). Mate choice. New York, Cambridge Univ. Press.

WILLSON, M. F. 1966. Breeding ecology of the yellow-headed blackbird. Ecol. Monogr. 36: 51-77.

WINGFIELD, J. C. 1984. Androgens and mating systems: testosterone-induced polygyny in normally monogamous birds. Auk 101: 665-671.

WITTENBERGER, J. F. 1980. Vegetation structure, food supply, and polygyny in bobolinks (Dolichonyx oryzivorus). Ecology 61: 140-150.

WITTENBERGER, J. F., & R. L. TILSON. 1980. The evolution of monogamy: hypotheses and evidence. Ann. Rev. Ecol. Syst. 11: 197-232.

WOOTTON, J. T., E. K. BOLLINGER, & C. J. HIBBARD. 1986. Mating systems in homogenous habitats: the effects of female uncertainty, knowledge costs, and random settlement. Am. Nat. 128:499-512.

YASUKAWA, K., & W. A. SEARCY. 1982. Aggression in female red-winged blackbirds: a strategy to ensure male parental investment. Behav. Ecol. Sociobiol. 11: 13-17.

ZIMMERMANN, J. L. 1966. Polygyny in the dickcissel. Auk 83: 534-546.

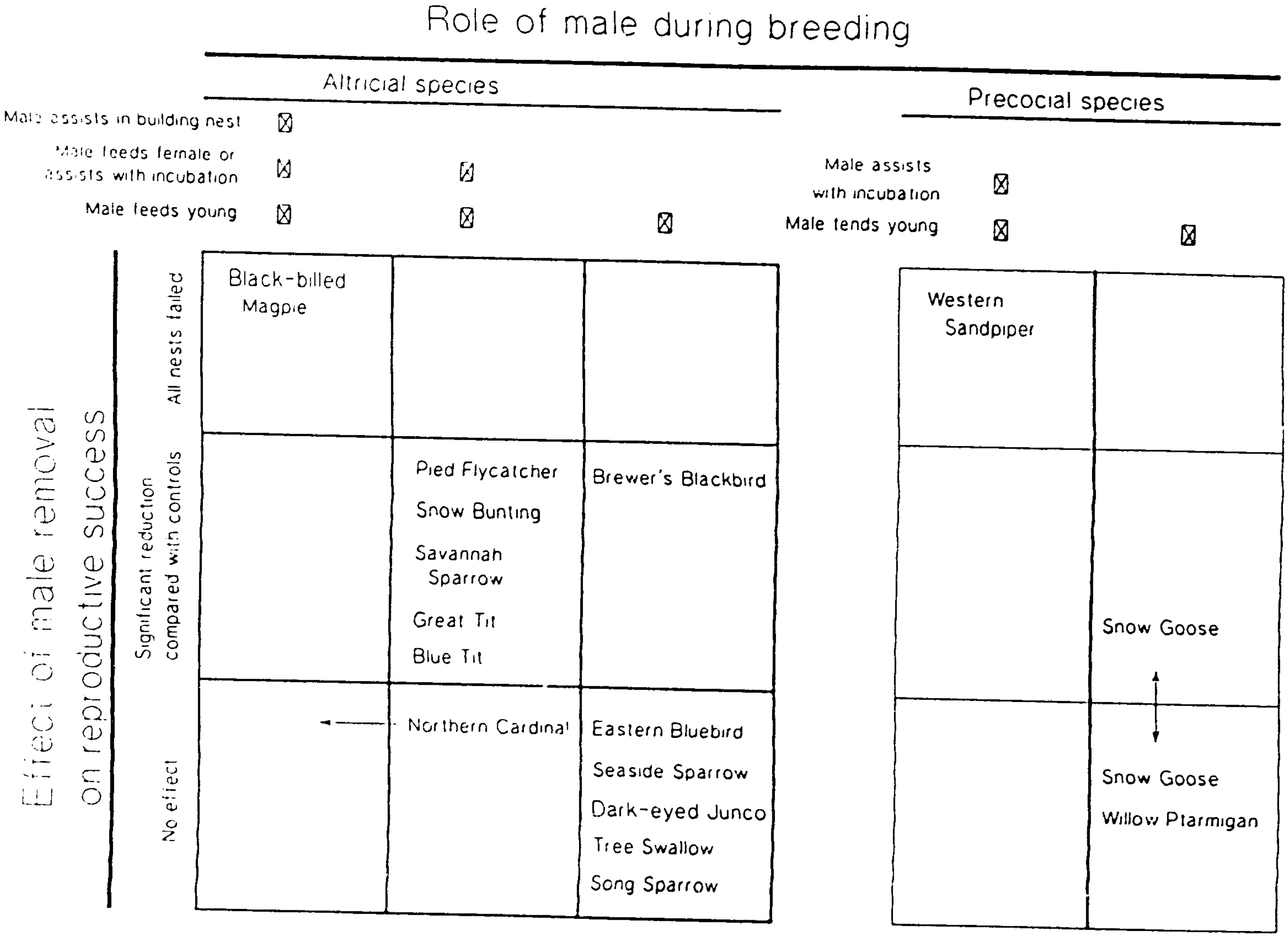
II. EVIDENCE FOR OBLIGATE MALE PARENTAL CARE IN BLACK-BILLED MAGPIES

INTRODUCTION

Most species of birds are monogamous, in contrast to the widespread occurrence of polygyny in other vertebrates (Lack 1968; Møller 1986). Since males contribute more parental care in monogamous than polygynous birds (Verner and Willson 1969; Møller 1986), monogamy has often been explained by a need for male parental care in order to produce offspring successfully (Lack 1968, Emlen and Oring 1977, hypothesis 1 of Wittenberger and Tilson 1980). However, this association does not necessarily indicate what factors maintain monogamy in bird populations. Male parental care would only explain monogamy in a population when 1) females cannot rear any offspring without male parental care (hypothesis 1 of Wittenberger and Tilson 1980) or 2) the reduced amount of male parental care often associated with secondary mate status (e.g., Lifjeld et al. 1987) makes pairing with unmated males more profitable to females than pairing with already-mated males (hypothesis 2 of Wittenberger and Tilson 1980). Experimental removal of males can indicate how important male parental care is for female reproductive success and, thereby, its significance in the maintenance of monogamy.

Almost all male removal studies have found that unaided females were able to raise successfully some offspring (e.g., Weatherhead 1979, Gowaty 1983, Lyon et al. 1987). Only one study found that females could not produce any young without male parental care (Western Sandpiper, *Calidris mauri*; Erkmann 1983). In altricial birds, the ability of unaided females to raise young successfully suggests that most species are monogamous because it is advantageous to females (hypothesis 2), and not to both sexes (hypothesis 1; Wittenberger and Tilson 1980: 201). However, hypothesis 1 of Wittenberger and Tilson (1980) may explain monogamy in more birds than thought previously because, relative to females, male removal studies have generally examined species with low levels of male parental care (Fig. II-1). There is a need for male removal studies in monogamous species with varying levels of male parental care so I can better understand the relative importance of male parental care versus other constraints in the maintenance of monogamy (Mock 1985)

Fig. II-1. The distribution of male removal studies in typically monogamous birds (listed by common name; scientific names and references are given below) in relation to the role of males during breeding. Data on the role of the male during breeding came from Verner and Willson (1969), the male removal study or personal communication (Song Sparrow, W. Hochachka). Arrows indicate differing results among studies. Behaviours under role of male during breeding indicate breeding activities of most males of a given species (if data were not available from the male removal study). 'X's above a column indicate that males participate in that behaviour. Snow Buntings were not included in the group of species with relatively large male parental investment (far left column) because it was not clear whether males that accompany females are contributing relatively more to parental investment, ensuring their paternity or both. Reproductive success was only compared between control and male removal groups using fledging success so estimates of reproductive success would be similar. Scientific names and references used: Snow Goose (Anser caerulescens), Martin et al. 1985; Western Sandpiper (Calidris mauri), Erckmann 1983; Willow Ptarmigan (Lagopus lagopus), Hannon 1984, Martin & Cooke 1987; Pied Flycatcher (Ficedula hypoleuca), Alatalo et al. 1982; Tree Swallow (Tachycineta bicolor), P. Dunn unpubl. data; Black-billed Magpie, this study, Blue Tit (Parus caeruleus), Sasvari 1986; Great Tit (Parus major), Sasvari 1986, Bjorklund & Westman 1987; Eastern Bluebird (Sialia sialis), Gowaty 1983; Northern Cardinal (Cardinalis cardinalis), Richmond 1978; Savannah Sparrow (Passerculus sandwichensis), Weatherhead 1979; Seaside Sparrow (Ammodramus maritimus), Greenlaw & Post 1985; Song Sparrow (Melospiza melodia), Smith et al. 1982; Dark-eyed Junco (Junco hyemalis), Wolf et al. in press; Snow Bunting (Plectophenax nivalis), Lyon et al. 1987; Brewer's Blackbird (Euphagus cyanocephalus), Patterson et al. 1980.


Role of male during breeding
Altricial species
Precocial species
Male assists in building nest ☒
Male feeds female or assists with incubation ☒ ☒
Male feeds young ☒ ☒ ☒
Male assists with incubation ☒
Male tends young ☒ ☒
Effect of male removal on reproductive success
All nests failed
Significant reduction compared with controls
No effect
Black-billed Magpie
Pied Flycatcher
Snow Bunting
Savannah Sparrow
Great Tit
Blue Tit
Brewer's Blackbird
Northern Cardinal
Eastern Bluebird
Seaside Sparrow
Dark-eyed Junco
Tree Swallow
Song Sparrow
Western Sandpiper
Snow Goose
Snow Goose
Willow Ptarmigan

This paper describes a male removal experiment designed to evaluate the contribution of male parental care to reproductive success among Black-billed Magpies (Pica pica). Black-billed Magpies are monogamous corvids with apparently long-term pair-bonds and small differences between the sexes in terms of total energetic investment during breeding (Mugaas and King 1981). The total energetic investments of male and female magpies are similar because males provide most of the food eaten by their mates during incubation, which has a relatively low energetic cost for females (Mugaas and King 1981). Magpies may engage in extra pair-bond copulations, although these appear to be rare, and there is no evidence of subsequent male assistance in these cases (Birkhead 1979, Buitron 1983). In the absence of information on genetically effective matings, I consider that magpies pair monogamously because they maintain a prolonged and essentially exclusive relationship with one partner during the breeding season (Wittenberger and Tilson 1980).

METHODS

The study was conducted on 2 areas in the North Saskatchewan River valley in Edmonton, Alberta, Canada during April - June 1985-87. One study area included Kinsmen and Queen Elizabeth Parks, and the other study area was Riverside Golf Course. In 1987 I also included magpie nests on the University of Alberta campus and in a nearby residential area (Campus-Windsor Park). The general habitat types were similar to those described by Hochachka and Boag (1987).

Nests were checked at least 3 times each season to determine laying date (date of clutch initiation), clutch size, and number of young fledged. Laying date was determined directly for all nests by inspection of nests before and during laying and by back-dating from the observed number of eggs (assuming that one egg was laid/day, plus a gap of one day at some point in laying; Hochachka 1985: 12). Fledging success was taken to be the number of young in the nest at 20 days of age (approximately 1 week before fledging). Nestling age was determined from a known hatch date or by calculating nestling age from a logistic growth equation for bill depth (C. Scharf, unpubl. data). In 1987, nestlings of known age were weighed to determine if young in nests of failure was indicated by the loss of all eggs or young.

Nests were observed approximately once per week from mid-April to late-May between 0800 and 1800 h. Observers watched nests from approximately 20 m away. This is closer than most previous studies; however, magpies in the city of Edmonton have habituated to heavy human activity near their nests, so I do not believe that my presence influenced their behavior. Each observation session consisted of ten 3 minute periods (each period separated by approximately 3-5 minutes) in 1985 and one 60 minute period in 1986 and 1987. An initial nest was chosen randomly every week, after which nests were picked systematically for observation during that week. The time of day that control and unaided females were observed did not differ during the incubation or nestling periods (*t*= -0.03, df= 11, *P*= 0.98 for incubation; *t*= -1.64, df= 11, *P*= 0.13 for the nestling period; times were arcsine transformed). During each observation period, observers recorded the total number of trips inside the nest by both males and females (feeding trips could not be distinguished from other trips) and the length of time control and unaided females spent on the ground (mostly foraging) and sitting in trees and on the nest. Unaided and control females were observed for 85 and 108 hours, respectively. However, my analyses were confined to 81 and 33 hours of observation on unaided and control females, respectively, because males and females could not be distinguished reliably at control nests where neither bird was marked individually and because of missing data for some behaviors. Therefore, my observations at control nests only come from pairs in which the sex of each bird was known (one or both birds were marked with unique combinations of plastic, colored leg-bands).

Within each study area, territories were chosen randomly for removal of males, although territories where males were removed in previous years were excluded from removals in subsequent years. Magpies were caught with an array of fishing-line nooses attached to wire wickets sunk into the ground around a live, decoy magpie (Scharf 1985a). Birds were classified to age (yearling or adult) based on the length of the black tip of the 10th primary (Scharf 1985b: 94) and to sex based on wing length and beak size (Scharf 1987). Classification of age based on the length of the black tip of the 4th primary (Erpino 1968) was not an accurate method of classifying age in this population (Scharf 1985b: 94). Removed magpies were kept in an aviary. Males assigned for removal were not marked prior to their capture so the territorial status of captured males was determined by 1) their location prior to capture (near the removal nest or another territory), 2) by the response of the female toward the male that was caught (before and during capture attempts) and 3) by the presence of other birds on the territory immediately after capture of males presumed to be territory holders. I assumed that I caught the territory holder if no other bird was seen with the female at the removal nest on the day of capture. When males assigned as controls could be caught they were measured, color-banded and held for 30 minutes before release, to control for the possibility that female magpies might desert their nest immediately if males disappear for short periods of time. However, females did not desert nests within 1 day of banding of their mates, nor immediately after their own banding, so I do not believe that capture and banding caused any of the observed nest desertions. Number of visits to the nest by observers was similar between control and unaided nests to control for human disturbance.

Laying date and clutch size of control and male removal (unaided) females were compared with two-way ANOVA's (main effects were treatment and study area) each year to determine if there were any a priori differences that may have biased the fledging success results. Laying date and clutch size were approximately normally distributed; however, fledging success of all nests (both male removals and controls) was not normally distributed because of nest failures (zero fledging success) among the male removal group. The ten 3-minute observation periods during each observation session in 1985 were combined and multiplied by two to make nest visit rates equivalent to the 60 minute observation sessions in 1986 and 1987. To analyze nest visit data, I first calculated a mean rate of visits for each nest from multiple observations to obtain independent samples. These means were calculated separately for the incubation and nestling periods. Individual means for each nest were then analyzed with two-way ANOVA's in which the main effects were treatment and year. The year effect controlled for the difference in length of observation sessions between 1985 and 1986-87. Multi-way ANOVA's were performed with the General Linear Models procedure of the Statistical Analysis System (SAS Institute, 1982), and tests of significance were based two-tailed and were considered significant at the 0.05 probability level. Means are presented with their standard errors.

RESULTS

Twenty-nine male magpies were trapped at 28 nests chosen for removal of males (a territorial male and a replacement male were trapped at the same nest in 1987). I attempted to remove half of the males during laying or early incubation and the other half during late incubation. However, difficulties in trapping males led to a removal schedule of 2 before laying, 19 during laying or the first half of incubation, and 5 during the last half of incubation or early post-hatch. In addition, 2 more males were removed from their territories, but the stage of nesting was not known at the time of removal. I was unable to remove additional territorial males because magpies on most territories did not usually approach the decoy and nooses after three trapping attempts or during late incubation.

Following the removal of presumed territorial males, replacement males were seen assisting territorial females at 9 of 28 nests (32%). All of these replacement males were seen defending the nest against intruders (other magpies or human observers) or feeding the female at least once. Females were not observed with another male for at most 5-13 days after removal at seven of these nests and for a maximum of 2 days at the other two nests. Eight of these nine nests were analyzed separately for the effect of replacement males on fledging success. The remaining nest was included in the sample of unaided females because I were able to remove the replacement male (a yearling) less than 5 days after it appeared. Except for this nest, my repeated attempts to remove replacement males were unsuccessful. Another potential case of replacement involved a male (color code RAOG) neighbor that was seen near the nest of an unaided female in 1987. However, this male was not considered a replacement because it did not appear to assist the widowed female (during 11 hr of observation). Replacement males were seen at 1) both nests where the male was removed prior to laying, 2) at two of 19 nests where males were removed during laying or the first half of incubation, 3) at two of five nests where males were removed during the second half of incubation or known at the time of male removal.

Unaided females

I examined laying date and clutch size at control nests and nests of unaided females to see if there were any a priori differences that could have biased comparisons of fledging success. Laying date for the first egg in a clutch and clutch size (Table II-1) did not differ between control nests and nests of unaided females nor among study areas in any year (two-way ANOVA's for each year, main effects were treatment and study area; $\underline{P}>0.09$ for laying date each year; $\underline{P}>0.11$ for clutch size each year). The fledging success data could not be tested for differences among years and study areas using data from nests of unaided females because these data were not normally distributed (all nests failed). Therefore, I tested for study area and year effects with data from control nests only. I also excluded 1987 data from the Campus study area in order to avoid empty cells in the two-way ANOVA design. When only control nests were examined, there was a significant difference in fledging success among years (two-way ANOVA, main effects were year and study area; $\underline{F}=4.38$, df= 2,72, $\underline{P}= 0.016$), but there was no difference among study areas ($\underline{F}= 2.84$, df=1,72, $\underline{P}= 0.096$). Inspection of the least-squares means for each year indicated that the difference among years was due to a low fledging success in 1986 (see also Table II-1).

No young fledged from the 20 nests where females were unaided (Table II-1), while the rate of nest failure for all control nests was 48% (51 / 106 nests, Table II-2). I tested whether nests of unaided females failed at a significantly higher rate than control nests by using a randomization test (Sokal and Rohlf 1981) that estimated the probability of finding the observed number of nest failures at male removal nests among a randomly-chosen sample (of equal size) of control nests in the same year and study area. Ten thousand random samples (size of each sample = no. of nest failures at male removal nests) were drawn with replacement from control nests in each corresponding year and study area to calculate the probability values in Table II-2. Two of seven of these simulations resulted in a significant outcome ($\underline{P} \leq 0.05$), meaning that the observed rate of nest failure among male removal nests would not be expected by chance alone (for a given study area and year category). An overall probability value was estimated by

Table II-1. Reproductive parameters of black-billed magpies at control and male removal nests with and without replacement males in Edmonton, Alberta, April-June 1985-1987. No renests are included.

		Laying date			Clutch size			Fledging success[a]		
Year	Treatment	$\bar{X}$	SE	N[b]	$\bar{X}$	SE	N[b]	$\bar{X}$	SE	N[b]
1985										
	Controls	20 Apr	1.3	23	6.0	0.3	26	2.3	0.4	26
	Male removals									
	aided[c]	23 Apr	5.2	5	6.8	0.5	5	2.2	0.9	5
	unaided	22 Apr	3.2	7	6.9	0.3	7	0.0	0.0	7
1986										
	Controls	18 Apr	1.5	20	5.9	0.5	14	0.9	0.2	25
	Male removals									
	aided[c]	19 Apr		1	3.0		1	0.0	0.0	3
	unaided	23 Apr	4.9	3	5.3	1.2	3	0.0	0.0	3
1987										
	Controls	18 Apr	0.9	32	6.8	0.2	26	1.6	0.3	55
	Male removals									
	aided[c]									
	unaided	20 Apr	1.8	9	6.7	0.5	7	0.0	0.0	10

---

[a] Number of young fledged per female; includes nest failures.

[b] Number of nests.

II-2. Number of nesting attempts by black-billed magpies that fledged at least one young cessfully (S) or failed (F) to produce young and the probability (P) of finding the observed ber of nest failures at nests of unaided females among all control nests in a given study area and r (randomization test, see text for explanation).

	Kinsmen- Q.E. Parks					Riverside Golf Course					Campus-Windsor Park				
	Unaided females		Control			Unaided females		Control			Unaided females		Control		
r	F	S	F	S	P	F	S	F	S	P	F	S	F	S	P
5	4	0	7	5	0.118	3	0	2	12	0.004					
5	1	0	5	0	1.0	2	0	8	12	0.159					
7	4	0	2	5	0.006	1	0	6	14	0.286	5	0	21	7	0.228

the total number of tests made (N=7; Table D.30 in Zar 1974). The probability that two tests (each with a probability of 0.05 or less) would be significant, out of seven tests altogether, is 0.04. Therefore, I concluded that even though our sample sizes for male removal nests were low, the failure of all 20 nests would not be expected by chance.

Time of nest failure was known in relation to hatch for 13 nests of unaided females (only nests in which the male was removed before the latter half of incubation); of these, 7 nests were lost or deserted after hatch (54%). Nests of control birds showed a similar pattern: nine of 16 nests failed after hatch (56%; $G = 0.04$, df= 1, $P > 0.75$). The maximum number of days between male removal and nest failure (our nest checks were not made often enough to determine the exact date of failure) averaged 22.2±2.1 d. (n=20 nests). There was no relationship between timing of male removal (relative to hatch date) and time to failure of the nest (midpoints of ranges were used when exact dates were not known; $r^2 = 0.04$, df= 19, $P = 0.38$). I found little direct evidence of predation on nests (2-10% of nests, Table II-3); however, the cause of most nest failure was unknown (75-86%). More nest failures appeared to be associated with spring snowstorms (20-39%) than with predation (Table II-3). Body mass of nestlings <4 days old was similar between nests of unaided (13.8±0.3 g, mean±SE, N= 11 nestlings) and paired (13.6±1.1 g, N= 38) females ($t = 0.18$, df= 47, $P > 0.5$), but at 5-9 days of age body mass was lower in nests of unaided (24.1±1.2 g, N= 8) than paired (42.9±4.2 g, N= 22) females ($t = 4.16$, df= 28, $P < 0.001$). Most nests of unaided females failed after nestlings reached 9 days of age, so we do not have any data for later ages. Although my data are limited, they suggest that starvation may have been the cause of nest failure when males were removed.

I thought that unaided females would change their behavioral patterns to compensate for the loss of male parental care. However, I found no differences between unaided and paired females in the total time sitting, time spent in the nest or time spent on the ground (Table II-4). During both the incubation and nestling periods, number of nest visits/hr did not differ between unaided and paired females, although there was a trend ($P = 0.09$) toward more nest visits by unaided than paired females during incubation (Table II-4). During incubation, the total rate of visits at control nests (i.e., both the male and female) was 1.8 times greater than the rate at nests of unaided

Table II-3. Causes of total nest failure in black-billed magpie nests, Edmonton, Alberta, April-June 1985-1987.

	Predation[a]		Desertion of nest[b]		Unknown		Total[c]	
Treatment	%	N	%	N	%	N	%	N
Control	3	1	17	6	81	29	100	36
Unaided female	10	2	15	3	75	15	100	20

[a] Feathers or cracked eggs were found in or near the nest.

[b] Cold eggs or dead young were found in the nest. This could also have been due to predation on the female parent.

[c] Thirty-nine percent (N= 14) of control nests and 20% (N= 4) of nests of unaided females failed within two days of a snowstorm.

Table II-4. Behavior of Black-billed Magpies at control and male removal nests in Edmonton, Alberta, April-June 1985-1987. Observations of nests of unaided females during incubation only include nests at which the male was removed during laying or early incubation. Times are out of one hour (in min.). Note that times do not sum to 60 min. because time spent flying and moving in trees was not included, and total time sitting includes time spent on the nest. Sample sizes are the number of nests.

Period/Treatment	Total observation time (hr.)	Nest visits/hr						Females only								
		Total			Female only			Total time sitting			Time spent in nest			Time spent on ground		
		X	SE	N	X	SE	N	X	SE	N	X	SE	N	X	SE	N
Incubation																
Control	26	2.5	0.4	9	0.8	0.2	9	51.7	4.2	9	43.1	6.5	9	2.2	1.4	9
Unaided females	69	1.4	0.2	13	1.4	0.2	13	53.0	2.3	13	45.6	3.7	13	2.7	1.4	13
P			0.002			0.09			0.53			0.74			0.81	
Nestling																
Control	7	4.4	1.7	6	1.6	1.2	5	42.5	6.8	6	22.5	11.0	5	8.5	5.6	6
Unaided females	12	1.8	0.4	7	1.8	0.4	7	45.0	5.6	7	38.0	10.6	4	10.7	3.9	7
P			0.02			0.95			0.92			0.91			0.99	

Probability of no difference between behaviors at nests of control and unaided females. Probability values are from a two-way ANOVA (main effects were treatment and year). All interactions were non-significant.

females, and during the nestling period it was 2.4 times greater at control nests (Table 4). The difference in total nest visit rate during the nestling period was not due to differences in the age of young in nests of unaided versus paired females (7.9±2.1 days old in control nests, 8.9±2.0 days old in nests of unaided females; $\underline{t}$= 0.36, df= 14, $\underline{P}$>0.5).

Widows with replacement males

Females with replacement males produced as many fledglings as control females in 1985 ($\underline{t}$= 0.1, df=29, $\underline{P}$> 0.9), but in 1986 females with replacement males produced fewer fledglings (Table II-1), although the sample size was too small for testing in 1986 (the one replacement male in 1987 was removed). When replacement males assisted widows, nest failure rates were 20% (1/5) in 1985 and 100% (3/3) in 1986, compared with rates of 35% (9/26) and 52% (13/25) at control nests in 1985 and 1986, respectively. It appears that widows with replacement males can produce as many, or almost as many, offspring as control females. However, except for the potential replacement male in 1987 (RAOG), I never observed males associating simultaneously with a widowed female and another female, and we did not know the breeding status of replacement males. If male ROAG were breeding simultaneously with two females, then it would have produced fewer fledglings than monogamous males, because ROAG produced one fledgling at his original nest and no offspring were produced at the nest of the unaided female that he visited.

DISCUSSION

In contrast to almost all other male removal studies, female Black-billed Magpies that lacked male assistance were unsuccessful in raising any young. This indicates that male parental care is more important in Black-billed Magpies than any other passerine in which males have been removed experimentally thus far (Fig. II-1). Buitron (1988) found a similar effect of loss of male parental care on fledging success in two cases when males disappeared prior to fledging. However, after fledging, two unaided birds (1 male and 1 female) were able to raise 4-6 young to independence (Buitron 1988). It should be noted that my conclusions depend on two assumptions. First, it could be argued that my sample of unaided females was not a random sample of the entire population, but just of those females that for some reason were not able to attract a replacement male. The females that gained a replacement male may have been better quality parents, and they may have been able to raise offspring alone. My evidence to suggest that this was not true came from the one widowed female that gained a replacement male, but subsequently failed to produce any young after I removed the replacement male. To my knowledge, there is also no evidence that characteristics related to a female's ability to attract mates is correlated with quality as a parent. Second, my results do not necessarily indicate that an absolute need for male parental care maintains monogamy in magpies, as implied by hypothesis 1 of Wittenberger and Tilson (1980). Hypothesis 1 would only apply if monogamy were advantageous to both sexes. There is still the potential for male magpies to produce more offspring by aiding two females, if two females can each produce some offspring with a fraction of the male's total parental care. I use data from our study and others to argue below that monogamy is also advantageous to male magpies.

Information on replacement males that were neighbors could suggest whether males can successfully split their parental care between two females. In this study I found no evidence that replacement males were neighbors. However, only one of eight widows with replacement males had a neighbor that was banded. A potential replacement male (RAOG) was seen at more than one nest in this study, but this male only assisted the female on his original territory. Even assuming that male RAOG was bigamous, this male would not have increased his fledging success above that of monogamous males. I suspect that most replacement males came from flocks of non-breeding magpies present throughout the breeding season.

I also could not find any other studies in which male magpies increased their reproductive success by splitting their parental care between two nests. Baeyens (1981a, pers. comm.) reported two cases of "bigamy" that arose when males were captured and a neighboring male annexed the territory and remaining mate. However, in these cases the eggs were rotten or the young were dead in the neighboring male's nest, so these cases might be considered renesting attempts rather than simultaneous bigamy. In addition, no eggs were laid during these new associations and the former pair-bond was restored when the captive males were released (after 4-18 d.). In cases where males disappeared before eggs were laid, replacement males bred successfully with the widowed females (Baeyens 1981a, pers. comm.; see also Buitron 1988). Therefore, although Black-billed Magpies may mate with more than one bird in a breeding season, it appears that "bigamy" is sequential (after nest failure), rather than simultaneous. Even in cases where replacement males may be breeding simultaneously with two females, it appeared that they were no more successful than monogamous males (Baeyens pers. comm., this study). In summary, monogamy is probably advantageous to both male and female magpies because completely unaided females produce no offspring, and males do not appear to profit from polygyny. To my knowledge, this is the first experimental evidence reported for obligate male parental care in a passerine.

If reproductive success invariably falls to zero following male removal, then one might hypothesize that unaided females should desert their nest or attempt to gain a new mate. Instead of deserting immediately, unaided females remained at their nests for over 2.5 weeks following removal of their mates (see also Shannon 1958, Baeyens 1981a). These females might remain at the nest if gaining a replacement male at the first nest is less costly (in terms of reproductive success) than renesting. Successful renesting is still possible throughout the nestling period in this population (mid-May to early June; e.g., 73% (8/11) of renests were successful in 1987; c.f. Erpino 1986b). Nevertheless, 68% (19/28) of all unaided females did not gain a replacement male and about half continued nesting until after hatch. I cannot explain why these females did not desert their nests earlier. Replacement males may become more available later in the breeding season (after other nests fail) or it may be possible for unaided females to raise a few offspring in years of high food abundance (Lyon et al. 1987).

Behavioral observations suggested that unaided females were not able to compensate significantly for the loss of male parental care. Before and after hatch, unaided females made fewer visits to the nest than the total visits of both the male and female in control pairs. This diffference is likely due to the male providing most of the incubating female's food and the increasing participation of females in nest visits as the nestling period progresses (Buitron 1988). During incubation, control and unaided females spent similar amounts of time in the nest (71-76%) and on the ground (4-5%).

Buitron (pers. comm.) found that an unaided female made more feeding trips and had a lower nest attendance rate when her mate disappeared during incubation. My results are similar in that unaided females tended to increase their rate of nest visits, but I cannot explain the lack of difference in nest attendance between unaided and control females. Unaided females may compensate for the loss of male feeding by foraging more often while they are on the ground; however, I did not record direct measures of feeding rate. Buitron (1988) also found an increase in feeding rate by an unaided female when its mate disappeared 2 days after the young fledged from the nest. However, this increased feeding rate was still lower than it had been when both parents were present. In contrast to Buitron (1988), I may not have found an increase in the nest visit rate of unaided females during the nestling period because the birds I observed had young nestlings (mean= 7 d. old), and they may have been spending more of their time brooding the young. Other studies have reported that females spend over 60% of their time in the nest during the early nestling period (Erpino 1986b, 67%; Buitron 1988, 72%). In this study I found that unaided females spent a similar percentage of time in their nests (63%, Table II-4); however, control females only spent 38% of the time they were observed in their nest. The small sample size in this study for control nests during the nestling period may be the cause of the discrepancy among studies.

Why is male parental care essential?

Buitron (1988) suggested that male and female magpies were so specialized in their types of parental care that both parents were needed to produce offspring. This may be true in terms of physiological adaptations for incubation and brooding (e.g., the male has no brood patch); however, magpies can alter some behaviors such as the rate of food delivery to nestlings (Buitron 1988) and the nest visit rate during incubation (Buitron pers. comm., this study). One major role of males may be supplying incubating and brooding females with most of their food (Baeyens 1981a; pers. obs.). Adding food increases the number of young leaving successful nests (i.e., those that produce at least one fledgling), although it did not decrease the rate of nest failure in this population (Hochachka and Boag 1987). Although my data are limited, the lower body mass of young in nests of unaided females suggests that starvation may have been the cause of nest failure among unaided females. I could not find any difference in the cause of nest failures between unaided and paired females; however, the cause of nest failure was unknown in most cases. A contributing cause of nest failure may be spring snowstorms that appear to cause many nest failures (Table II-3; c.f. Buitron 1983b: 225). Male parental care may also be important in magpies for protection of eggs and young against predators (Baeyens 1981b, Buitron 1983b). However, nest predation did not appear to be the major cause of total nest loss in this study (3-10%) or others (mean= 27 ± 6%, n= 6 populations; Baeyens 1981b, Tatner 1982, Balança 1984, Reese and Kadlec 1985, Buitron 1988). Total nest failure from all causes may be a major limiting factor in magpie reproduction (mean nest failure rate= 46 ± 4%, N= 14 populations; Hogstedt 1980, Baeyens 1981b, Vines 1981, Møller 1982, Tatner 1982, Seel 1983, Balança 1984, Hochachka 1985, Reese and Kadlec 1985, Buitron 1988). Although I are not sure of the cause of nest failure in this study, it may be possible to determine why male parental care is so important by examining the mechanism of nest failure in greater detail.

Most other male removal studies have also not determined why male removal had a significant effect on reproductive success. Several authors have suggested that feeding nestlings may be the primary benefit of male parental care (Alatalo et al. 1982, Bjorklund and Westman 1986, Lyon et al. 1987). This conclusion was based on a lower body mass at fledging among young of unaided females. However, feeding ability may not be the ultimate cause of lower reproductive success if unaided females have to spend more time in other activities (e.g., predator defense) that subsequently reduce feeding rate. This possibility, plus the potential for interactions between feeding rate and predation (Wolf et al. in press), indicate that only carefully designed experiments can determine why male parental care is important.

Male parental care and monogamy in other species

If, among species, female reproductive success is correlated positively with male parental care, then one may expect to find a greater reduction in reproductive success following male removal in species with relatively greater male parental care. This relationship is not clear-cut (Fig. II-1), although there appears to be a trend toward greater loss of reproductive success among species in which the male contributes to building the nest, incubating (or feeding the female while she incubates), and feeding nestlings than among species in which the male mainly feeds or tends the young (Fig.

II-1). Figure I-1 may be confounded by differing times of male removal in each study. However, the effect on reproductive success was not associated with the period of male removal in these studies (removal periods were laying, incubation and nestling; $\underline{G}$= 0.79, df= 2, $\underline{P}$= 0.67). The effect of male removal on reproductive success may also be influenced by the relative extent of male investment in each breeding activity, rather than just whether or not the male assisted in a particular activity. A more quantitative and less arbitrary means of comparing species (and also of predicting where they may fit into the scheme in Fig. II-1) may involve estimating energy expenditure of males and females during breeding (e.g., Mugaas and King 1981; Beissinger 1987). However, energy expenditure may be a biased estimator of parental investment if males engage in risky behaviors (e.g., predator defense) that may be relatively low in energy expenditure (see also Bryant et al. 1984).

Wolf et al. (in press) have reviewed male removal studies of passerines. They concluded that male removal had the greatest effect on reproductive success in species that nested in cavities or bred at higher latitudes (both are correlated with larger clutch sizes; Wolf et al. in press). Species with larger initial clutch sizes might benefit relatively more from male parental care because the value of male parental care is greater with larger clutches (Patterson et al. 1980). Data from studies of passerines in my Fig. II-1 suggest an almost significant trend toward larger clutch size among species with a significant decrease in reproductive success following male removal (4.3 ± 0.5 eggs, $\underline{N}$= 5 studies vs. 6.9 ± 1.1 eggs, $\underline{N}$= 6 studies; $\underline{t}$= 2.2, df= 7, $\underline{P}$= 0.064). However, this trend may not continue with species that always fail following male removal; magpie clutch size in this study averaged 6.2 eggs.

Both this study and the study by Wolf et al. (in press) indicate gaps in our understanding of what factors maintain monogamy in different species and populations of birds. Patterns of male parental care will not completely explain monogamy (e.g., Fig. II-1); however, an understanding of how male parental care varies across monogamous species and why it is important in each species will allow us to examine the relative importance of other constraints (e.g., breeding synchrony, environmental variability, variance in territory quality) on breeding behavior.

LITERATURE CITED

ALATALO, R. V., A. LUNDBERG, & K. STAHLBRANDT. 1982. Why do Pied Flycatcher females mate with already-mated males? Anim. Behav. 30: 585-593.

BAEYENS, G. 1981a. Functional aspects of serial monogamy: the magpie pair-bond in relation to its territorial system. Ardea 69: 145-166.

-----------. 1981b. Magpie breeding success and Carrion Crow interference. Ardea 69: 125-139.

-----------. 1981c. The role of the sexes in territory defence in the Black-billed Magpie (*Pica pica*). Ardea 69: 69-82.

BALANÇA, G. 1984. Le déterminisme du succès de la reproduction chez une population de Pies Bavardes (*Pica pica*). Gibier Faune Sauvage 4: 5-27.

BEISSINGER, S. R. 1987. Anisogamy overcome: female strategies in Snail Kites. Am. Nat. 129: 486-500.

BIRKHEAD, T. R. 1979. Mate guarding in the Magpie *Pica pica*. Anim. Behav. 27: 866-874.

BJORKLUND, M., & B. WESTMAN. 1986. Adaptive advantage of monogamy in the Great Tit (*Parus major*): an experimental test of the polygyny threshold model. Anim. Behav. 34: 1436-1440.

BRYANT, D. M., C. J. HALLS, & P. TATNER. 1984. Reproductive energetics of two tropical bird species. Auk 101: 25-37.

BUITRON, D. 1983a. Extra-pair courtship in Black-billed Magpies. Anim. Behav. 31: 211-220.

----------. 1983b. Variability in the responses of Black-billed Magpies to natural predators. Behaviour 87: 209-236.

----------. 1988. Female and male specialization in parental care and its consequences in Black-billed Magpies. Condor 90: 29-39.

EDEN, S. F. 1985. The comparative breeding biology of magpies *Pica pica* in an urban and a rural habitat (Aves: Corvidae). J. Zool. 205: 325-334.

EMLEN, S. T., & L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197: 215-223.

ERKMANN, W. J. 1983. The evolution of polyandry in shorebirds: an evaluation of of hypotheses. Pp. 114-168 *in* Social Behavior of Female Vertebrates (S. K. Wasser, Ed.). New York, Academic Press.

ERPINO, M. J. 1968a. Age determination in the Black-billed Magpie. Condor 70: 91-92.

----------. 1968b. Nest-related activities of Black-billed Magpies. Condor 70: 154-165.

GOWATY, P. A. 1983. Male parental care and apparent monogamy among Eastern Bluebirds (*Sialia sialis*). Am. Nat. 121: 149-157.

GREENLAW, J. S., & W. POST. 1985. Evolution of monogamy in Seaside Sparrows, *Ammodramus maritimus*: tests of hypotheses. Anim. Behav. 33: 373-383.

HANNON, S. J. 1984. Factors limiting polygyny in the Willow Ptarmigan. Anim. Behav.

32: 153-161.

HOCHACHKA, W. M. 1985. The effect of food availability on Black-billed Magpie reproduction. Unpubl. M.S. Thesis, University of Alberta.

HOCHACHKA, W. M., & D. A. BOAG. 1987. Food shortage for breeding Black-billed Magpies (*Pica pica*): an experiment using supplemental food. Can. J. Zool. 65: 1270-1274.

HOGSTEDT, G. 1980. Prediction and test of the effects of interspecific competition. Nature 283: 64-66.

KLEIMAN, D. G. 1977. Monogamy in mammals. Quart. Rev. Biol. 52: 39-69.

LACK, D. 1968. Ecological adaptations for breeding in birds. London, Methuen.

LIFJELD, J. T., T. SLAGSVOLD, & G. STENMARK. 1987. Allocation of incubation feeding in a polygynous mating system: a study of Pied Flycatchers *Ficedula hypoleuca*. Anim. Behav. 35: 1663-1669.

LYON, B. E., R. D. MONTGOMERIE, & L. D. HAMILTON. 1987. Male parental care and monogamy in Snow Buntings. Behav. Ecol. Sociobiol. 20: 377-382.

MARTIN, K., F. G. COOCH, R. F. ROCKWELL, & F. COOKE. 1985. Reproductive performance in Lesser Snow Geese: are two parents essential? Behav. Ecol. Sociobiol. 17: 257-263.

MARTIN, K,. & F. COOKE. 1987. Bi-parental care in Willow Ptarmigan: a luxury? Anim. Behav. 35: 369-379.

MOCK, D. W. 1985. Avian monogamy: the neglected mating system. Pp. 6-15 in Avain monogamy (P. A. Gowaty and D. W. Mock, Eds.). Ornithol. Monogr. 37.

MØLLER, A. P. 1982. Characteristics of magpie *Pica pica* territories of varying duration. Ornis Scand. 13: 94-100.

----------. 1986. Mating systems among European passerines: a review. Ibis 128: 234-250.

MUGAAS, J. N., & J. R. KING. 1981. Annual variation of daily energy expenditure by the Black-billed Magpie. Studies Avian Biol. No. 5.

PATTERSON, C. B., W. J. ERCKMANN, & G. H. ORIANS. 1980. An experimental study of parental investment and polygyny in male blackbirds. Am. Nat. 116: 757-769.

REESE, K. P., & J. A. KADLEC. 1985. Influence of high density and parental age on the habitat selection and reproduction of Black-billed Magpies. Condor 87: 96-105.

RICHMOND, A. W. 1978. An experimental study of advantages of monogamy in the Cardinal. Ph.D. dissertation, Bloomington, Indiana Univ.

SAS INSTITUTE, INC. 1982. SAS users guide: statistics, 1982 ed. Cary, North Carolina, SAS Inst.

SASVARI, L. 1986. Reproductive effort of widowed birds. J. Anim. Ecol. 55: 553-564.

SCHARF, C. 1985a. A technique for trapping territorial magpies. N. A. Bird-Bander 10 34-36.

----------. 1985b. The role of social dominance in winter flocks of Black-billed Magpies. Ph.D. dissertation, Edmonton, University of Alberta.

---------. 1987. Sex determination of the Black-billed Magpie, Pica pica. Can. Field-Nat. 101: 111-114.

SEEL, D. C. 1983. Breeding of the magpie Pica pica on Angelsey, North Wales. Bangor Inst. of Terr. Ecol. Occ. Paper No. 15.

SHANNON, G. R. 1958. Magpie's rapid replacement of dead mate. Brit. Birds 51: 401-402.

SMITH, J. N. M., Y. T. YOM-TOV, & R. MOSES. 1982. Polygamy, male parental care, and sex ratio in Song Sparrows: an experimental study. Auk 99: 555-564.

SOKAL, R. R., & F. J. ROHLF. 1981. Biometry. N.Y., W. H. Freeman and Co.

TATNER, P. 1982. The breeding biology of magpies Pica pica in an urban environment. J. Zool. 197: 559-581.

VERNER, J., & M. F. WILLSON. 1969. Mating systems, sexual dimorphism, and the role of male passerine birds in the nesting cycle. Ornithol. Monogr. No. 9.

WEATHERHEAD, P. J. 1979. Ecological correlates of monogamy in tundra-breeding Savannah Sparrows. Auk 96: 391-401.

WITTENBERGER, J. F., & R. L. TILSON. 1980. The evolution of monogamy: hypotheses and evidence. Ann. Rev. Ecol. Syst. 11: 197-232.

WOLF, L., E. D. KETTERSON, & V. NOLAN Jr. 1988. Paternal influence on growth and survival of Dark-eyed Junco young: do parental males benefit? Anim. Behav. 36: 1601-1618.

ZAR, J. H. 1974. Biostatistical analysis. Englewood Cliffs, New Jersey, Prentice Hall.

III. FOOD ABUNDANCE, POLYGYNY AND MALE PARENTAL CARE IN TREE SWALLOWS

INTRODUCTION

The abundance and distribution of food is thought to have a major influence on the mating systems of vertebrates (Emlen and Oring 1977, Oring 1982). Relatively low food abundance may necessitate male parental care in a given brood and favor monogamy. Abundant food levels may reduce the importance of male parental care and allow males to seek additional females for mating (if they can take advantage of the "extra" time available to seek additional mates; Emlen and Oring 1977). There have been many interspecific studies of mating systems and food abundance in birds to support the hypothesis that food abundance influences mating behavior (e.g. Crook 1964, Wittenberger 1978, Orians 1980, Beehler 1985). However, interspecific studies cannot separate the effects of phylogeny and environment, which makes inferences about causation more difficult (Jarman 1982). Few studies have examined the influence of food abundance on mating behavior within a species (Harmeson 1974, Wittenberger 1980, Davies and Lundberg 1984, Quinney 1986, Simmons et al. 1986). The influence of food abundance on the need for male parental care is an important test of mating system theory.

Male removal studies have been used to examine the importance of male parental care to reproductive success. These studies have generally found that male parental care increases reproductive success, but it is not an absolute necessity (e.g., Weatherhead 1979, Smith et al. 1982, Gowaty 1983, Greenlaw and Post 1985, Bart and Tornes 1989; but see Erkmann 1983, Chapter II). However, the effect of male removal varies among studies (Wolf et al. 1988), and it may vary among years (Lyon et al. 1986, Bart and Tornes 1989). Without information on food availability it will not be possible to determine how much of the variation among studies is due to ecological or phylogenetic constraints. Previous studies of mating systems have used experimental manipulations of nesting cover, food or sex ratio to determine if resources or competitors limit polygyny (Pleszczynska and Hansell 1980, Ewald and Rohwer 1982, Smith et al. 1982, Davies and Lundberg 1984, Hannon 1984); however, experimental tests of the need for male parental care have not been made previously in habitats with different levels of food availability.

The need for male parental care in tree swallows (*Tachycineta bicolor*) may be influenced by food abundance (Quinney 1986). Two studies of tree swallows in southern Ontario reached different conclusions about the importance of male parental care to reproductive success (Leffelaar and Robertson 1986, Quinney 1986). Based on removals of males, Leffelaar and Robertson (1986) suggested that male parental care was necessary to feed and raise a full brood of young and, therefore, was a sufficient explanation for the maintenance of monogamy. In contrast, Quinney (1983, 1986) suggested that male parental care was not always an absolute necessity and that polygyny may occur when food abundance is sufficiently great that it becomes advantageous to females to become the secondary mate of a polygynous male.

In this paper I investigate the influence of local variation in food abundance on male parental care and the maintenance of monogamy in tree swallows. We studied tree swallows in two habitats that appeared to differ in food abundance and nest-box occupancy rate. High rates of nest-box occupancy may be associated with higher rates of polygyny (Quinney 1986). Data collected one year before we began this study suggested that swallows at my study site occupied more nest-boxes in lakeshore (69%, 18/26 nest-boxes) than in roadside/agricultural habitat (45%, 9/20; G. L. Holroyd, pers. comm.), and based on lone females feeding nestlings, we suspected that polygyny may have been occurring at the lakeshore. Visits to these areas during egg-laying suggested that aerial insect abundance was greater at the lake than the road site. A third area next to a marsh appeared to have been intermediate between the lake and road sites in insect abundance. Most of my comparisons, however, will be made between the presumed extremes in food abundance at the lake and road sites.

To examine the effect of food abundance on the need for male parental care I removed mated, male swallows in each habitat. Assuming that food abundance was lower at the road than the lake, I expected that: 1) natural cases of polygyny would be more common at the lake than the road, and 2) simulated polygyny (i.e., unaided females) would be more advantageous at the lake because the need for male parental care would be lower in a high food area. In this population of tree swallows polygynous males rarely assist secondary females (P. Dunn unpubl. data), so the reproductive success of experimentally-unaided and naturally-occurring secondary females was similar within sites (see below).

METHODS

Study animal

Tree swallows nest readily in nest-boxes provided by man. At my study area in central Alberta, Canada, tree swallows have a single brood of altricial nestlings each year. Clutch size varies from 3 to 8 (annual means= 6.1 to 6.7 eggs) in central Alberta. Eggs are incubated by the female for about 14 days. During incubation the male guards the nest, but does not incubate. Young fledge from the nest at 18-20 days of age, and both sexes feed the nestlings. Foraging occurs both on and off the territory. Polygyny occurs in 5 (Quinney 1983) to 8% (this study) of territorial males, and it can occur in two ways: 1) two females nesting in the same nest-box (Quinney 1983) or 2) two females nesting in separate nest-boxes defended by the same male (this study). In the first case, the male and both females appear to feed all the young in a nest-box, while in the second case, the male almost always feeds the young in the nest of the primary female and the secondary female must feed the young unaided (P. Dunn pers. obser.). In this study, polygyny in males was inferred from: 1) observations of males copulating with two females, 2) defence by a male of the nest-box occupied by the presumed secondary female (the female that he copulated with) and 3) observation of only a female feeding nestlings (polygynous males rarely fed the young in nests of secondary females). Copulations in tree swallows occur on the nest-box or perches within the territory. All three criteria were fulfilled in the cases of polygyny used for analysis.

Study area

Tree swallows were studied on and near the southeast shore of Beaverhill Lake, Tofield, Alberta during May-July 1986-88. Six areas with 13-50 nest-boxes each were established in lakeshore (areas A and B) marsh (area C) and roadside/agricultural habitats (areas D,E and F, Fig. III-1). Individually-marked swallows from one habitat were never observed foraging in habitats used by swallows in other parts of the study area (e.g.,

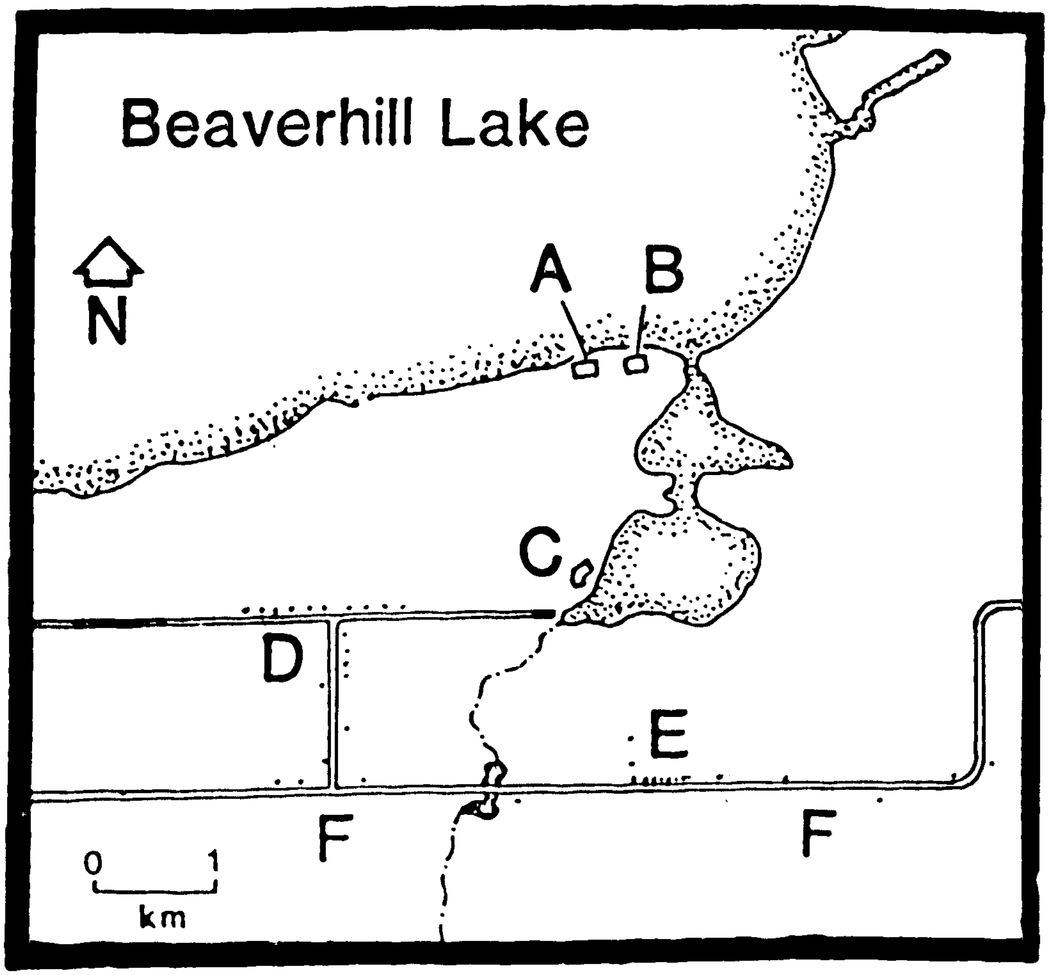


Fig. III-1. Sketch map (scale is approximate) of tree swallow nest boxes at and near Beaverhill Lake, Tofield, Alberta, May-Jul 1986-88. Letters refer to grids and fencelines where boxes were spaced 24 m apart. Area 'F' consisted of boxes spaced 400 m apart along a nest-box trail. Dots represent the approximate location of boxes along roadsides (areas D, E and F).

birds at the road were never seen foraging at the marsh or lake). Maximum distances from the nest-box that birds were seen flying were generally less than 300 m. Nest-boxes were generally spaced 24 m apart in areas A-E (close to the spacing used by Leffelaar and Robertson [1986] and Quinney [1983, 1986]) and approximately 400 m apart in area F. Some nest-boxes in areas A, B and C had additional boxes placed around them in a spiral at 1, 4, 8, 16 m. Details of this experiment are presented in Chapter V. Nest-boxes in area F were part of a "nest-box trail" established in the late 1970's. In roadside/agricultural habitat nest-boxes were placed along fencelines (Fig. III-1). All boxes were in the same location each year except in area D where boxes were moved 700 m west after 1986 (to keep boxes away from a temporary pond) and in area E where boxes were only used in 1987. Within lake and road sites there were no differences among areas in laying date (except among road areas in 1986), clutch size, fledging success or insect abundance (for the road site areas D and E were compared in 1987).

Estimation of insect abundance

To sample aerial insects, I used "tow-nets" that have proven effective for sampling the insects eaten by tree swallows (Quinney and Ankney 1985). The insect sampling technique and equipment were identical to those described by Hussell and Quinney (1987). These nets collect all of the taxa and size classes of insects delivered to nestlings, although not in the same proportion as in the nestlings' diet. Insects fly or are blown into the tow-nets and are collected in a jar of 70% ethanol at the rear. Two nets were placed 2 m above the ground in each of lakeshore (areas A and B), marsh (area C) and roadside (area D, and also area E in 1987) habitats each year. Many birds forage near this height at my study area. In southern Ontario, Holroyd (1972) found that tree swallows spent 47% of their foraging time below 4.6 m. The nets were opened manually at dawn and closed at dusk each day. Hourly wind speeds were calculated for each net at each site to correct for variation in the amount of air sampled/day by each net. These hourly wind speeds were estimated from regressions based on wind speed measurements made at each net (with hand-held anemometers) and wind speeds recorded at an Environment Canada weather stations (Elk Island National Park, 30 km away and Edmonton International Airport, 80 km away) and included a correction for low wind speed (see Hussell and Quinney 1987). Insect biomass was calculated by counting the number of insects in different size and taxon categories and multiplying that number by the mean dry biomass of each size and taxon category. An insect biomass index (IBI) was calculated by dividing the daily insect biomass by the km of wind passing through the net while it was operating on that day. I did not include insects over 13 mm long in the insect biomass index calculation because they are wider than the average gape of adult swallows (Quinney and Ankney 1985), and are rarely fed to nestlings (0.7%, Quinney and Ankney 1985; this study). Insects less than 1 mm were excluded for similar reasons.

Capture, marking and determination of age and sex

Swallows were caught in the nest box (Cohen and Hayes 1984, Magnusson 1984) throughout the breeding season and individually color-marked on the breast with felt-tip ink markers. Birds were classified to sex by the presence of a brood patch in females or cloacal protuberance in males. Yearling (SY= second calendar year of life) and adult (ASY= after second calendar year) females were distinguished by plumage differences (Hussell 1983). Data from yearling females were generally excluded, except in the analysis of return rates, because other studies have found differences between yearlings and adults in clutch size and fledging success (DeSteven 1978).

Male removal experiment

At each site, male removal and control nests were chosen randomly from nests that did not have polygynous males or were not being used in other experiments. Over three years, males were collected from 9 nests during laying (all in 1987), 28 nests during incubation and 16 nests between hatch and 7 days of age (nestlings can fledge after 16 days). Number of visits to the nest by observers was similar between control and unaided nests to control for human disturbance. I checked the data from unaided and control groups for differences in timing of male removal that may have biased my analyses. Date of male removal (relative to hatch date) did not differ among sites (P= 0.16, F= 1.8, df= 3,43; 2-way ANOVA, main effects were site and year). However, timing of male removal did differ among years (P< 0.001, F= 20.3, df= 2,43) because an effort was made in 1987 to remove males throughout laying, incubation and the early nestling periods, while I only attempted to remove males around the time of hatch in 1986 and 1988.

Estimation of settlement date

The date that females settle on a territory and establish pair-bonds must be known to compare the mating decisions of monogamous and secondary females under similar conditions (i.e., seasonal changes in habitat quality could otherwise confound the analysis). Accurate settlement data were not available in 1986 and 1987 (the years when polygyny was observed), so I have assumed that there was a positive relationship between settlement date and nest-initiation date in 1986 and 1987, based on data from 1988 (r^2= 0.58, $\underline{P}$= 0.001, df= 63). Exact nest initiation dates were not available to estimate settlement date in 1986 and 1987, so estimates were made of nest initiation date based on the minimum time to build a nest (3 days, P. Dunn, unpubl. data) and the amount of nesting material in the box (categories were: 1) a few pieces of grass, 2) sparse [a light cover of grass], 3) medium [a nest cup < 3 cm high] and 4) ready to lay [a nest cup > 5 cm high]). Settlement date was estimated in 1988 from 10 1-min. scans made daily at each nesting area. During each scan the number of birds perched or within 5 m of each nest-box was recorded. Settlement date was the first date of three consecutive days during which two birds were seen on or near a nest-box.

Estimation of reproductive success

Each nest-box was visited every 2-3 days around the time of clutch initiation to determine laying date and clutch size. One or two days before the calculated hatch date, nests were checked daily to determine hatching date. Nests were visited on day 16 of the nestling period to weigh nestlings just before fledging (which usually occurred at 18-20 days of age). Body mass of nestlings was used to assess body condition at fledging. Fledging success was the number of nestlings in the nest at 16 days of age minus birds found dead in the box on visits >20 days after hatch. Two measures of reproductive success of control (paired) and unaided females were compared to determine if male parental care made a significant contribution to the reproductive success of the pair. First, the percentage of nests that produced at least one young (successful nests) was used as an estimate of predation intensity and the rate of abandonment. Second, fledging success of successful nests was used to estimate starvation and partial predation.

For the purpose of comparing insect abundance with timing of breeding, we defined three periods during breeding: egg-formation/laying, incubation and nestling. The laying period was defined as 4 days before the date of the 10th percentile of clutch initiation to 2 days before the date of the 90th percentile of clutch completion. These values were chosen based on studies of egg formation (Schifferli 1976) and timing of fertilization (Leffelaar and Robertson 1984). The nestling period was from 15 days (approximate length of incubation) after the 10th percentile of clutch completions to 30 days (approximate length of incubation and nestling periods) after the 90th percentile of clutch completions. The incubation period was the period between the laying and nestling periods. Hussell and Quinney (1987) defined their periods slightly differently, although any discrepancies between studies are likely to be minor (e.g., over 85% of females began laying during the laying period defined by Hussell and Quinney 1987).

Females were weighed when their nestlings were 16 days old to determine if females at male removal nests weighed less than control females (possibly because of increased parental care). Body mass of most birds was measured between 1500 and 1800 hr Rate of return to the study area was analysed from banded swallows nesting in 1986 and 1987 to determine how many offspring and parents recruited subsequently into the breeding population.

Observations of parental care

Observations of individually-marked females at control and male removal nests were made every 2-3 days. Males and females could be distinguished at every control nest because at least one member of the pair (usually the female) was marked. An initial nest was chosen randomly for focal observation every 2-3 days (at the start of a new series of observations), after which nests were picked systematically for observation. Observation sessions were 20 minutes long and were spread as evenly as possible among three periods of the day morning (sunrise to 0900), midday (0900 to 1500), and evening (1500 to 2000). During each observation session observers recorded all visits by the female and male inside the nest-box and, for the female only, the following behaviors time spent inside the nest-box, sitting on the box or post, flying and perched at the entrance hole looking into or out of the nest-box. The method of recording behaviors (except number of nest visits) changed each year in an attempt to improve the methods (e.g., stopwatches were used in 1986 and 1987, but electronic metronomes were used in 1988). Therefore, behavioral data have been analysed separately for each year.

The mass of each food bolus given to nestlings might differ between unaided and control females and between habitats. To examine these possibilities, I collected food boluses from nestlings fitted with pipe-cleaner collars (e.g., Walsh 1979). These collars prevented nestlings from swallowing food boluses. Collars were placed on all young in a nest during an observation period (separate from the ones above), which lasted until the female made 3-4 trips inside the nest-box. Boluses were retrieved from nestlings and dried in an oven at 95 C for three hours prior to weighing.

Statistical analyses

Homogeneity of variances was tested with the Bartlett-Box F test (Norusis, 1986) prior to using analysis of variance (ANOVA) to examine laying date, clutch size, fledging success and various behaviors. If variances could not be made homoscedastic through a transformation, then an appropriate non-parametric test was substituted. No interaction terms from ANOVA were significant unless noted otherwise. All tests of independence in 2X2 tables were performed with the G-test and William's correction (Sokal and Rohlf 1981). Tests of independence with 3-way tables were performed using log-linear models in the HILOGLINEAR procedure of SPSS/PC+ (Norusis 1986), while logit models (i.e., for dependent variables such as nesting success) were fitted using the LOGLINEAR procedure. Means are presented with their standard errors. All statistical tests were two-tailed.

RESULTS

Did insect availability differ among sites?

Mean insect biomass (IBI) did not differ among sites (lake, marsh, road) when data from the entire breeding season were analysed (Fig. III-2, Table III-1; $\underline{P}$ for site effect= 0.34 in a 2-way ANOVA with year, nesting period and study site as main effects).

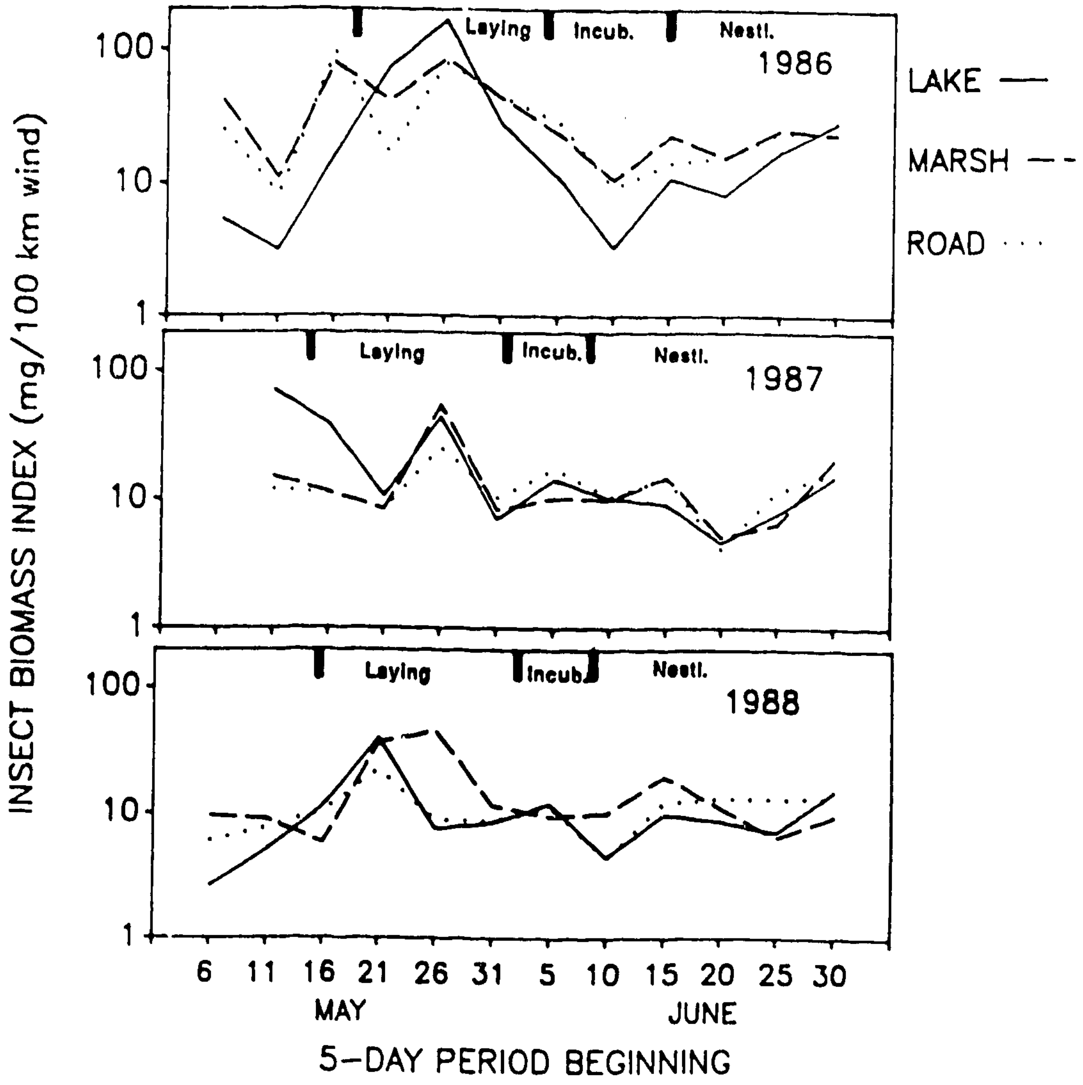


Fig. III-2. Insect biomass index for lake, marsh and road habitats near Beaverhill Lake, Alberta, May-Jul 1986-88. Values are 5-day means of ln-transformed IBI. Nesting periods are defined in methods. The maximum and minimum dates for all sites are given for each nesting period in the figure.

Table III-1. Insect biomass index (mg/100 km wind)[1] at Beaverhill Lake, Alberta, 1986-1988. Nestling periods are defined in methods.

		Laying			Incubation			Nestling		
Year	Site	$\bar{x}$	(95% CI)	n[2]	$\bar{x}$	(95% CI)	n[2]	$\bar{x}$	(95% CI)	n[2]
1986										
	Lake	68.0	(30.3-152.9)	16	9.0	(4.0-20.2)	9	11.7	(7.2-19.0)	19
	Marsh	58.6	(25.9-132.3)	15	17.6	(6.4-48.8)	10	21.5	(13.0-35.7)	18
	Road[3]	36.2	(18.7-70.1)	16	17.5	(6.2-49.3)	9	18.7	(12.0-29.2)	17
1987										
	Lake	28.7	(15.9-52.1)	17	7.5	(1.6-34.0)	6	8.9	(5.9-13.5)	21
	Marsh	15.8	(8.9-28.0)	12	14.0	(6.1-32.4)	10	8.3	(4.6-14.9)	21
	Road[3]	12.4	(6.6-23.5)	12	14.2	(8.5-23.5)	12	9.8	(5.8-16.6)	18
1988										
	Lake	14.4	(7.1-28.7)	14	10.1	(6.4-15.7)	10	7.6	(5.0-11.5)	22
	Marsh	21.6	(10.4-44.7)	16	10.2	(4.3-24.3)	8	10.2	(6.3-16.4)	24
	Road[3]	10.6	(5.5-20.1)	17	12.0	(7.4-19.5)	7	10.2	(6.4-16.2)	23

[1] Mean IBI was estimated by calculating the arithmetic mean of ln-transformed IBI and then converting back to mg/100 km wind by taking the antilog of the transformed mean. Calculation of 95% CI from Sokal and Rohlf (1981: 420-421).

[2] Days of insect sampling.

[3] Only data from insect nets on grid D. Insects were only sampled on grid E in 1987.

However, there were significant interactions between nesting period and year and between study site and year. Year effects were caused by greater mean IBI in 1986 than in 1987 or 1988 (1987 and 1988 did not differ, Fig. III-2; $\underline{P} < 0.001$ for year effect, $\underline{F} = 17.2$, df= 2, 437). The study site and year interaction was probably caused by a greater mean IBI at the lakeshore than the road in 1986 (Fig. III-2). When analysed by nesting period, mean IBI tended to differ among lake, marsh and road sites only during the laying season (Table III-1; 2-way ANOVA's with year and site as main effects; $\underline{P} = 0.067$ for site effect during laying, $\underline{F} = 2.76$, df= 2, 126). This difference was mostly due to greater mean IBI at the lake than the road.

The reproductive performance and mating decisions of swallows may depend more on the maximum insect biomass rather than biomass averaged over several days. Maximum IBI tended to be greater at the lake than the road (paired t-test on ln-transformed IBI; two-tailed $\underline{P} = 0.12$, t= -1.7, df= 2). Maximum IBI was similar at the road (76 mg/ 100km wind) and the lake (60 mg/ 100 km wind) in 1988, but in 1986 and 1987 maximum IBI was approximately two times greater at the lake than the road (1317 vs. 458 mg/ 100 km wind in 1986 and 131 vs 58 mg/ 100 km wind in 1987). There was a drought in 1988, and this may have reduced peak insect abundance at all sites. If only 1986 and 1987 data are considered, then there was a stronger tendency for greater maximum IBI at the lake than the road (paired t-test, two-tailed $\underline{P} = 0.081$, t= -7.7, df=1)

In addition to differing in mean and maximum insect biomass, the various sites could have differed in terms of the distribution of that biomass among size classes of insects, and this could have affected the availability of insects for swallows. Here I only present data for the lake and road sites during the nestling period in 1987 because most comparable data from the diet of birds was collected at that time. During the nestling period in 1987, 1-3 mm insects were found more frequently and 3-5 and 5-7 mm insects were found less frequently in the insect nets at the road than the lake site (Fig. III-3; G= 208, df=4, $\underline{P} = 0.0001$). In terms of biomass, the 3-5 mm insect class offered the greatest available food source at the lake; while at the road, insects in the 1-3 mm size class offered the greatest food source (Fig. III-3).

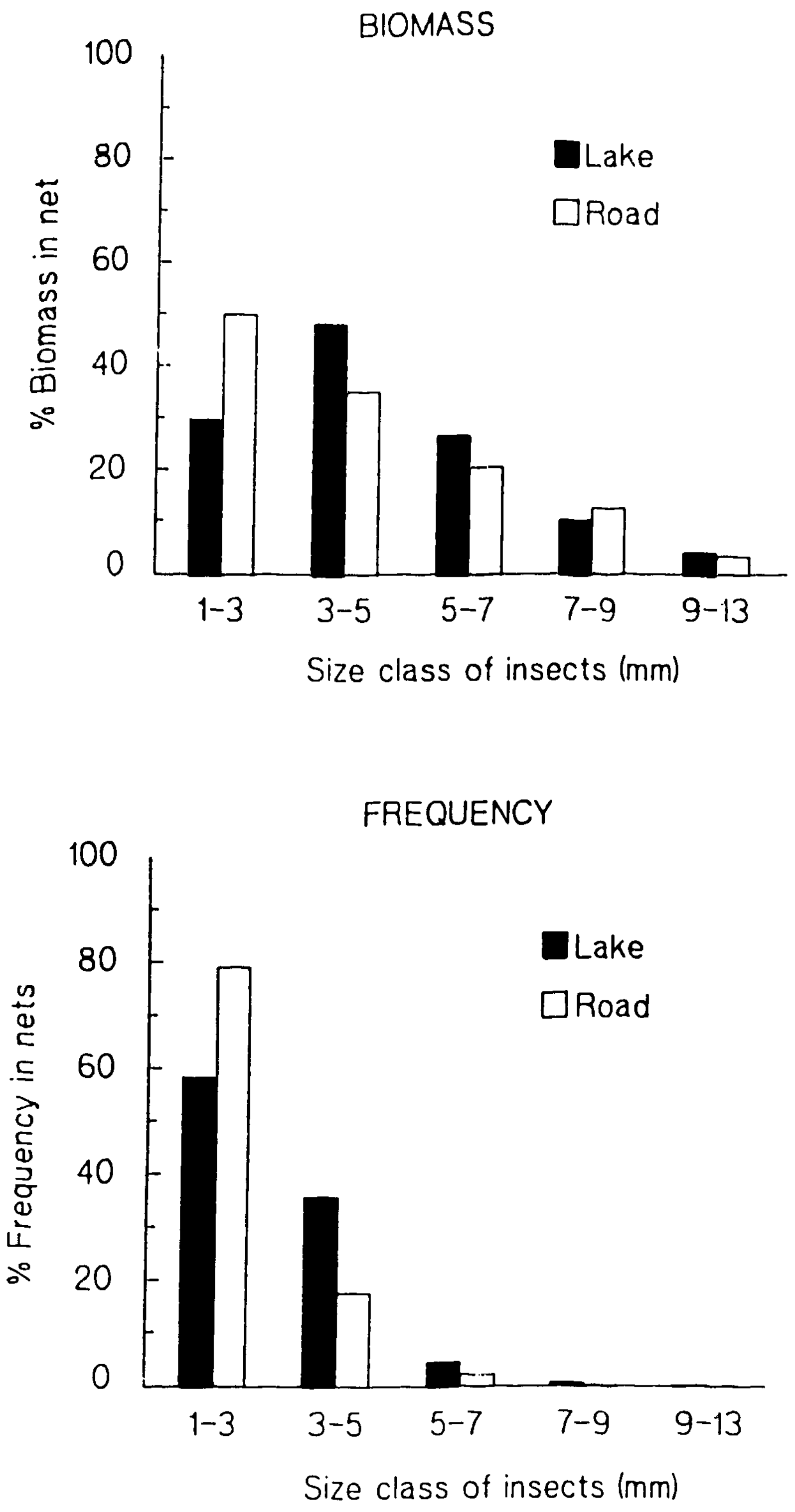


Fig. III-3 Biomass (%) and frequency (%) of insects collected by tow-nets in Lakeshore and Roadside habitats during the nestling period in 1987. Percentages are based on the number of insects collected by tow-nets.

Natural polygyny

There were 7 cases of natural polygyny in 1986 (8%, 3/39) and 1987 (7%, 4/56) and one potential case in 1988. The potential case of polygyny in 1988 involved a female that lost her mate on 30 May 1988 (the last day of laying for this female). A neighboring male was seen with this female within 4 days and he copulated with her 7 and 10 days after the male died. It is possible that he could have fertilized some of this female's eggs during earlier copulations that I did not observe. Six of seven cases of polygyny occurred at the lakeshore (there was one case at the marsh in 1986). If polygyny is associated with high insect abundance early in nesting, then the one case of polygyny at the marsh site may have been due to a relatively high mean IBI during laying in 1986 (Table III-1).

Settlement dates were examined so that the fledging success of secondary females at the lake and marsh was only compared with that of monogamous females at the road that settled at the same time. Secondary females at the lake and marsh (4 ASY, 2 SY) settled from 7-13 May (10± 1.1 May) while monogamous females at the road (n=10, all ASY) settled from 7-14 May (10± 1.2 May; $\underline{P}$= 0.71, $\underline{t}$= -0.38). Only one nest of a monogamous female was excluded from subsequent analyses in order to compare females that settled concurrently. For successful nests, the fledging success of secondary females at the lake and marsh (5.5±0.6, n=6, includes two SY females) was as high as the fledging success of monogamous females at the road (5.1±0.8, n=7; $\underline{P}$= 0.73, t= -0.4) and lake (5.1±0.4, n= 35, $\underline{P}$= 0.96, t= 0.06) sites (1986 and 1987 data). Fledging success of the potential secondary female at the lake in 1988 (7 fledglings) was also relatively high. Clutch size was generally greater at the lake than the road (see next section), although this was not true for secondary females, probably because of the small sample size. Fledging success relative to initial clutch size was examined with ANCOVA to determine if partial loss of eggs or young occurred differentially among monogamous females at the road and secondary females at the lake and marsh. For a given clutch size there was no difference in fledging success between monogamous females at the road and secondary females at the lake and marsh (only 1986 and 1987 data on successful females; ANCOVA's with clutch size as the covariate, $\underline{P}$= 0.93, $\underline{F}$= 0.01, df= 1,10; slopes were homogeneous $\underline{P}$= 0.37). Therefore, in either absolute or relative terms, secondary females at the lake did not suffer a cost from loss of male parental care.

Male removal experiment

Secondary mate status may only be chosen by females that are in the best condition or habitat, so I removed males to determine if a randomly-chosen female would also incur no cost by choosing polygyny. Males were removed at 16 nests from the lakeshore, 5 nests from the marsh and 25 nests at the road site. I first checked for differences in laying date and clutch size that could have confounded the analysis of my experimental results. There were no differences in laying date or clutch size between control and unaided females (Tables III-2, 3). However, the earliest male removals were made late in the egg-laying period, so I did not expect an effect.

Overall, laying date was later in 1986 than in 1987 or 1988 (Table III-2), possibly because of a major snowstorm on 13-14 May 1986. A smaller snowstorm occurred on 19 May 1987 and no snowstorms occurred in May 1988. Laying date was generally earlier at the lakeshore than the road area (Table III-2). There were significant interactions between treatment and site and between year and site in the analysis of laying date (Table III-2). However, these interactions were not present in the subset of data used to analyse fledging success (see below). Clutch size did not differ among years; however, it was greater at the lakeshore than the road area (Table III-3). This difference in clutch size was probably due to earlier laying and a stronger negative relationship between clutch size and laying date at the lakeshore than the road area. There was a significant negative relationship between clutch size and laying date at the lakeshore (Spearman rank correlation $\underline{r}$= -0.39, $\underline{P}$< 0.001, $\underline{N}$= 93), but not at the roadside ($\underline{r}$= -0.19, $\underline{P}$= 0.21, $\underline{N}$= 44; data from areas D and E).

Fledging success was analysed from three years of data on nests of 46 unaided and 164 control adult (ASY) females. Data were collected from an additional 34 yearling (SY) females (7 unaided and 27 control); however, those data were only used in the analysis of return rate. If male parental assistance had a cumulative effect, then one would expect to see a positive correlation between the timing of male removal and subsequent fledging success. However, there was no relationship between timing of male removal (relative to hatch date) and subsequent fledging success in this study ($\underline{P}$>

Table III-2. Laying date of adult (ASY) tree swallows, Beaverhill Lake, Alberta, 1986-1988[1]. Only includes birds with known clutch size. Does not include data from nests of primary or secondary females or renests.

	1986			1987			1988		
	X	SE	*n*	*X*	SE	*n*	*X*	SE	*n*
Control									
Lake	26 May	0.6	8	23 May	0.7	27	24 May	0.4	43
Marsh	25 May	1.0	4	22 May	0.8	11	23 May	0.7	19
Road	28 May	1.1	10	27 May	0.7	11	24 May	0.8	20
Unaided									
Lake	26 May	2.2	3	20 May	0.8	5	22 May	0.4	6
Marsh	29 May		1	22 May	1.4	4			
Road	28 May	1.5	7	28 May	0.7	9	25 May	1.1	6

[1] P values for each effect in a 3-way ANOVA: Treatment $P= 0.28$; Year $P= 0.0001$; Site $P= 0.01$; Treatment X Site $P= 0.047$; Year X Site $P= 0.007$; Treatment X Year $P> 0.60$.

Table III-3 Clutch size of adult (ASY) tree swallows, Beaverhill Lake, Alberta, 1986-1988[1]. Does not include data from nests of primary or secondary females nor renests. Five nests with unknown laying dates are included.

	1986			1987			1988		
	$\bar{X}$	SE	*n*	$\bar{X}$	SE	*n*	$\bar{X}$	SE	*n*
Control									
Lake	6.8	0.2	8	6.6	0.3	27	6.6	0.1	43
Marsh	6.3	0.3	4	6.5	0.4	11	[illegible]	0.1	19
Road	5.9	0.3	12	5.8	0.3	12	6.4	0.2	20
Unaided									
Lake	7.0	0.0	3	7.2	0.2	5	6.8	0.2	6
Marsh	7.0		1	5.8	0.8	4			
Road	6.1	0.3	9	5.9	0.4	9	6.3	0.2	6

[1] *P* values for each effect in a 3-way ANOVA (marsh site data were excluded to avoid empty cells in the ANOVA design): treatment *P*= 0.16; year *P*= 0.79; Site *P*= 0.0001; all interactions *P*> 0.16.

0.5, r^2= 0.001, N= 52). Therefore, male removal data from throughout the breeding season were pooled for analysis.

Nest failures.-- Sample sizes were too small to compare the rate of nest failure (no young fledged) of control and unaided females among sites (no nests of unaided females failed in 1986 or 1987 at the lake, and no nests of unaided females failed at the road in 1988). After pooling study sites, there was no difference between control and unaided females in the frequency of nests that failed (P= 0.46, Table III-4). The rate of nest failure was higher in 1988 (56%) than in 1987 (19%) or 1986 (19%) because of predation by weasels (Mustela erminea) on almost all of the nests in areas C and B (P= 0.002 for year effect, Table III-4). Only 1-2 nests were depredated in 1986 and 1987, when most nest failure was due to starvation or abandonment. The rate of nest failure was similar between control and unaided females, but different among years, so I only analysed fledging success for successful nests.

Fledging success at successful nests.-- Fledging success was analysed in absolute and relative terms to determine if differences between the lake and road were due to larger initial clutch sizes at the lake or to differential loss of eggs or young after laying. Absolute fledging success refers to the number of fledglings, while relative fledging success was absolute fledging success adjusted for initial clutch size (with ANCOVA). Analysis of relative fledging success of control females at the lake and road was confounded by annual differences. Relative fledging success at the road site was lower in 1987 than in 1986 or 1988 (Fig. III-4, P= 0.023, F=4.2, df= 2,34, slopes were homogeneous P= 0.93). However, relative fledging success did not differ among years at the lake site (year effect P= 0.90, slopes were homogeneous P= 0.41). I compared relative fledging success separately for each year because of this potentially confounding effect.

For a given clutch size, relative fledging success of control females at the lake and road were similar in 1986 and 1988. However, in 1987 females at the lake produced more fledglings for a given clutch size than females at the road (Fig. III-4, P=0.027, F=5.4, df= 1,31). Slopes of the regression lines were generally homogeneous, except in 1988 (P= 0.084) when females at the road tended to produce

Table III-4. Nest failure rate (%) among control and unaided adult (ASY) females[1]. Data include 7 control nests in 1988 in which clutch size was unknown and 3 nests in which relaying began within 4 days of a snowstorm in 1987. One control nest with unknown fledging success in 1986 was excluded.

	Nests producing					
	1986		1987		1988	
	No Fledglings (%)	Total N	No Fledglings (%)	Total N	No Fledglings (%)	Total N
Control	13	23	13	50	58	89
Unaided	23	13	29	21	42	12

[1] Log-linear model; Year: P= 0.002, X^2= 12.3, df= 2; Treatment: P= 0.46, X^2= 0.02, df= 1;

Interaction: P= 0.19, X^2= 3.4, df=2 .

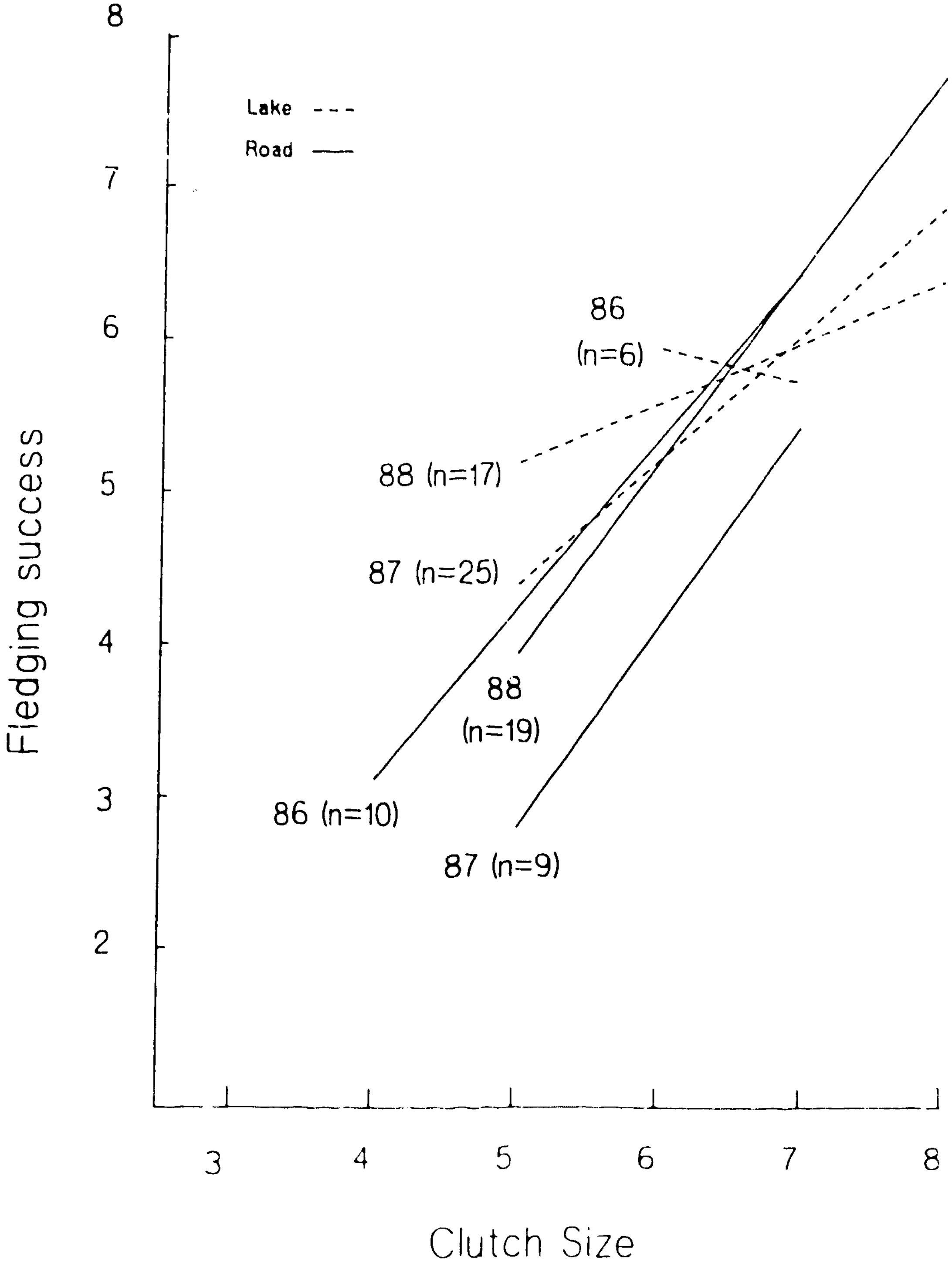


Fig. III-4. Relative fledging success of successful adult (ASY) control females.

The interaction effect was due mostly to lower fledging success at the road than the lake in clutches of 5-6 eggs, rather than better production at the road than the lake in clutches of 7-8 eggs (Fig. II-4; the effect on the interaction term was more pronounced when clutches of 5-6 eggs were omitted from analysis [$\underline{P}$=0.78] than when clutches of 7-8 eggs were omitted [$\underline{P}$= 0.42]). In absolute terms, mean fledging success of control females was greater at the lake than the road (Table III-5; 2-way ANOVA on lake and road data only, $\underline{P}$ for site effect= 0.039, $\underline{P}$ for year effect= 0.36, interaction $\underline{P}$= 0.10). This occurred because mean clutch size was greater at the lake than the road and fledging success was related positively to clutch size at both sites ($\underline{P}$= 0.004, r^2= 0.41, n=48 at the lake; $\underline{P}$< 0.001, r^2= 0.75, n= 38 at the road).

It appeared that control females would produce more fledglings by breeding at the lakeshore, but was this also true for unaided females (the hypothetical secondary females)? Unaided females probably incur the same cost from losing male parental care as naturally-occurring secondary females, because at the lake secondary and unaided females produced similar numbers of fledglings (Fig. III-5). As in the analysis above, relative fledging success was analysed by each year. There were not enough data in 1988 to perform an ANCOVA; however, in 1986 and 1987 unaided females produced similar numbers of fledglings (for a given clutch size) as control females at the road ($\underline{P}$= 0.49 for 1986 and $\underline{P}$= 0.12 for 1987). In absolute terms, fledging success of unaided females at the lake (6.2±0.3, n= 11) was greater than that of control females at the road (5.2±0.3, n=38; $\underline{P}$= 0.018, t= -2.5, df= 33).

If food abundance affected the need for male parental care and food was more available at the lakeshore than the road site, then I would expect that unaided females at the lakeshore would produce more fledglings than unaided females at the road site. Relative to initial clutch size, loss of male parental care had a more detrimental effect on fledging success of unaided females at the road than at the lakeshore site ($\underline{P}$= 0.03, $\underline{F}$= 5.1, df= 1, 26; slopes were homogeneous, $\underline{P}$= 0.81; Fig. III-5). For the most common clutches of 6 and 7 eggs, unaided females at the road raised 0.5 and 1.75 fewer fledglings, respectively, than unaided females at the lakeshore. In absolute terms, fledging success of unaided females was also greater at the lakeshore (6.2±0.3, n= 11) than at the road (4.6±0.3, n= 18; $\underline{P}$= 0.002, t= -3.3, df= 27).

TableIII-5. Fledging success at successful nests (fledged at least 1 young) of adult (ASY) tree swallows, Beaverhill Lake, Alberta, 1986-1988[1].

	1986			1987			1988		
	$\bar{X}$	SE	*n*	$\bar{X}$	SE	*n*	$\bar{X}$	SE	*n*
Control									
Lake	5.8	0.2	6	5.7	0.2	25	5.8	0.4	17
Marsh	5.8	0.4	4	5.1	0.5	9	5.0		1
Road	5.5	0.2	10	4.0	0.7	9	5.7	0.3	19
Unaided									
Lake	6.0	0.6	3	6.4	0.4	7	5.0	0.6	1
Marsh	7.0		1	3.0	0.0	2			
Road	4.7	0.4	6	4.3	0.8	6	4.7	0.7	6

[1] *P* values for each effect in a 3-way ANOVA (marsh site data were excluded to avoid empty cells in the ANOVA): treatment *P*= 0.60; Year *P*= 0.62; Site *P*= 0.014; all interactions *P*> 0.05.

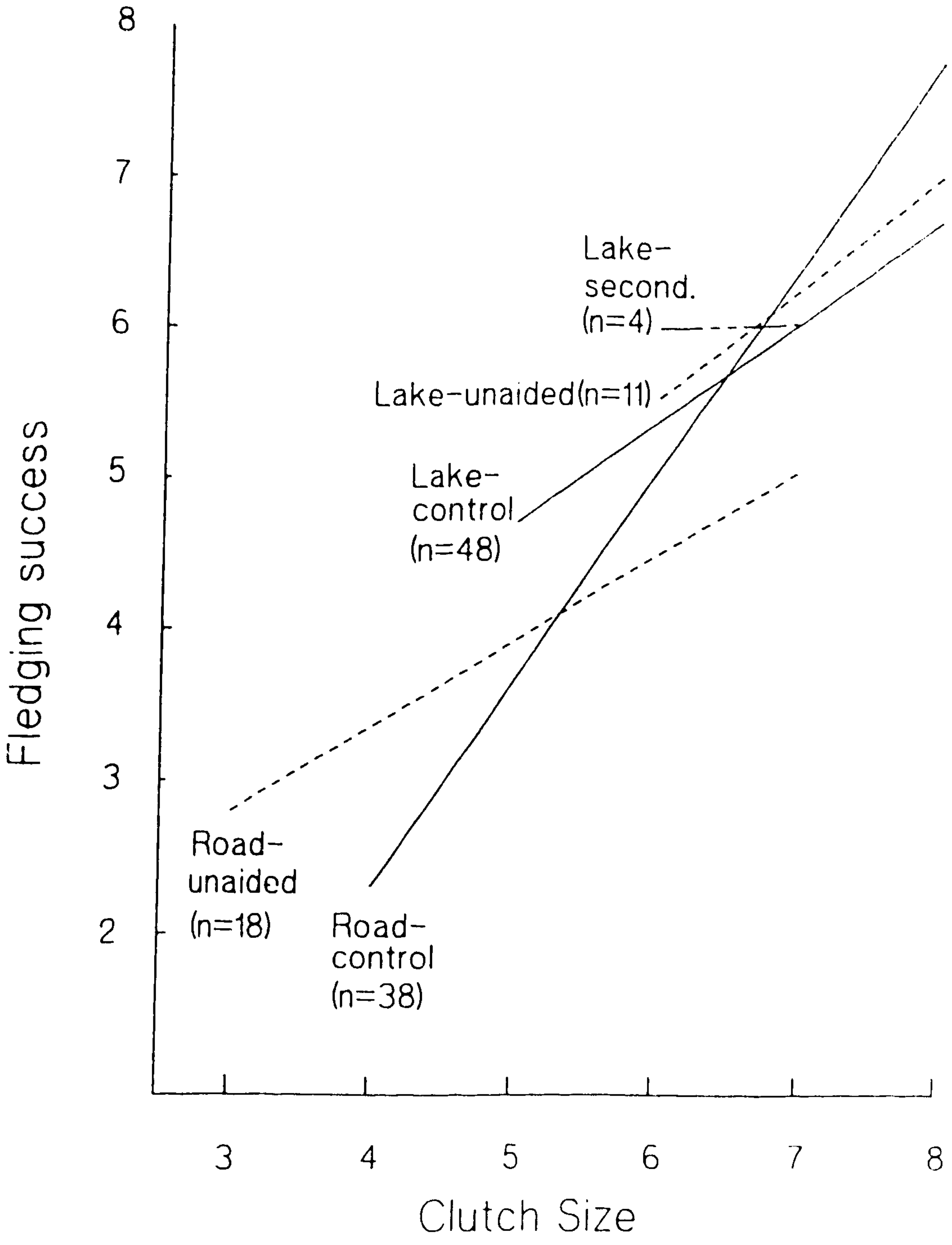


Fig III-5 Relative fledging success of successful adult (ASY) females in Lakeshore and Roadside habitats. Data for secondary females only from the lake in 1986 and 1987 Lines are least-squares regression lines

In summary, fledging success was greater at the lake than the road for control females, because of a larger initial clutch size at the lake. Larger clutch size also appeared to be responsible for greater fledging success of unaided females at the lake than control females at the road (in absolute terms). In both absolute and relative terms, unaided females at the lakeshore had greater fledging success than unaided females at the road. Based on both relative and absolute fledging success of unaided females, secondary mate status would appear to be more advantageous at the lake than the road.

Behavior of control and unaided females

During the nestling period in 1986-88, 39 control and 30 unaided adult females were observed for a total of 128 and 107 hr, respectively. Because the same individuals were observed several times throughout the nestling period, I used averages of each behavior calculated from multiple observations of the same bird (only nests with at least 3 observation sessions were analysed). This technique assumes that: 1) even though brood size and age may influence the behavior of females, they have the same relative effect on the behavior of unaided and control females (i.e., similar slopes), and 2) observations of unaided and control females were distributed similarly. These were valid assumptions in my case because the slopes of the regression lines for nest visit rate and all other behaviors did not differ between unaided and control females ($P > 0.05$; ANCOVA for each year and behavior, with brood size or age as the covariate and treatment as the grouping variable), and there was no difference between unaided and control females in the distribution of brood sizes or ages when my observations were made (Kolomogorov-Smirnov tests for each year; $P > 0.32$). Therefore, comparisons of the behaviors of unaided and control females did not need to control for brood size or age because they had similar effects on each group of females. There was also no significant correlation between the number of observations/nest and the mean value of any behavior I measured (separate Pearson correlations for control and unaided females, $P > 0.28$). Observations of birds at the marsh site are presented in Table III-6, but were not included in these analyses to avoid empty cells in the ANOVA design (almost all nests at the marsh were depredated in 1988).

Nest visit rate.--Averaged over the entire nestling period, unaided and control

Table III-6. Mean nest visits of adult (ASY) tree swallows per 20 minute observation period during the nestling period, Beaverhill Lake, Alberta, 1986-1988. Data from the Marsh site were excluded to avoid missing cells in the ANOVA.

	1986			1987			1988			P values for each main effect in a 3-way ANOVA		
	$\bar{X}$	SE	*n*	$\bar{X}$	SE	*n*	$\bar{X}$	SE	*n*	*Treatment*	*Year*	*Site*
Total nest visits												
Control (male and female)												
Lake	7.2	0.7	6	5.8	1.5	7	5.9	0.6	5			
Marsh	7.6	1.2	3	4.5	0.6	5						
Road	9.3	0.4	4	8.1	1.7	3	4.9	0.8	6			
Unaided female										0.005	0.003	0.14
Lake	5.6	0.8	3	4.8	0.5	6	4.3	1.0	4			
Marsh	5.1		1	2.7	1.0	2						
Road	6.1	1.1	5	6.6	0.4	3	3.6	0.6	6			
Female nest visits										0.11	0.0004	0.038
Control female only												
Lake	4.5	0.3	6	3.4	0.8	7	3.1	0.3	5			
Marsh	7.6	1.2	3	3.2	0.3	5						
Road	6.4	0.6	4	3.9	1.0	3	3.4	0.8	6			

Table III-6). However, the rate of total nest visitation (males and females combined) did not differ between the two sites (Tables III-6). Unaided females made fewer total nest visits than the combined visits of the male and female at control nests (Table III-6). Although unaided females did not appear to compensate fully in terms of total number of nest visits (Table III-6), from the perspective of individual nestlings it appeared that in two of the three years unaided females were able to visit them as often as control females (Fig. III-6). In 1987 and 1988 the per capita nest visit rate was similar at nests of unaided and control females (Fig. III-6; i.e., there was no difference between control and unaided females in the slopes or intercepts of regression lines for total nest visits versus brood size; ANCOVA, P> 0.27). However, in 1986 the per capita nest visit rate was lower at nests of unaided than control females (Fig. III-6, a difference of 1.1 visits/nestling/hr; P= 0.014 for the intercept term, df= 1,19, F= 7.25).

Other behaviors were examined for differences between sites (within treatment groups) using ANCOVA's with brood size as the covariate. No differences were found between the lake and road, so sites were pooled in subsequent analyses. Unaided females spent less time sitting (on the box or post) than control females; however, it was not obvious what other behaviors unaided females were spending more time in, if they were spending less time sitting (Table III-7).

Feeding rate of nestlings at the road and lake sites.-Females might be able to compensate for differences between sites in food abundance or for the loss of the male by increasing the mass or changing the composition of each food bolus fed to nestlings. I examined mean dry biomass/bolus by collecting food boluses (N= 42) from collared nestlings in nests of 7 control and 9 unaided females in 1987 and 1988. There was no difference between control and unaided females in the mean brood size or brood age during the days that these nests were sampled (t-tests, P>0.24, df=14). Mean dry biomass/food bolus did not differ between all unaided (0.051±0.006 g, n= 22) and control (0.042±0.005 g, n= 19) females (t= -1.1, P= 0.27, df= 39). However, boluses of unaided females at the road tended to be lighter than those of unaided females at the lake site (P= 0.096, t-1.75, df=20; 0.037±0.006 g at the road vs. 0.058±0.008 g at the lake). Even though total nest visits per nestling were similar between unaided and control groups in most years, a slightly lower nest visit rate (Fig. III-6) and bolus mass

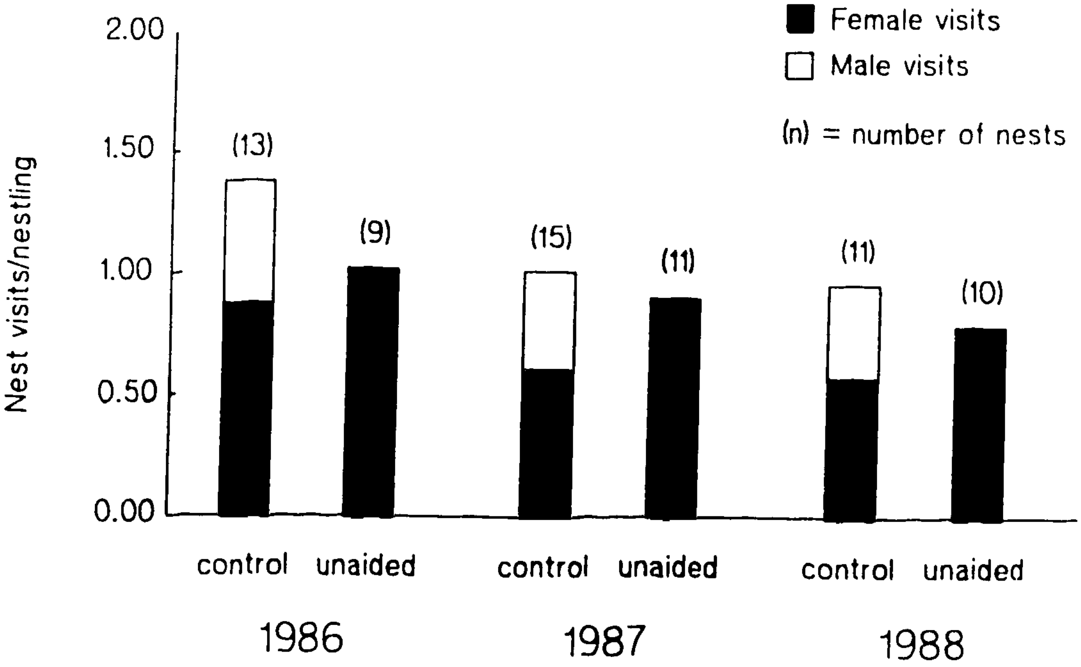


Fig. III-6. Mean nest visits per nestling (during 20 minute observation periods) for adult (ASY) females, Beaverhill Lake, Alberta, 1986-88. The top of each bar indicates the total number of nest visits (male and female combined for control nests) per nestling.

Table III-7. Behavior of control and unaided adult (ASY) female tree swallows during the nestling period, Beaverhill Lake, Alberta, 1986 - 1988. Times are out of 20 min. observation periods (in sec.).

	1986			1987			1988			P values from 2-way ANOVA's		
	$\bar{X}$	SE	n	$\bar{X}$	SE	n	$\bar{X}$	SE	n	Treatment	Year	Interaction
In Box												
Control	288.5	39.1	13	212.7	45.2	15	403.9	44.3	11	0.198	0.009	0.49
Unaided	305.2	69.2	9	327.6	31.1	11	424.7	55.7	10			
Sitting												
Control	22.5	10.1	13	45.6	14.2	15	83.7	26.2	11	0.017	0.005	0.82
Unaided	2.8	1.9	9	10.0	4.3	11	45.9	18.8	10			
Flying												
Control	828.9	38.1	13	836.9	50.4	15	599.7	43.4	11	0.727	0.0001	0.51
Unaided	865.4	68.7	9	761.4	41.1	11	595.7	54.3	10			
At Hole												
Control	59.4	13.8	13	100.8	8	15	112.6	23.0	11	0.570	0.003	0.46
Unaided	24.2	5.3	9	83.2	15.7	11	133.8	31.3	10			

could have combined to produce a lower rate of food delivery to nestlings of unaided females at the road than the lake. This may have been a contributing cause of the lower fledging success (both relative and absolute) of unaided females at the road than the lake.

Prey size selection by parents.-The condition of unaided and control females could be affected if foraging for their nestlings is more difficult at the road than the lake area. I examined this possibility by comparing the size distribution of insects found in food boluses with the size distribution of insects available at each site (from net samples). Insect taxa were pooled in these analyses because a previous study found little evidence for prey selection based on taxa (Quinney and Ankney 1985). In this study I found that over 92% of the diet was composed of dipterans. The size classes of insects in the diet of nestlings of unaided and control females did not differ within sites (Fig. III-7). However, there were differences between the lake and road sites in the size classes of insects fed to nestlings (Fig. III-7; log-linear model with site, insect size class and treatment as main effects, P= 0.035, df= 4, X^2= 10.3). At the lake, females fed their young mostly 3-5 mm insects (the most abundant size class), while at the road nestlings were fed relatively more 5-7 mm insects (the third most abundant size class; Fig. III-3,7). The largest insects (9-13 mm) formed the majority (by biomass) of the diet of nestlings at the lake, while at the road the diet was composed mostly of 5-7 and 9-13 mm insects (Fig. III-7). This difference in prey selection was not due to different availability of 9-13 mm insects because these insects were equally abundant at the lake and road sites during the nestling period (Fig. III-3). Therefore, females at the road were feeding their nestlings a greater proportion (% frequency) of larger, less abundant prey than females at the lakeshore. This difference suggests that foraging may have been more costly for females at the road than the lake site. More difficult foraging may have contributed to lighter food boluses, and subsequently more starvation, at nests of unaided females at the road. It could also have reduced the body condition of fledglings and parents and their subsequent rate of return to the study area.

Body mass of nestlings

I used body mass as an index of nestling body condition just prior to fledging. A variety of factors could have confounded the analysis of body mass of nestlings

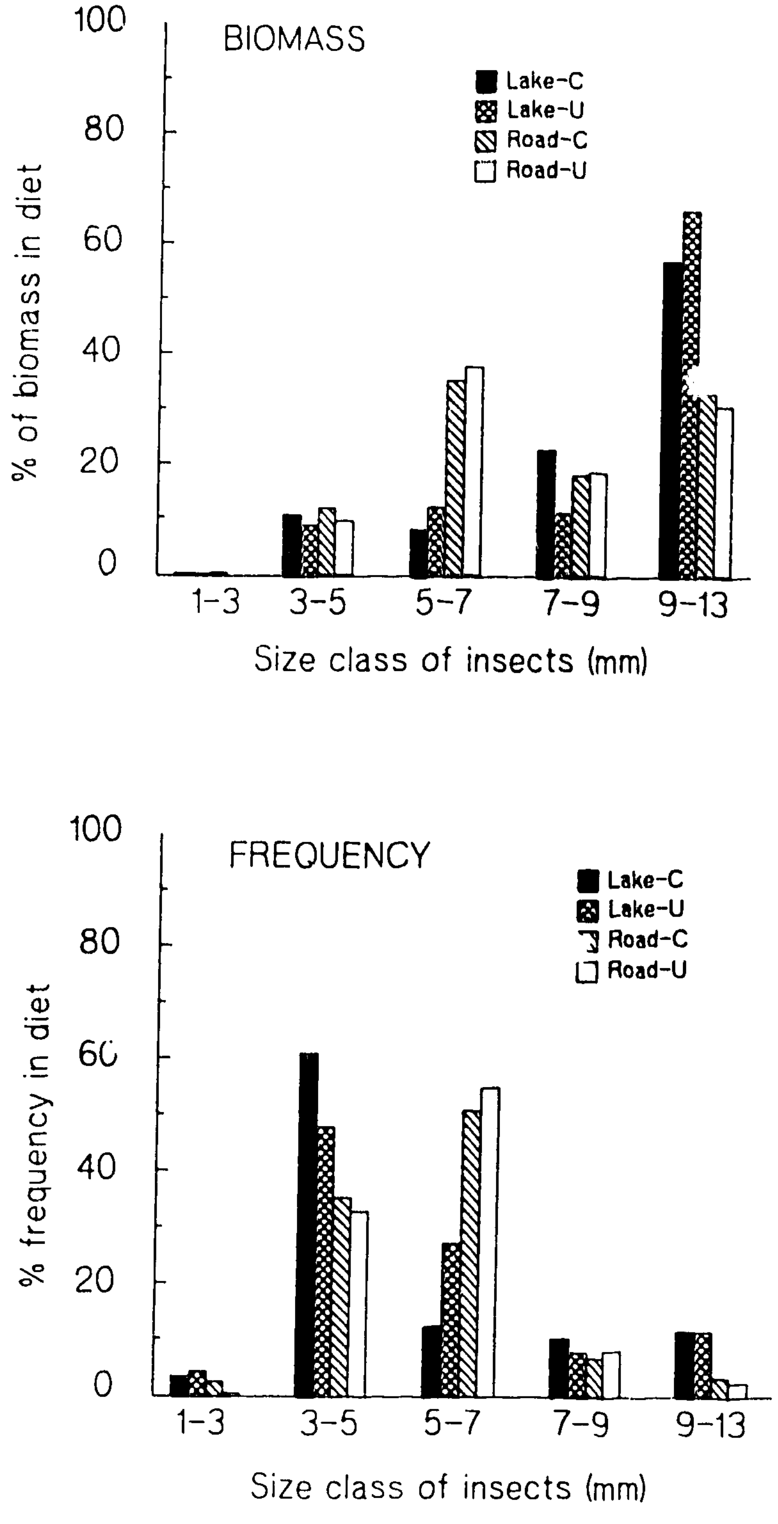


Fig. III-7. Biomass (%) and frequency (%) of insects in the diet of tree swallow nestlings in Lakeshore and Roadside habitats, Jun 1987-88. 'C'= Control and 'U' = unaided female nests (measured on day 16). In this analysis a mean nestling mass was calculated for each brood to avoid lack of independence among samples. Prior to examining the effect of male removal on mean nestling mass, I tested for effects of brood reduction, timing of male removal, year and study site on mean nestling mass. Regression analysis indicated that brood reduction (clutch size-brood size/clutch size; arcsin transformed) was not related to mean nestling mass on day 16 ($\underline{r}^2$= 0.02, $\underline{P}$= 0.10, df= 1, 118), nor was timing of male removal related to mean mass ($\underline{r}^2$= 0.03, $\underline{P}$= 0.38, df= 1, 28). Mean nestling mass on day 16 was also not influenced by year (2-way ANOVA, $\underline{P}$= 0.30, $\underline{F}$= 1.2, df= 2, 114; main effects were year and treatment). There was also no difference between lake and road nests in mean nestling body mass, so these sites were pooled (separate ANCOVA's for control and unaided females with brood size as the covariate and lake or road as the group; $\underline{P}$> 0.22 for site effects; slopes were homogeneous, $\underline{P}$> 0.14).

Only brood sizes of 3, 5, 6 and 7 young (on day 16) had more than 3 samples in each treatment category (Fig. III-8). Among these broods, mean nestling mass on day 16 was affected by male removal ($\underline{P}$= 0.008, $\underline{F}$= 7.35, df= 1,86) although the effect was not the same for all brood sizes (i.e., there was an interaction between treatment and brood size, $\underline{P}$= 0.011, $\underline{F}$= 3.93, df= 3, 86, 2-way ANOVA, main effects were treatment and brood size). Brood size also tended to have an effect on fledging mass ($\underline{P}$= 0.059, $\underline{F}$= 2.56, df= 3, 86). The significant interaction effect was caused by lower fledgling mass in brood sizes 3 and 7 of unaided females ($\underline{t}$-tests, $\underline{P}$= 0.048 and 0.009, respectively; Fig. III-8). Mean nestling mass did not differ in nests of control and unaided females with the most common brood sizes of 5 and 6 young ($\underline{t}$-tests, $\underline{P}$= 0.68 and 0.69 respectively, Fig. III-8).

Body mass of female parents

In contrast to the effect on mean nestling mass, control and unaided adult female parents weighed on day 16 had similar body mass (ANOVA, $\underline{P}$= 0.17 for treatment effect, $\underline{P}$= 0.49 for site effect). At the lakeshore, control and unaided females weighed 21.0±0.3 g (n= 24) and 20.8±0.2 g (n= 7), respectively, while at the road, control and unaided females weighed 21.1±0.4 g (n= 9) and 20.2±0.5 g (n= 9), respectively. Mean

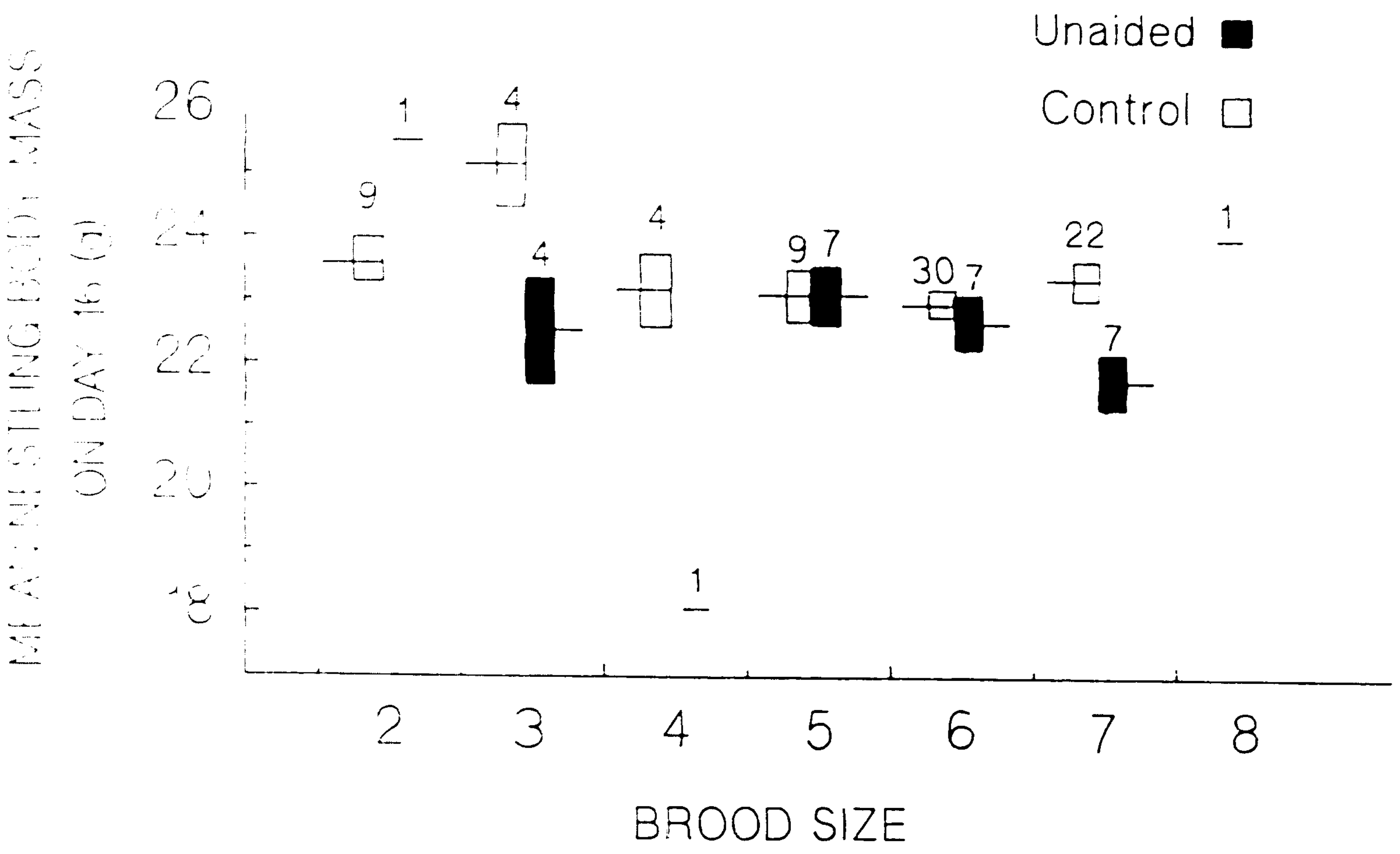


Fig. 18. Mean body mass (g) of tree swallow nestlings on day 16 (just before fledging). Beaverhill Lake, Alberta, 1986-88. Only includes data from nests of adult (ASY) females. Horizontal line is the mean, while the bar indicates one SE above and below the mean. Numbers above the bars are sample sizes.

body mass of adults also did not differ between the lake and road sites for either control (P= 0.83, F= 0.05, df= 1,30) or unaided females (P= 0.72, F= 0.13, df= 1,13) after controlling for brood size with ANCOVA (slopes were homogeneous in both tests, P> 0.41).

Return rate of fledglings and parents

Ten fledglings were known to return to the study area in subsequent years (all except 2 were born in 1986 and returned in 1987). Eight of these birds were from control nests (8/645 banded fledglings from control nests; 1.24%) and two were from nests of unaided females (2/169 fledglings from nests of unaided females; 1.18%). These return rates were not significantly different (G= 0.003, P>0.95, df= 1); however, the probability of a type II error is likely high with such small sample sizes. Among returning fledglings from control nests, 5 were from nests at the lake, 1 was from the marsh, 2 were from the road and 1 was from a nest-box in aspen forest near the lakeshore. The returning fledglings from nests of unaided females came from 1 lake and 1 road nest. Broods that had at least one individual return in subsequent years did not differ in mean nestling mass (on day 16) from broods that had no individual return (22.5±0.7 g, for 4 control broods with returning young vs. 23.5±0.2 g for 49 control broods with no returning young; P= 0.072, F= 3.33, df= 1,73; 2-way ANOVA, main effects were treatment and whether or not an individual returned). The 10 birds that returned the next year weighed only 0.03±0.4 g more than the mean body mass of other nestlings in their broods. Only one of the 10 returning birds was the heaviest nestling in its brood on day 16.

There was no difference between control and unaided female parents in the direct return rate to the study area. Among adult females, 28% (25/88) of control and 23% (8/35) of unaided females returned to the study area the next year (G= 0.39, P> 0.4, df= 1). For all females, 27% (31/114) of control and 22% (9/41) of unaided females returned the next year (G= 0.44, P> 0.4, df= 1). If this 5% difference in return rate were real, then I would need a total sample size of 1200 females to be 80% certain (i.e., the power of the test= 0.80) of finding a significant difference at an alpha level of 0.05 (Sokal and Rohlf 1981: 766). Unaided and control females that bred at the lake and road returned to the study area at similar rates the next year (Log-linear model, P> 0.5, df=1). Fledging success in the next year (for birds that did not change sites) was not affected by breeding location (site effect P= 0.32, F= 1.06, df= 1,23) or treatment (P= 0.87, F= 0.026) in the previous year (2-way ANOVA; data included 10 unsuccessful nests and 5 SY females).

DISCUSSION

During laying, the food supply of tree swallows was greater near the shore of Beaverhill Lake than at the road site 2 km away. Food availability (IBI) may have also been greater at the lake during the nestling period if females at the road fed their young larger, less abundant prey. As predicted, I found that natural polygyny occurred generally in areas with greater food abundance (during laying), and naturally-occurring secondary females in good habitat (lake) produced more fledglings than monogamous females in poorer habitat (road). When secondary mate status was simulated by removing males, I again found that unaided females at the lake produced more fledglings than monogamous females at the road. This supports Quinney's (1983) suggestion that female tree swallows will choose polygyny when it becomes more advantageous to mate with an already-mated male in an area with a superior food supply than with a unmated male in an area with a lower food supply. It is often assumed that the major cost of choosing secondary mate status is the loss of male parental care (Weatherhead 1979, Wittenberger and Tilson 1980). However, in this study loss of male parental care did not reduce fledging success (within a habitat). The occurrence of polygyny and its success appeared to be influenced more by food conditions during laying than during the nestling period (when male parental care is presumably most important). Within the range of food levels studied here, polygyny appeared to be influenced more by the ability of females to lay large clutches than by a need for male parental care.

While food abundance may influence where and if females will chose polygyny, low food abundance (within the range studied here) does not necessitate biparental care. The varying explanations for monogamy in tree swallows (Leffelaar and Robertson 1986; Quinney 1983, 1986) are probably best reconciled as responses by populations to geographic variation in food abundance. Food availability may have been so low at Leffelaar and Robertson's study area that biparental care was necessary. At Quinney's study area, food may have been sufficiently abundant that polygyny was favorable to some females. Assuming that the reproductive success of unaided females equals that of secondary females, it appeared that males on my study area would benefit from polygyny, and females would benefit from secondary mate status at the lake site. Although females might have incurred little or no cost by becoming a secondary mate at the road (unaided and control females produced similar numbers of fledglings at the road), this may never have occurred because secondary mate status was more profitable at the lake. If there were only a small number of females each year that had to choose between monogamy at the road and secondary mate status at the lakeshore, then polygyny might not occur at the road site.

Polygyny may have been more costly for females than I suggest if the lower body mass of nestlings of unaided females reduced the subsequent survival of fledglings. Nestlings weighed less in large broods of 7 young, but not in nests with the most common brood sizes of 5 and 6 young. Overall, the difference in mean nestling mass between nests of control and unaided females was only 2.3 % of the body mass of young from nests of unaided females. Most studies of the survival of fledglings in relation to body mass, including DeSteven's (1980) study of tree swallows, have found little difference in body mass between birds that returned (or reached independence) and disappeared. The mean difference in body mass of young that returned versus disappeared was 1.4±0.3% (Ross and McLaren 1981, Groves 1984, Harris and Rothery 1985, Gibbs 1988, Wolf et al. 1988). The same value in studies in which body mass had a significant effect on return rate was 5.7±0.9% (Gibbs 1988, Patterson et al. 1988, Sullivan 1988). These studies suggest that the difference in body mass of nestlings found in this study was not large enough to affect survival. Despite the difference in body mass of nestlings, there was no difference in their rate of return. Return rate of fledglings from nests of unaided females in this study (1.2%) was similar to the return rate from unmanipulated nests in Alberta (1.3%; Pinel 1980) and Saskatchewan (0.8%; Houston and Houston 1987).

Unaided females had higher rates of nest visits, and presumably higher parental effort, than control females. Quinney (1986) described one nest at which an unaided female delivered almost as many meals (234/day) to her brood a. broods of the same age (6-12 days old) and size (3 nestlings) raised by two parents (272 meals/day). Leffelaar and Robertson (1986) also found that the feeding rates of three unaided females increased during the nine hours that their mates were held in captivity, and feeding rates of two unaided females increased for several days after their mates disappeared. A related study of food-provisioning in tree swallows (Hussell 1988) indicated that parents respond to increased hunger signals from their nestlings (e.g., when food supply is lower) by increasing their feeding rate (at least in the short term). However, it is important to note that nest visit rate may not be a good measure of feeding rate in tree swallows because parents probably adjust the size of food boluses, and not nest visits, to changes in food supply and the demands of their young (Hussell 1988). In this study, unaided females may have maintained similar nest visit rates as controls, but the amount of food received by nestlings may have been lower because unaided females at the road tended to collect smaller food boluses than unaided females at the lake. Male removal studies that have reported per capita feeding rates indicate that young in nests of unaided females generally receive as many visits as young fed by both parents (Smith et al. 1982, Greenlaw and Post 1985, Wolf et al. unpubl data, this study). Although per capita nest visit rates may be similar in these studies, there is still the possibility that unaided females may be providing lower quality or smaller food items or less food overall.

Unaided females at the road site tended to bring lighter food boluses to their nestlings than unaided females at the lakeshore. This difference in prey fed to nestlings may be the mechanism for greater loss of young in nests of unaided females at the road than at the lake site (relative fledging success was lower at the road). Quinney (cited in Hussell 1988) also found a non-significant tendency for food boluses to be lighter in an area with relatively lower food abundance (mean IBI). Larger insects were relatively [illegible] common at the road than the lake site, and this may have made foraging more difficult for unaided females at the road compared with unaided females at the lakeshore.

If unaided females are expending more energy toward parental care than paired females, one might expect that unaided females would weigh less than control females by the end of the nestling period (all else being equal). Body mass of breeding adults has been suggested as a predictor of subsequent survival (Hussell 1972, Askenmo 1977, Nur 1984b), so unaided females might also return at a lower rate the next year. However, at the end of the nestling period, there was no difference in body mass between unaided and paired females, nor did body mass differ between habitats. Studies of other species have shown a significantly lower body mass in unaided females when compared with paired females: lesser snow goose (Anser caerulescens, Martin et al. 1985), blue and great tits (Parus caeruleus and P. major Sasvari 1986), and willow ptarmigan (Lagopus lagopus, Martin and Cooke 1987; when males were removed at hatch, but no body mass change occurred when males were removed during incubation). In this study, there was no difference in return rates of unaided and control adults in the next year. Similar return rates have been found in most other male removal studies (Gowaty 1983, Martin and Cooke 1987), although Hannon (1984) found a difference in return rate in one year, but not another.

Most other male removal studies in typically monogamous species have found that male parental care is helpful, but not a necessity (Weatherhead 1979, Patterson et al. 1980, Alatalo et al. 1982, Smith et al. 1982, Martin et al. 1985, Greenlaw and Post 1985, Sasvari 1986, Bjorklund and Westman 1987, Lyon et al. 1987, Wolf et al. 1988; but see Erkmann 1983, Chapter II. In these cases monogamy may be maintained in the population because the loss of male parental care associated with secondary mate status makes monogamy almost always more advantageous to females than polygyny (hypothesis 2 of Wittenberger and Tilson 1980). However, some male removal studies have found that loss of male parental care had little or no effect on reproductive success (lesser snow geese, Martin et al. 1985; willow ptarmigan, Hannon 1984, Martin and Cooke 1987; eastern bluebirds, Sialia sialis, Gowaty 1983; northern cardinals Cardinalis cardinalis, Richmond 1978, and tree swallows, this study).

If male parental care is not important for reproductive success in some species then why do not males desert their mates and search for other mating opportunities? Bart and Tornes (1989) have presented three hypotheses for the maintenance of monogamous pair-bonds in cases where the value of male parental care is low. Only one of these hypotheses is applicable to tree swallows. Bart and Tornes (1989) suggest that if male parental care is generally not costly to males, then there might not be strong selection against providing male parental care. This hypothesis is unlikely to be a complete explanation because it does not consider the probability that males will find alternative mating opportunities. It may not be costly to provide male parental care, but if there are other mating opportunities then males should take advantage of them (assuming they are not too costly). In tree swallows there are probably few alternative mating opportunities, except for extra-pair copulations (Lombardo, 1986; pers. obs.) and polygyny. Even though polygyny may be advantageous to female tree swallows if food abundance is relatively high, polygyny may be uncommon because intrasexual competition for nest-boxes prevents most males from gaining a territory large enough that two females can breed without one female excluding the other (Hannon 1984, Arcese 1989, see Chapters V and VI).

Quinney (1986) presented evidence from a few nests of unaided tree swallows that suggested food abundance could influence the need for male parental care. I can compare my results directly with Quinney's results because I have used the same methods to sample insect abundance (Hussell and Quinney 1987). Quinney (1986) found that in an area of relatively high food abundance an unaided female could raise a brood of three young as well as two parents with the same size brood in an area of lower food abundance. Quinney's areas of high and low food abundance differed by 14.6 mg of insect biomass/ 100 km wind during the nestling season (Hussell and Quinney 1987), while my lake and road areas in Alberta did not differ in insect biomass during the nestling period (Table III-8; a mean difference of 3.5 mg/ 100 km wind). Relative to Quinney's study areas, all of our sites in central Alberta were relatively high in food abundance throughout the breeding season (Table III-8). This may explain why unaided females produced as many offspring as control females at both the lake and road sites. However, unaided females at the road site produced fewer offspring than unaided females at the lakeshore. In addition, nest-box occupancy tended to be lower at the road than the lake site and all of my known cases of natural polygyny occurred at the lake (n=6) or marsh (n= 1) sites. These results suggest that the road site was somehow poorer in quality for unaided (and presumably secondary) females, even though the IBI was high (relative to Quinney's poorest site) and similar among my sites during the nestling period.

Table III-8. Insect biomass index (IBI) in Ontario and Alberta. Values are the arithmetic means, standard errors and ranges of the back-transformed yearly means for 1977-1984 in Ontario and 1986-1988 in Alberta.

	Laying season				Nestling season				
Location	$\bar{X}$	SE	range	n^1	$\bar{X}$	SE	range	n^1	Source
Ontario									
Sewage Lagoon	39.1	7.6	7.2-77.2	8	17.9	3.3	7.2-38.2	8	Hussell and Quinney (1987)
Backus Field	3.1	0.4	1.6-5.2	8	3.3	0.3	1.7-4.5	8	
Alberta									
Lake	37.0	16.0	14.4-66.0	3	9.4	1.5	7.6-11.7	3	
Marsh	32.0	13.4	15.5-58.6	3	13.3	4.1	8.3-21.5	3	This study
Road	19.7	8.3	10.6-36.2	3	12.9	2.9	9.8-18.7	3	

---

[1] Number of years of sampling.

A superior food supply and limited nest sites may both be required for polygyny to occur in tree swallows (Quinney 1983). A greater mean IBI at the lake than the road during laying may have made the lake site appear better at the time polygynous females chose a nesting area. In addition, nest-box occupancy was higher at the lakeshore (about 90%) than the road site (about 60%) in 1987 and 1988, but it was about the same in 1986 (both 50-60%). Even though nest sites were not limiting in 1986, there were still two cases of polygyny at the lake and none at the road site. Whatever its cause, the difference in fledging success between unaided females at the lakeshore versus the road (mean difference= 1.3 young for clutches of 6 and 7 eggs) may have been always sufficient to favor polygyny at the lakeshore rather than the roadside.

LITERATURE CITED

Arcese, P. 1980. Intrasexual competition and the mating system in primarily monogamous birds: the case of the song sparrow. Animal Behaviour 38: 96-101.

Askenmo, C. 1977. Effects of addition and removal of nestlings on nestling weight, nestling survival and female weight loss in the pied flycatcher *Ficedula hypoleuca* (Pallas). Ornis Scandinavia 8: 1-8.

Bart, J., and A. Tornes. 1989. Importance of monogamous male birds in determining reproductive success. Evidence for house wrens and a review of male-removal studies. Behavioral Ecology and Sociobiology 24: 109-116.

Beehler, B. 1985. Adaptive significance of monogamy in the trumpet manucode *Manucodia keraudrenii* (Aves:Paradisaedae). Pages 83-99 *in* P. A. Gowaty and D. W. Mock, Editors. Avian monogamy, Ornithological Monograph 37.

Cohen, R. R., and D. J. HAYES. 1984. A simple unattached nest-box trapping device. North American Bird-Bander 9:10-11.

Crook, J. H. 1964. The evolution of social organisation and visual communication in the weaver birds (Ploceinae). Behaviour supplment 10: 1-78.

Davies, N. B., and A. Lundberg. 1984. Food distribution and a variable mating system in the dunnock, *Prunella modularis*. Journal of Animal Ecology 53: 895-912.

DeSteven, D. 1978. The influence of age on the breeding biology of the tree swallow *Iridoprocne bicolor*. Ibis 120:516-523.

-----------. 1980. Clutch size, breeding success, and parental survival in the tree swallow. (*Iridoprocne bicolor*). Evolution 34: 278-291.

Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223.

Erkmann, W. J. 1983. The evolution of polyandry in shorebirds: an evaluation of hypotheses. Pages 114-168 *in* S. K. Wasser, Editor. Social behavior of female vertebrates, New York, Academic Press.

Gibbs, H. L. 1988. Heritability and selection on clutch size in Darwin's medium ground finches (*Geospiza fortis*). Evolution 42: 750-762.

Gowaty, P. A. 1983. Male parental care and apparent monogamy among eastern bluebirds (*Sialia sialis*). American Naturalist 121:149-157.

Greenlaw, J. S., and W. Post. 1985. Evolution of monogamy in seaside sparrows, *Ammodramus maritimus*: tests of hypotheses. Animal Behaviour 33:373-383.

Groves, S. 1984. Chick growth, sibling rivalry, and chick production in American black oystercatchers. Auk 101: 525-531.

Hannon, S. J. 1984. Factors limiting polygyny in the willow ptarmigan. Animal Behaviour 32: 153-161.

Harmeson, J. P. 1974. Breeding ecology of the dickcissel. Auk 91: 348-359.

Harris, M. P., and P. Rothery. 1985. The post-fledging survival of young puffins *Fratercula arctica* in relation to hatching date and growth. Ibis 127: 243-250.

Holroyd, G. L. 1972. Resource use by four avian species of aerial insect feeders.

Unpubl. M.Sc. thesis, Toronto, Univ. Toronto.

------------. 1975. Nest site availability as a factor limiting population size of swallows. Canadian Field Naturalist 89:60-64.

Houston, M. I., and C. S. Houston. 1987. Tree swallow banding near Saskatoon, Saskatchewan. North American Bird Bander 12: 103-108.

Hussell, D. J. T. 1972. Factors affecting clutch size in arctic passerines. Ecological Monograph 42:317-364.

------------. 1983. Age and plumage color in female tree swallows. Journal of Field Ornithology 54: 312-318.

------------. 1988. Supply and demand in tree swallow broods: a model of parent-offspring food-provisioning interactions in birds. American Naturalist 131: 175-202.

Hussell, D. J. T., and T. E. Quinney. 1987. Food abundance and clutch size of tree swallows <u>Tachycineta</u> <u>bicolor</u>. Ibis 129: 243-258.

Jarman, P. J. 1982. Prospects for interspecific comparison in sociobiology. Pages 323-342 <u>in</u> King's College Sociobiology Group, Cambridge, Editors Current problems in sociobiology, Cambridge, Cambridge Univ. Press.

Lack, D. 1968. Ecological adaptations for breeding in birds. London, Methuen.

Leffelaar, D., and R. J. Robertson. 1986. Equality of feeding roles and the maintenance of monogamy in tree swallows. Behavioral Ecology and Sociobiology 18:199-206.

Lombardo, M. P. 1986. Extrapair copulation in the tree swallow. Wilson Bulletin 98: 150-152.

Lyon, B. E., Montgomerie, R. D., and Hamilton, L. D. 1987. Male parental care and monogamy in snow buntings. Behavioral Ecology and Sociobiology 20: 377-382.

Magunsson, A. 1984. Ny fangstmetod for holkfaglar. Var Fagevarld 4: 318.

Martin, K., F. G. Cooch, R. F. Rockwell, & F. Cooke. 1985. Reproductive performance in lesser snow geese: are two parents essential? Behavioral Ecology and Sociobiology 17:257-263.

Martin, K., & F. Cooke. 1987. Bi-parental care in willow ptarmigan: a luxury? Animal Behaviour 35:369-379.

Mock, D. W. 1985. An introduction to the neglected mating system. Pages 1-10 <u>in</u> P. A. Gowaty and D. W. Mock, Editors. Avian Monogamy, Ornithological Monograph 37.

Murray, B. G. Jr. 1984. A demographic theory on the evolution of mating systems as exemplified by birds. Evolutionary Biology 18: 71-140.

Norusis, M. J. 1986. SPSS/PC+ advanced statistics. Chicago, SPSS Inc.

Nur, N. 1984a. The consequences of brood size for breeding blue tits. II. nestling weight, offspring survival and optimal brood size. Journal of Animal Ecology 53: 497-518.

------------. 1984b. The consequences of brood size for breeding blue tits. I. adult survival, weight change and the cost of reproduction. Journal of Animal Ecology 53: 479-496.

Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. American

Naturalist 103: 589-603.

-----------. 1980. Some adaptations of marsh-nesting blackbirds. Monographs in Population Biology 14.

Oring, L. W. 1982. Avian mating systems. Pages 1-92 in D. S. Farner and J. R. King, Editors. Avian biology, vol. VI. New York, Academic Press.

Patterson, I. J., G. M. Dunnet, and S. R. Goodbody. 1988. Body weight and juvenile mortality in rooks Corvus frugilegus. Journal of Animal Ecology 57: 1041-1052.

Pinel, H. W. 1980. Reproductive efficiency and site attachment of tree swallows and mountain bluebirds. Blue Jay 38: 177-183.

Pleszcsynska, W., and R. I. Hansell. 1980. Polygyny and decision theory: testing of a model in lark buntings (Calamospiza melanocorys). American Naturalist 116: 821-830.

Quinney, T. E. 1983. Tree swallows cross a polygyny threshold. Auk 100: 750-754.

-----------. 1986. Male and female parental care in tree swallows. Wilson Bulletin 98: 147-150.

Quinney, T. E., and C. D. Ankney. 1985. Prey size selection by tree swallows. Auk 102: 245-250.

Quinney, T. E., D. J. T. Hussell, and C. D. Ankney. 1986. Sources of variation in growth of tree swallows. Auk 103: 389-400.

Richmond, A. R. 1978. An experimental study of advantage of monogamy in the cardinal. Unpubl. Ph.D. diss. Indiana Univ., Bloomington.

Sasvari, L. 1986. Reproductive effort of widowed birds. Journal Animal Ecology 55: 553-564.

Schifferli, L. 1976. Factors affecting weight and conditions in the house sparrow particularly when breeding. Unpubl. Ph.D. diss. Univ. of Oxford, Oxford.

Simmons, R. B., B. MacWhirter, P. Barnard, and G. C. Hansen. 1986. The influence of microtines on polygyny, productivity, age, and provisioning of breeding northern harriers: a 5-year study. Canadian Journal of Zoology 64: 2447-2456.

Smith, J. N. M., Y. T. Yom-Tov, and R. Moses. 1982. Polygamy, male parental care, and sex ratio in song sparrows: an experimental study. Auk 99: 555-564.

Sokal, R. R., and F. J. Rohlf. 1981 Biometry. New York, W. H. Freeman.

Sullivan, K. A. 1988. Ontogeny of time budgets in yellow-eyed juncos: adaptation to ecological constraints. Ecology 69: 118-124.

Walsh, H. 1978. Food of nestling purple martins. Wilson Bulletin 90: 248-260.

Weatherhead, P. J. 1979. Ecological correlates of monogamy in tundra-breeding savannah sparrows. Auk 96: 391-401.

Wittenberger, J. F. 1978. The evolution of mating systems in grouse. Condor 80: 126-137.

-----------. 1979. The evolution of mating systems in birds and mammals. Pages 271-349 in P. Marler and J. G. Vandenbergh Editors. Handbook of behavioral neurobiology, vol. 3, social behavior and communication, New York, Plenum Press.

-----------. 1980. Vegetation structure, food supply, and polygyny in bobolinks (Dolicnonyx oryzivorus). Ecology 61: 140-150.

Wittenberger, J. F., and R. L. Tilson. 1980. The evolution of monogamy: hypotheses and evidence. Annual Review of Ecology and Systematics 11: 197-232.

Wolf, L., E. D. Ketterson, and V. Nolan Jr. 1988. Paternal influence on growth and survival of dark-eyed junco young: do parental males benefit? Animal Behavior 36: 1601-1618.

IV. FEMALE-FEMALE AGGRESSION AND THE MAINTENANCE OF MONOGAMY IN TREE SWALLOWS

INTRODUCTION

The polygyny threshold model (Verner 1964, Verner and Willson 1966, Orians 1969) has been a leading hypothesis to explain the maintenance of monogamy in populations of birds and mammals (Wittenberger and Tilson 1980). One of the model's assumptions is that the reproductive success of already-mated females is reduced when additional females settle and mate polygynously (Garson et al. 1981). This reproductive cost may occur because the amount of male parental care received by each female is reduced or because of deleterious effects of increased density on predation or food availability. If the reproductive costs of sharing a territory outweigh the costs of excluding another female, then selection should favor female behaviors that exclude potential secondary mates (e.g., chasing or displaying toward intruders). The polygyny threshold model predicts that polygyny can be more advantageous to some females than monogamy if the costs of polygyny are more than compensated for by breeding on a higher quality territory. However, female aggression could force some females to mate monogamously even when their reproductive success would have been greater had they mated polygynously.

Until recently, the evidence presented to suggest that female-female aggression maintains monogamy has mainly been limited to observations of female aggression toward models or playbacks of their calls (Table IV-1). Much of this evidence supports the maintenance of monogamy hypothesis, but it does not preclude several alternative hypotheses. These alternatives include 1) females are aggressive to prevent complete takeovers of their territories and 2) females are aggressive to prevent intraspecific brood parasitism (egg-dumping, Gowaty and Wagner 1988). These three hypotheses are not exclusive, however, the maintenance of monogamy hypothesis can be separated from the two alternatives by examining the costs of polygyny and the pattern of female aggression.

Several predictions can be made from this hypothesis concerning the maintenance of monogamy. First, already-mated females should attempt to exclude

Table IV. Studies of female settlement and aggression in birds. Blanks indicate no data available and ?= results are not known definately.

Species	Evidence	Did primary females incur a cost?	Did female aggression limit the no. of mates?	Source
Polygynous				
Pied flycatcher (*Ficedula hypoleuca*)	Females aggressive toward other females, but not males (presentations of live models)	No	Yes?	Alatalo et al. (1982) Breiehagen and Slagsvold (1989)
Western meadowlark (*Sturnella neglectus*)	Females aggressive toward playbacks of their calls	No		Dickinson et al. (1987)
Red-winged blackbird (*Agelaius phoeniceus*)	More settlement after female removals		Yes	Hurly and Robertson (1985)
	1) Removal of a) primary and b) secondary females did not affect no. of birds that settled	No	No	Searcy (1988), also Milks and Picman (unpubl. data)
	2) Experimental increases in female aggression did not affect harem size			
Yellow-headed blackbird (*Xanthocephalus xanthocephalus*)	Primary females equally aggressive as secondary and tertiary females (during laying)	No?	No	Lightbody and Weatherhead (1987)
Marsh wren (*Cistothorus palustris*)	1) Monogamous and primary females equally aggressive to playbacks of calls (during prelaying, but after settlement of secondary female?)		No	Leonard and Picman (1987)
	2) Secondary females settle after most bachelor male become mated, [illegible] after primary females start to incubate			
Monogamous				
Willow ptarmigan (*Lagopus lagopus*)	Females unable to exclude secondary females after experimental increase in male territory size (assumes terr. quality also did not increase)	No?	Yes?	Hannon (1984)
Tree swallow (*Tachycineta bicolor*)	1) Primary females not very aggressive toward secondary females.	No	No	This study

[illegible] Studies of female settlement and aggression in birds. Blanks indicate no data available and ?= results are not known definately.

Species	Evidence	Did primary females incur a cost?	Did female aggression limit the no. of mates?	Source
Tree swallow (cont.)	2) Secondary females settled when monogamous females were most aggressive, not afterwards			
Yellow warbler (Dendroica petechia)	Primary female aggressive toward secondary female (after laying)		Yes?	Hobson and Sealy (1989)
Eastern bluebird (Sialia sialis)	Females more aggressive toward female than male mounts (during laying)	No?[1]	No?	Gowaty (1983), Gowaty and Wagner (1988)
Seaside sparrow (Ammodramus maritimus)	Only one observation of female agression, and nest placement random, not at center of territory to maximize access to resources	No?[1]	No?	Greenlaw and Post (1985)
Song sparrow	Settlement of secondary females reduced on territories where females spent more time in alert behavior (food supplemented territories)	Yes?	Yes	Arcese (1989)

[1] Based on no cost to unaided females (Gowaty 1983, Greenlaw and Post 1985).

intruders if sharing a territory with another female incurs a cost to the primary female. Second, one might predict that before settlement of a secondary female the primary females of polygynous males would have been less aggressive toward female intruders than monogamous females. This assumes that monogamous females are better able to exclude secondary females than are primary females. This comparison assumes that level of female aggression is not correlated with territory or mate quality. Third, once secondary females have settled, primary females should continue to be aggressive toward the secondary female to displace it from the territory (at least until the primary female begins laying or incubation). This assumes that there is not a net cost to female aggression before laying or incubation. Fourth, the pattern of settlement by secondary females can be used to suggest if female aggression plays a role in limiting male pairing success (Leonard and Picman 1987). In several bird species female aggression toward intruders is greatest during nest-building and laying (Leonard and Picman 1987, Robertson et al. 1986, c.t htbody and Weatherhead 1987, Gowaty and Wagner 1988). If this aggression limits settlement by secondary females, then one would expect to find most settlement of secondary females after primary females started incubation and aggression declined (female aggression model of Leonard and Picman 1987). However, if female aggression does not limit the settlement of secondary females, then secondary females should settle at the same time, or slightly later, than monogamous females.

In this study I examined the potential for female aggression to limit polygyny in tree swallows. Approximately 5 (Quinney 1983) to 8% (this study) of tree swallow males are polygynous, and female tree swallows attack and sometimes kill intruders (Robertson et al. 1986). These conditions indicate that there is potential for female-female aggression to maintain monogamy as the predominant (apparent) mating system in this species. I compared the reproductive success of monogamous and primary females and the settlement patterns of monogamous and secondary females to determine if female aggression had the potential to maintain monogamy in tree swallows. The second prediction (above) could not be tested because very little aggression data were collected before the settlement of the secondary female.

Study area and methods

Tree swallows were studied near the southeast shore of Beaverhill Lake, Tofield, Alberta during May-July 1986-88. This study used two grids of 50 nest-boxes each within 50 m of the lakeshore and one grid of 32 boxes near a marsh 1 km away. All nest-boxes were spaced 24 m apart, except for several spirals of boxes in each of the three grids (see Chapter V for more details). The aggression data used here were not influenced by the number of boxes on a male's territory (G= 2.38, P= 0.12, df=1; categories were strong and mild/none responses by females toward intruders versus 1 or >1 nest-box). Swallows used in this study were caught in the nest box (Cohen and Hayes 1984, Magnusson 1984) early in the nesting season and uniquely color-marked on the breast with felt-tipped ink markers. Birds were classified to sex by the presence of a brood patch in females or cloacal protuberance in males. Yearling (SY= second calendar year of life) and adult (ASY= after second year) females were distinguished by plumage differences (Hussell 1983). Each nest-box was visited every 2-3 days to determine when two birds occupied the box (settlement date; 1988 only), and when nest-building and egg-laying started (all years). Clutch size and fledging success were determined from regular nest visits during the incubation and nestling periods.

Primary and secondary females were the first and second females to settle and establish pair-bonds with a male. Settlement date of females was estimated as explained in Chapter III. This information was used to compare: 1) the reproductive success of monogamous and primary females that settled during the same time period and 2) the settlement pattern of monogamous and secondary females. Settlement dates of two monogamous females were omitted from the first analysis because they settled after all primary females had settled.

There were 7 cases of natural polygyny in 1986 (8%, 3/39) and 1987 (7%, 4/56). Polygyny in males was inferred from 1) observations of males copulating with two females, 2) defence by a male of the nest-box occupied by the presumed secondary female (the female that he copulated with) and 3) observation of only a female feeding nestlings (polygynous males rarely fed the young in nests of secondary females).

Aggressive behavior of primary and monogamous females was estimated to determine if primary females were aggressive toward secondary females (prediction 3) and how seasonal changes in aggression of monogamous females related to the settlement of secondary females (prediction 4). Every 3 days an initial nest was chosen randomly for focal observation, after which the remaining nests were chosen systematically. Observation sessions were 20 minutes long during which observers recorded: total number of intruders, number and type of responses by resident males and females (either together or separately) and, when possible, the age, sex or identity (based on color-marks or nest location) of intruders. An intrusion was recorded when another swallow entered the territory of the pair under observation (half-way to the next occupied box, usually 12 m). Responses of resident females were grouped into two categories for analysis: mild (including no response and chattering) and strong (chases, physical contacts or perched outside entrance hole (hole-guarding)). Cases where the female was out of sight or in the nest-box when an intrusion occurred were excluded from analysis (Robertson et al. 1986). In most cases the sex of intruders was not known; therefore, female aggression was analyzed two ways: 1) responses by resident females toward birds with SY plumage (brown-blue plumage; all females) and 2) attacks by resident females toward all intruders. The second analysis might bias the analysis of seasonal patterns of aggression if there are changes in the proportion of female intruders throughout the season and resident females differentially attack female intruders. However, two previous studies of aggression in tree swallows (using both live birds and models) demonstrated that females attack adult (blue plumage; either sex, but most adult intruders are male) and subadult intruders with equal frequency (Lombardo 1987, Stutchberry and Robertson 1987). This suggests that resident females attack all intruders at the same rate regardless of sex. Data presented here are only from 1986 because this was the only year in which observation sessions were conducted throughout the breeding season. Statistical tests were the same as those described for Chapters III and IV. All statistical tests were two-tailed. Means are presented with their standard errors.

Results

Do primary females suffer a reproductive cost? -- Fledging success was used in this analysis as the best available estimate of reproductive success. Laying date and clutch size of monogamous and primary females were compared to determine if differences in these variables could have influenced the analysis of fledging success. There was no difference between the laying dates of monogamous (24 May ± 0.58, n=34) and primary (25 May ± 1.6, n=6) females at the lakeshore (F= 0.32, P= 0.58 for effect of mate status, df= 1, 36; 2-way ANOVA, main effects were year and female mate status). Similarly, there was no difference between the clutch size of monogamous (6.7 ± 0.13 eggs, n= 34) and primary (6.7 ± 0.4 eggs, n= 6) females at the lakeshore (F= 0.02, P= 0.90 for effect of mate status, df= 1, 36). The one primary female at the marsh started laying her clutch of 6 eggs on 22 May 1986, which is similar to the means for monogamous females at the marsh site (clutch size= 6.5 ± 0.3 eggs n= 6, laying date= 26 May ± 1.0; n= 6). At the lakeshore, the fledging success of primary females (6.0 ± 0.4, n= 6) was similar to that of monogamous females (5.1 ± 0.4, n= 34, F= 1.8, P= 0.19 for effect of mate status, df= 1, 36). This indicates that compared with monogamous females, primary females suffered no loss of fledging success when secondary females settled and bred on the same territory. This result might be expected as males in this species make almost all of their feeding trips to the nest of the primary female. However, there is probably a reduction in nest-guarding by the male, because polygynous males spend much of their time at the nest of the secondary female only after the primary female has started incubation.

Further support for no cost of polygyny to primary females comes from the male removal experiment described in Chapter III. With a larger sample size (n=32 successful nests of ASY females, Table III-5), I found that experimentally created secondary females did not suffer lower reproductive success. This suggests that primary females would also not incur a cost from polygyny because male removal was an extreme test in which females received no male parental care (primary females actually have most of a male's parental care). Therefore, both natural and experimental cases of polygyny suggest that primary females incur no significant reproductive cost.

Are primary females aggressive toward secondary females? -Both systematic watches (6 h. of observation on 6 primary females) and irregular observations (on a daily basis) before egg-laying indicated that primary females did not spend much time in aggression toward secondary females after they settled. During systematic watches of primary females only 1 aggressive interaction toward a secondary female was recorded and this was a relatively short chase (less than 5 sec.). Primary females appeared to ignore secondary females (and vice versa) throughout the breeding season.

Settlement of secondary females.-- Date of settlement of secondary females was compared with that of monogamous females using nest initiation dates. Mean nest initiation date of monogamous adult females (11 May ± 0.82, n= 35, range= 6-23 May) was 4 days earlier than that of secondary females (15 May ± 2.3, n= 7, range= 9-22 May). This difference was almost significant (t= 1.96, P= 0.057, df= 40). Nevertheless, secondary females did not settle after monogamous females started to lay eggs, as might be expected if they were being excluded by already-mated females. Mean settlement date of secondary females (estimated using the 1988 regression equation; 10 May ± 1.2) was earlier than the mean laying date of adult monogamous females (24 May ± 0.6; t= 9.7, P= 0.0001, df= 40).

The seasonal pattern of female aggression was examined from 130 h. of observation of monogamous females in 1986. Monogamous females responded strongly toward subadult (known female) intruders more frequently during nest-building-laying (86%, 6/7) than during the nestling period (60%, 6/10); however, the difference was not significant (G= 1.3, P= 0.26, df= 1; no subadult intruders were seen during incubation, so that period was not included). When all intruders were included, there were significantly more strong responses during nest-building and laying (44%, 28/63 intruders) than during the incubation (17%, 4/23) and nestling periods (29%, 12/42; G= 6.5, P= 0.038, df= 2). In summary, secondary females settled during nest-building and laying when monogamous females were most aggressive, not afterwards as predicted by the maintenance of monogamy hypothesis.

Discussion

None of the three predictions of the female-female aggresssion hypothesis that were tested were supported in this study: 1) polygyny was not costly to primary female swallows, 2) primary females were not very aggressive toward secondary females, and 3) secondary females settled during nest-building and laying when monogamous females were most aggressive toward intruders, not afterwards. Few data were collected in this study on aggression toward known sex intruders (SY females); however, my general observations are consistent with the observations of others (including studies using model presentations) that females are most aggressive during nest-building and laying when the risk of nest usurpation, egg-dumping or polygyny is greatest (Lombardo 1987, Robertson et al 1987). During the nestling period there are more intruders (many are exploring for future nest-sites), but resident birds are rarely aggressive toward them (Lombardo 1987, pers. obs.). Female aggression also did not limit the number of mates acquired by males in some populations of yellow-headed blackbirds (Xanthocephalus xanthocephalus, Lightbody and Weatherhead 1987), marsh wrens (Cistothorus palustris, Leonard and Picman 1987) and red-winged blackbirds (Agelaius phoeniceus, Searcy 1988); however, in red-winged blackbirds this may vary geographically (see Hurly and Robertson 1985, Searcy 1988). In cases where females do not incur a cost from polygyny, aggression by females during nest-building and laying may be maintained to prevent nest-site usurpation or to prevent intraspecific brood parasitism (nest-site defence and anti-kleptogamy hypotheses of Gowaty 1981).

Several studies of female aggression have concluded that already-mated females may be aggressive toward potential secondary females to ensure their mate's full parental care (Yasukawa and Searcy 1982, Hurly and Robertson 1985, Breiehagen and Slagsvold 1989, Hobson and Sealy 1989, but see Arcese 1989). However, most of these studies have not tested the maintenance of monogamy hypothesis in a rigorous manner. The most that can be concluded from the majority of these studies is that females are aggressive during the breeding season and it may affect the settlement patterns of other females, but we do not know why these females are aggressive (Table IV-1). Future studies should determine 1) if there is a cost of polygyny to primary females and 2) how female-female aggression affects the settlement of secondary females and the frequency of nest usurpation and egg-dumping. If primary females suffer lower reproductive success than monogamous females and female aggression delays or prevents the settlement of secondary females, then it would suggest that females are aggressive to prevent loss of reproductive success from sharing a territory (i.e., the maintenance of monogamy hypothesis would be supported). To my knowledge only one study suggests that both of these conditions apply in a population of birds

(Arcese 1989, Table IV-1). If there were no cost of polygyny to females, but females were still aggressive toward intruders (as this study and a few others indicate), then one would have to examine the nest usurpation and egg-dumping hypotheses (these are not exclusive; Gowaty and Wagner 1988). One of the most direct ways to study these two hypotheses would be to alter the aggressiveness of females (e.g., with implants of testosterone) and examine the subsequent effects on the frequency of nest usurpation and egg-dumping.

The data available in this study and others do not allow one to determine whether nest-usurpation or egg dumping is a larger risk to the reproductive success of female tree swallows. Limited breeding opportunities with males may produce intense competition among females and a relatively high risk of eviction (11% [6/55] of nests were usurped in Ontario), and most (5/6) evicted females did not appear to renest successfully (Leffelaar and Robertson 1985). However, in this study the risk of nest usurpation (2%, 3/156 nests in which at least one egg was laid) was lower than the rate in Ontario (G= 6.3, P= 0.012, df= 1). Egg-dumping in a New York population of swallows appeared to occur at about the same rate as nest usurpation in Ontario, but more frequently than nest usurpation in Alberta (9% of nests in New York had 2 eggs laid in a 24 h. period, Lombardo 1988; comparable data were not available from this study). Estimates of egg-dumping based on the occurrence of two eggs laid in a nest in one day may be biased (MacWhirter 1989), so the cost to females of egg-dumping and nest usurpation is worth further investigation.

Other predictions could be tested from the female-female aggression hypothesis (see Searcy 1988). For example, I did not conduct removal experiments of females and their replacements to compare settlement rates with and without a female present, nor did I manipulate aggressive levels with implants of testosterone and subsequently compare the number of females that settled (e.g., Searcy 1988). However, in tree swallows comparison of the number of replacement females that settled on female removal and unmanipulated territories would be difficult to interpret because tree swallow males only gain one extra mate (compared with up to 5 mates in red-winged blackbirds; Searcy 1988). My attempts to increase secondary female settlement through an experimental reduction in aggressive behavior (with implants of the antiandrogen flutamide; Searcy and Wingfield 1980) were unsuccessful because the implants did not reduce female aggression. Given the low level of polygyny in tree swallows, it is probably not feasible to decrease the frequency of polygyny (or delay settlement of secondary females) by increasing female aggression with implants of testosterone.

Female tree swallows in this population were not aggressive toward intruders to prevent loss of male parental care. of tree swallows. Polygyny was not costly to females in this population, while female aggression could be very costly (some females are killed; Robertson et al. 1986). Females may be aggressive toward intruders because residents can incur significant reproductive costs from nest usurpation or egg-dumping than polygyny. Similar results have been found in studies of eastern bluebirds (*Sialis sialis*), seaside sparrows (*Ammodramus maritimus*) and yellow-headed and red-winged blackbirds (Table IV-1). Polygyny in tree swallows, and possibly these other species, did not appear to be influenced by a need for parental care (chapter III) nor by female aggression to prevent loss of male parental care (this chapter). Several alternative explanations for the maintenance of monogamy in tree swallows are examined in Chapters V and VI.

LITERATURE CITED

ALATALO, R. V., A. LUNDBERG, & K. STAHLBRANDT. 1982. Why do pied flycatcher females mate with already-mated males? Anim. Behav. 30: 585-593.

ARCESE, P. 1989. Intrasexual competition and the mating system in primarily monogamous birds: the case of the song sparrow. Anim. Behav. 38: 96-111.

BREIEHAGAN, T., & T. SLAGSVOLD. 1988. Male polyterritoriality and female-female aggression in pied flycatchers Ficedula hypoleuca. Anim. Behav. 36: 604-605.

COHEN, R. R., & D. J. HAYES. 1984. A simple unattached nest-box trapping device. N. A. Bird-Bander 9: 10-11.

DICKINSON, T. E., J. B. FALLS, & J. KOPACHENA. 1987. Effects of female pairing status and timing of breeding on nesting productivity in western meadowlarks (Sturnella neglecta). Can. J. Zool. 65: 3093-3101.

GOWATY, P. A. 1981. Aggression of breeding eastern bluebirds (Sialia sialis) toward their mates and models of intra- and interspecific intruders. Anim. Behav. 29: 1013-1027.

GOWATY, P. A., & S. T. WAGNER. 1988. Breeding season aggression of female and male eastern bluebirds (Sialia sialis) to models of potential conspecific and interspecific egg dumpers. Ethology 78: 238-250.

HANNON, S. J. 1983. Spacing and breeding density of willow ptarmigan in response to an experimental alteration of the sex ratio. J. Anim. Ecol. 52: 807-820.

HOBSON, K. A., & S. G. SEALY. 1989. Female-female aggression in polygynously nesting yellow warblers. Wilson Bull. 101: 84-86.

HURLY, T. A., & R. J. ROBERTSON. 1985. Do female red-winged blackbirds limit harem size? I. A removal experiment. Auk 102: 205-209.

HUSSELL, D. J. T. 1983. Age and plumage color in female tree swallows. J. Field Ornithol. 54: 312-318.

LEFFELAAR, D., & R. J. ROBERTSON. 1985. Nest usurpation and female competition for breeding opportunities by tree swallows. Wilson Bull. 97: 221-224.

LEONARD, M., & J. PICMAN. 1987. Female settlement in marsh wrens: is it affected by other females? Behav. Ecol. Sociobiol. 21: 135-140.

LIGHTBODY, J. P., & P. J. WEATHERHEAD. 1987. Interactions among females in polygynous yellow-headed blackbirds. Behav. Ecol. Sociobiol. 21: 23-30.

LOMBARDO, M. P. 1987. Attendants at tree swallow nests. III. Parental responses to live and stuffed-model attendants. Condor 89: 768-778.

LOMBARDO, M. P. 1988. Evidence of intraspecific brood parasitism in the tree swallow. Wilson Bull. 100: 126-128.

MACWHIRTER, R. B. 1989. On the rarity of intraspecific brood parasitism. Condor 91: 485-492.

MAGNUSSON, A. 1984. Ny fangstmeted for holkfaglar. Var Fagevarld 4: 318.

ORIANS, G. H. 1961. The ecology of blackbird (Agelaius) social systems. Ecol. Monog. 31: 285-312.

ORING, L. W. 1983. Avian mating systems. Pp. 1-92. in Avian Biology, Vol. VI (D. S. Farner and J. R. King, Eds.). New York, Academic Press.

QUINNEY, T. E. 1983. Tree swallows cross a polygyny threshold. Auk 100: 750-754.

ROBERTSON, R. J., H. L. GIBBS, & B. T. STUTCHBERRY. 1986. Spitefulness, altruism, and the cost of aggression: evidence against superterritoriality in tree swallows. Condor 88: 104-105.

SEARCY, W. A. 1988. Do female red-winged blackbirds limit their own breeding densities? Ecology 69: 85-95.

SEARCY, W. A., & J. C. WINGFIELD. 1980. The effects of androgen and antiandrogen on dominance and aggressiveness in male red-winged blackbirds. Horm. Behav. 14 126-135.

STUTCHBERRY, B. J., & R. J. ROBERTSON. 1987. Signalling subordinate and female status: two hypotheses for the adaptive significance of subadult plumage in female tree swallows. Auk 104: 717-723.

VERNER, J. 1964. Evolution of polygamy in the long-billed marsh wren. Evolution 18: 252-261.

VERNER, J., & M. F. WILLSON. 1966. The influence of habitat on mating systems of North American passerine birds. Ecology 47: 143-147.

WITTENBERGER, J. F., & R. L. TILSON. 1980. The evolution of monogamy hypotheses and evidence. Ann. Rev. Ecol. Syst. 11: 197-232.

YASUKAWA, K., & W. A. SEARCY. 1982. Aggression in female red-winged blackbirds a strategy to ensure male parental investment. Behav. Ecol. Sociobiol. 11 13-17.

V. A TEST OF THE POLYGYNY THRESHOLD MODEL IN TREE SWALLOWS

INTRODUCTION

The polygyny threshold model (Verner 1964, Verner and Willson 1966, Orians 1969) has been a leading hypothesis to explain the maintenance of monogamy in populations of birds and mammals (Wittenberger and Tilson 1980). This model assumes that females choose a breeding site from a variety of male territories based on the reproductive success that the female might expect to achieve on that territory. Polygyny will occur if male territories differ sufficiently in quality that some females are able to produce more offspring as a secondary female on a high quality territory than as a monogamous female on a poorer quality territory. In most birds, monogamy is thought to be the predominant mating behavior because there are few high quality male territories available that can compensate females for the costs of polygyny (e.g., loss of male parental care, increased nest predation or lower food availability; Wittenberger and Tilson 1980). The polygyny threshold model has gained widespread acceptance because several tests of its predictions have been fulfilled (Orians 1969, Cary and Nolan 1979, Pleszczynska and Hansell 1980, Quinney 1983).

However, several recent studies have suggested that the polygyny threshold model may not be valid with particular species because females settled randomly with respect to territory quality (Lightbody and Weatherhead 1988, Leonard and Picman 1988) or because loss of male parental care, a common result of polygyny, had no adverse effect on female reproductive success (e.g., Gowaty 1983, Hannon 1984, Searcy 1988, Lightbody and Weatherhead 1988). In some of these cases female settlement patterns were better explained by male territory size (Hannon 1984, Lightbody and Weatherhead 1987) or philopatry (Eliason 1986, Wootton et al. 1986, but see Yasukawa and Searcy 1986, Searcy 1988). In this paper, I test the assumptions and predictions of the polygyny threshold model in tree swallows, using both natural cases of polygyny and experimental manipulations.

The polygyny threshold model (Orians 1969) assumes that females choose a breeding location based on perfect knowledge of all available territories and an accurate assessment of the reproductive success that might be expected on a given territory

(Garson et al. 1981). This expected reproductive success may may not be realized if predation, or other mortality factors, influence the relationship between expected and realized reproductive success (Wittenberger 1979). Lastly, it is assumed that on similar quality territories secondary females produce fewer offspring than monogamous females because of the costs of polygyny (Wittenberger 1979). In this study, I examined this cost assumption with a male removal experiment because: 1) there were few cases of natural polygyny and 2) only females in the best condition or habitat may choose polygyny, and I wanted to determine if an average female would incur a cost. I removed males from randomly-chosen territories to simulate the loss of male parental care incurred by secondary females. This is an extreme test for tree swallows because in natural cases of polygyny secondary females may be benefiting from the territorial defence behavior of the male at both nests. In tree swallows, the male usually only feeds the nestlings at the nest of his primary mate, but he defends both boxes (P. Dunn, pers. obs.).

Predictions of the polygyny threshold model

Evidence that females choose among territories of varying quality is usually inferred from fulfillment of the predictions of the polygyny threshold model (Altmann et al. 1977, Garson et al. 1981, Lightbody and Weatherhead 1988). First, territory quality should be greater on the territories of polygynous than monogamous males, and these territory characteristics (e.g., food and nest sites) should affect female reproductive success if they are to be useful to females in assessing territory quality. Experimental manipulation of territory characteristics that are known or suspected of affecting female reproductive success provides the most rigorous test of this prediction. In this study, I added additional nest-boxes to randomly-chosen territories to increase territory quality and, thereby, increase the frequency of polygyny. Additional nest-boxes may affect female choice of breeding location and expected reproductive success if additional nest-boxes reduce the chance of having to share the same nest-box with another female (e.g., Quinney 1983). Sharing the same nest-box may reduce clutch size per female and increase brood reduction because of crowding in the nest. In tree swallows, it has also been suggested that nest sites are limiting (Holroyd 1975) and that the frequency of polygyny could be increased by adding more nest-boxes to territories (Quinney 1983).

Studies of other species have increased the frequency of polygyny by manipulating nesting cover (Pleszczynska and Hansell 1980) and food abundance (Ewald and Rohwer 1982, Davies and Lundberg 1984). The effect of food abundance on polygyny was examined in this study by comparing habitats with relatively high and low insect abundance (see chapter III for details). Second, the expected reproductive success of secondary females on high quality territories should be equal to, or greater, than that of monogamous females settling at the same time on poorer quality territories. This occurs because at any given time females attempt to maximize their reproductive success regardless of mate status. Third, females will settle first on the best quality territories and only these territories will be able to compensate polygynous females; therefore, female settlement date should be earlier on the territories of polygynous than monogamous males. Lastly, the order of territories settled by primary females will be correlated positively with the order chosen by secondary females (Altmann et al. 1977, Lightbody and Weatherhead 1988). This correlation is expected because each territory will have gone through two sets of comparisons of quality (by primary and then secondary females) and these should follow the same order as long as the final number of females per territory is the same (see Fig. I-2).

METHODS

Study areas, general field methods and the male removal experiment were described in Chapter III. The nest-box addition experiment is described below.

The first prediction of the polygyny threshold hypothesis was tested by adding additional nest-boxes to randomly-chosen boxes in each grid (prior to settlement). In 1986, 1 extra nest-box was added 1 m north of 10 randomly-chosen boxes in each grid of 30 nest-boxes at the lakeshore and marsh (Fig. V-1). After laying was completed, another nest-box was added 4 m south of the center box at 5 of the 10 clusters on each grid. In 1987 and 1988 the number of clusters was reduced to 5 on each grid, but 4 boxes were arranged in a spiral around the central box at distances of 1, 4, 8 and 16 m (Fig. V-1; similar to Robertson and Gibbs 1982). I also added extra boxes to area D in 1987 and 1988. Extra boxes were placed 1 m east and 4 m west of the center box at 4 randomly-chosen boxes (spirals were not possible along the

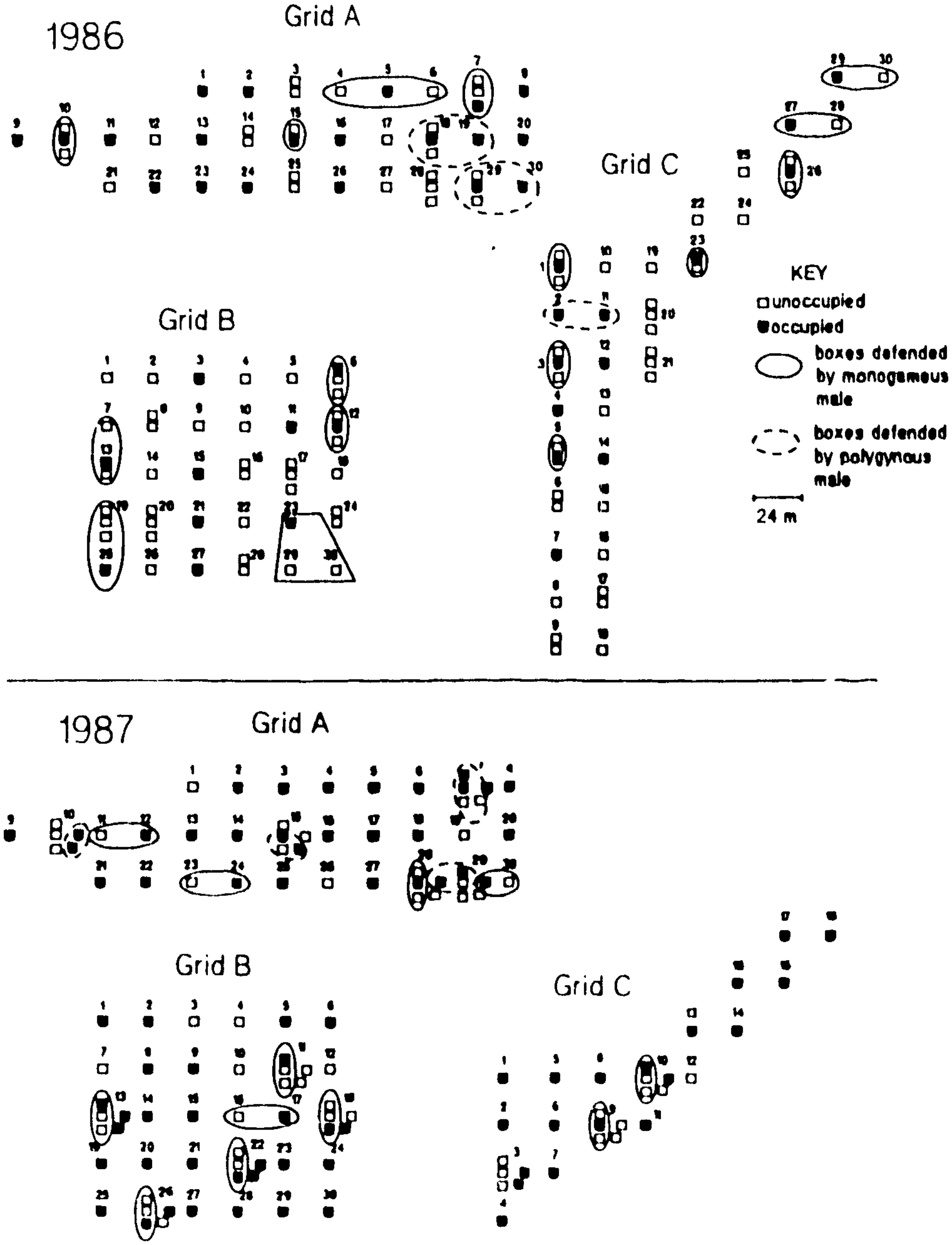


Fig. V-1 Map of tree swallow territories in 1986 and 1987. The number and location of nest-boxes was the same in 1988 as in 1987 (at areas A,B and C). There were no known cases of polygyny in 1988, so those nests are not included fenceline).

RESULTS

Male removal experiment: a test of the cost assumption

I removed males to determine if a randomly-chosen female would incur no cost from choosing polygyny. Males were removed at 16 nests from the lakeshore, 5 nests from the marsh and 25 nests at the road site. The detailed results of this experiment are presented in Chapter III. In summary, I found that fledging success and return rates of both nestlings and adults were similar for unaided and monogamous females (within a habitat). This suggests that secondary females were not incurring a cost from choosing polygyny.

Other assumptions

The polygyny threshold model also assumes that settlement of secondary females is not influenced by site fidelity or female aggression toward potential secondary mates. In tree swallows, female aggression did not limit the settlement of secondary mates because secondary mates settled at about the same time as monogamous females, when already-mated females were most aggressive toward intruders, not afterwards (Chapter IV). Site fidelity could have influenced the settlement of secondary females, but there were not enough data to test for an effect. Of seven known secondary females in 1986 and 1987, only one was a previously banded individual; it bred 38 m from its nest site the previous year. This suggests a high degree of site fidelity by some individuals; however, monogamous females also exhibit high site fidelity. Of 26 females that returned to breed the next year (only birds banded in 1986 or 1987), 18 (69%) returned to the same area and the median dispersal distance from the previously-used nest-box was 129 m (5.4 nest boxes away; range of distances= 0 to 5000 m).

Tests of predictions

There were 7 cases of natural polygyny in 1986 (8%, 3/39) and 1987 (7%, 4/56). Except for one case of polygyny at the marsh in 1986, all cases of polygyny occurred at the lakeshore. Only the number and spacing of nest-boxes differed between territories of monogamous and polygynous males. Other potential differences in territory quality were constant. Nest-boxes were identical with respect to size, height and orientation, and within a given habitat (lakeshore, marsh or roadside), food abundance was similar for all females because most foraging was conducted off the territory and within similar habitats (no color-marked swallows were seen foraging in habitats used by birds in other parts of the study area). If for some other reason particular territories were better than others, then one might also expect polygyny to occur in the same territory from one year to the next. However, there was no obvious pattern from 1986 to 1987 in the location of territories with polygynous males (Fig. V-1).

Only males that defended two or more nest-boxes were able to gain a second mate. However, only 20% (7/35 males) of males that defended at least two boxes gained a secondary mate (Fig. V-1). The spacing of additional boxes also had a significant effect on the mating behavior of males. Among territories with 2 or more boxes, those territories in which the two farthest boxes were over 5 m apart (the maximum distance apart for the 3 closest boxes in a cluster) were more likely to be occupied by polygynous males (38%, 6/16 territories) than territories that had boxes 5 m or less apart (5%, 1/19 territories; G= 5.9, P= 0.015). This suggests that defending an extra box is a necessary condition for achieving polygyny in this population, but it is not sufficient unless the second box is over 5 m from the primary female.

If number of nest-boxes or territory size is a measure of territory quality then female settlement date or fledging success should be correlated with these characteristics of the territory. I examined these relationships using only territories of monogamous males because it is necessary to control for female density when examining reproductive parameters. Among monogamous females, there were no correlations between fledging success or settlement date of females and number of nest-boxes on their mate's territory (Spearman rank correlations= -0.189 and 0.229, respectively, P > 0.10 for both, n=35; 1986 and 1987 data). There were also no correlations between fledging success or settlement date and diameter of the territory (based on the greatest distance between nest-boxes on a territory; Spearman rank correlations= -0.15, 0.26, P > 0.10 for both, n=35). In summary, males with two boxes that were over 5 m apart were more likely to become polygynous, but the spacing and number of boxes were not territory features that females could use as cues to increase their expected reproductive success.

The second prediction of the polygyny threshold model was supported. For successful nests of females that settled during the same time period, fledging success of secondary females at the lake and marsh (5.5±0.6, n=6, includes two SY females) was as high as the fledging success of monogamous females at the road (5.1±0.8, n=7 all ASY females; P= 0.73, t= -0.4; 1986 and 1987 data). Fledging success relative to initial clutch size was examined with ANCOVA to determine if the relationship between expected reproductive success (clutch size) and realized reproductive success (fledging success) was the same for secondary females at the lake and monogamous females at the road. For successful adult females, there was no difference between secondary females at the lake and monogamous females at the road in the slopes of these regression lines (ANCOVA with clutch size as the covariate, P= 0.72, F= 0.13, df= 1, 11). For a given clutch size there was also no difference in fledging success between secondary females at the lake and monogamous females at the road (only 1986 and 1987 data on successful ASY females; ANCOVA, P= 0.23, F= 1.61, df= 1, 12). Therefore, in either absolute or relative terms, concurrently settling secondary females in high quality habitat (lake) produced as many fledglings as monogamous females in poorer habitat (road).

The third prediction of the model was not supported by the tree swallow data. There was no difference between the settlement dates of primary and monogamous females on territories of polygynous and monogamous males, respectively (median date= 7 May for both groups; U= 136, P > 0.20, n= 7 and 31). Data for this comparison were pooled after no difference was found between years in settlement date (P > 0.10).

The fourth prediction of the polygyny threshold model was also rejected. The order of territories settled by primary and secondary females was not correlated positively (Spearman rank correlation = -0.23, P > 0.50, n=7). These results suggest that females are not choosing among territories within the lakeshore and marsh areas.

DISCUSSION

There was little support for the predictions of the polygyny threshold model in this population of tree swallows. Only one of the four predictions was supported and the assumption that polygyny was costly to females was violated. As predicted by the model, secondary females on high-quality territories (lake) produced as many offspring as monogamous females on poorer-quality territories (road). However, similar reproductive success would be expected in any situation where the cost assumption was violated. It appeared that within the lakeshore and marsh areas females were choosing territories randomly. Random settlement was suggested by the settlement patterns of polygynous females, because polygynous territories were not settled first (prediction three) and because territories with polygynous females were not settled in the same order by primary and secondary females (prediction four). Although females do not appear to be choosing particular territories, there is evidence that they are choosing among areas. At the lakeshore site, insect abundance was higher than at the road site, and this may have been the reason for a higher occupancy rate and earlier laying date (Chapter III). A similar pattern of choosing among sites, but settling randomly on particular territories has been reported in marsh wrens (Cistothorus palustris, Leonard and Picman 1988). If the polygyny threshold model, at least as it was originally formulated (Orians 1969), cannot explain polygyny in tree swallows, then what are the alternatives?

The sexy-son hypothesis (Weatherhead and Robertson 1979) has been proposed as a modification of the polygyny threshold model to explain polygyny in situations where secondary females on high-quality territories do not produce as many offspring as monogamous females on poorer-quality territories. The sexy-son hypothesis proposes that the short-term loss of reproductive success incurred by secondary females can be recouped by producing sons that inherit characteristics from their polygynous fathers that increase their chances of becoming polygynous. This is not a possible explanation for polygyny in this population of tree swallows because secondary females did not suffer a reproductive cost. The relative rarity of polygyny in tree swallows also means that secondary females could not recoup any short-term loss of reproductive success by producing sons that are likely to be polygynous (Quinney

1986).

Even if polygyny were not costly to females, they might still prefer mating polygynously with some males because they provide better protection against predators (this protection might be shared by two females on a territory). The results of the male removal experiment in this study (Chapter III) suggested that losing most male protection against predators had no effect on female reproductive success, so it seems unlikely that females are choosing among males that provide varying amounts of protection. Knapton (1988) has suggested that female eastern meadowlarks (Sturnella magna) may choose to mate polygynously with older males that provide better protection against predators. However, in his population polygynously mated females were more successful in breeding than monogamous females and polygyny was quite common (38-56% of males).

Polygyny might also occur if already-mated females are not able to exclude secondary females from settling. This hypothesis assumes that females attempt to exclude secondary females because they reduce the reproductive success of already-mated females (i.e., negative density-dependent effects on reproductive success). Again, this hypothesis could not apply to this study population, because: 1) primary females did not produce fewer offspring than monogamous females (Chapter IV) and 2) it is unlikely that primary females, which receive male aid, would do worse than unaided females which showed no loss of reproductive success. Some studies have suggested that female aggression could limit polygyny (Breiehagan and Slagsvold 1988, Arcese 1989); however, in these species already-mated females probably incur a cost when secondary females settle and breed (Chapter IV). Nevertheless, it is possible that female aggression limits settlement of secondary females as a non-adaptive consequence of aggression to prevent egg-dumping or nest usurpation (see Chapter IV). This assumes that already-mated females cannot distinguish between potential secondary females and females that might engage in egg-dumping or nest usurpation.

There is some evidence from tree swallows to support this hypothesis. First, already-mated females did not incur a cost when a secondary female settled and bred, yet they were aggressive toward intruders. Males, on the other hand, are less aggressive toward female intruders and may attempt to copulate with them (Stutchberry and Robertson 1987, P. Dunn pers. obs.). Second, egg-dumping and nest usurpation occur in tree swallows (Lombardo 1988, Leffelaar and Robertson 1985), and they have the potential to greatly reduce female reproductive success. Lastly, males in this study were more likely to becomo polygynous (5 vs. 38%) if they had two nest-boxes over 5 m apart. This suggests that females are defending an area immediately surrounding their nest-box and that secondary females are generally forced to nest outside this area. Monogamy is probably the most common pairing association in tree swallows because most males (56%, 20/36) do not have extra nest-boxes over 5 m from an occupied box. Male competition for nest-boxes is intense, and it may limit most males to defending one nest-box. However, other constraints must be operating as well, because only 38% of males with an extra box over 5 m away became polygynous One possible constraint is that at any given time the number of potential secondary females in the population may be low relative to the number of unmated males with nest-boxes. Nevertheless, a 38% rate of polygyny is similar to rates found in some populations of other species that are "typically" polygynous (15-31%, Harmenson 1974; 10-20% Pleszcsynska and Hansell 1980; 21-44% Wittenberger 1980; 13% Wootton et al. 1986; 47%, Leonard and Picman 1988).

Quinney (1983, 1986) suggested that polygyny in tree swallows was caused by a combination of limited nest-sites and high food abundance. This study supports that conclusion, but for a different reason. Quinney thought that polygyny was costly to female tree swallows and that they had to be compensated for that cost by breeding in areas of high food abundance. In this study polygyny also occurred in an area of high food abundance, but this was not because females were attempting to reduce the cost of polygyny. Polygyny would not have been costly in either lake or road habitats in this study (Chapter III). However, females could lay larger clutches at the lakeshore because of greater insect abundance during the laying period. insect abundance. Therefore, the best place to breed for a female in this study was the lakeshore, regardless of mate status. If there were greater competition among females for nest-boxes at the lakeshore and only a small number of females had to "choose" between monogamy and polygyny, then one might only find polygyny at the lakeshore (or other high quality habitats such as the marsh).

These results do not mean that the polygyny threshold model is invalid for tree swallows at Quinney's study area or anywhere else. In areas where territory quality is very high and homogeneous, the reproductive success of monogamous and secondary females may be so similar that there is no disadvantage to secondary mate status and females may be unable to distinguish differences in territory quality (it may also not be possible for researchers to find differences). Orians' (1969) graph of the polygyny threshold model shows this region in the upper right of Fig. 1. However, most discussions of the model concern the region where polygyny is costly to females (e.g., Garson et al. 1981; but see Wootton et al. 1986). Several recent studies (Wootton et al. 1986, Leonard and Picman 1988, Lightbody and Weatherhead 1988) found that polygyny occurs randomly in high quality homogeneous areas. Wootton et al. (1986) have modified the polygyny threshold model to emphasize the changes that occur as territory quality increases and the cost of polygyny decreases. It seems likely that Beaverhill Lake is a high-quality homogeneous habitat for tree swallows. Similar conditions may occur at Quinney's study area in Ontario because insect abundance is similar to that at Beaverhill Lake (Table III-8). However, the crucial test is whether or not secondary females incur a cost from polygyny. Quinney (1983, 1986) suggested that secondary females did not incur a cost, but he was not able to determine which female was the secondary (two females laid eggs in one nest and he assumed half of the fledglings were produced by each female). A better test would be to simulate the loss of male parental care experienced by secondary females with a male removal experiment. In other areas where insect abundance is much lower and polygyny appears to be costly (e.g., Leffelaar and Robertson 1986, P. Dunn unpubl. data), secondary females may be choosing relatively higher quality areas to offset the costs of polygyny. An examination of polygyny in various habitats would be an important test of the modified polygyny threshold hypothesis (Wootton et al. 1986).

LITERATURE CITED

ALTMANN, S. A., S. S. WAGNER, & S. LENINGTON. 1977. Two models for the evolution of polygyny. Behav. Ecol. Sociobiol. 2: 397-410.

ARCESE, P. 1989. Intrasexual competition and the mating system in primarily monogamous birds: the case of the song sparrow. Anim. Behav. 38: 96-111.

BREIEHAGAN, T., & T. SLAGSVOLD. 1988. Male polyterritoriality and female-female aggression in pied flycatchers *Ficedula hypoleuca*. Anim. Behav. 36: 604-605.

CAREY, M., & V. NOLAN, JR. 1979. Population dynamics of indigo buntings and the evolution of avian polygyny. Evol. 33: 1180-1192.

DAVIES, N. B., & A. LUNDBERG. 1984. Food distribution and a variable mating system in the dunnock, *Prunella modularis*. J. Anim. Ecol. 53: 895-912.

DESTEVEN, D. 1978. The influence of age on the breeding biology of the tree swallow *Iridoprocne bicolor*. Ibis 120:516-523.

ELIASON, B. C. 1986. Female site fidelity and polygyny in the blackpoll warbler (*Dendroica striata*). Auk 103: 782-790.

EWALD, P. W., & S. ROHWER. 1982. Effects of supplemental feeding on timing of breeding, clutch size and polygyny in red-winged blackbirds, *Agelaius phoeniceus*. J. Anim. Ecol. 51: 429-450.

GARSON, P. J., W. K. PLESZCZYNSKA, & C. H. HOLM. 1981. The "polygyny threshold" model: a reassessment. Can. J. Zool. 59: 902-910.

GOWATY, P. A. 1983. Male parental care and apparent monogamy among eastern bluebirds (*Sialia sialis*). Am. Nat. 121:149-157.

HANNON, S. J. 1984. Factors limiting polygyny in the willow ptarmigan. Anim. Behav. 32:153-161.

HARMESON, J. P. 1974. Breeding ecology of the dickcissel. Auk 91: 348-359.

HOLROYD, G. L. 1975. Nest site availability as a factor limiting population size of swallows. Can. Field Nat. 89:60-64.

KNAPTON, R. W. 1988. Nesting success is higher for polygynously mated females than for monogamously mated females in the eastern meadowlark. Auk 105: 325-329.

LEFFELAAR, D., & R. J. ROBERTSON. 1985. Nest usurpation and female competition for breeding opportunities by tree swallows. Wilson Bull. 97: 221-224.

-----------. 1986. Equality of feeding roles and the maintenance of monogamy in tree swallows. Behav. Ecol. Sociobiol. 18: 199-206.

LEONARD, M. L., & J. PICMAN. 1987. Female settlement in marsh wrens: is it affected by other females? Behav. Ecol. Sociobiol. 21: 135-140.

-----------. 1988. Mate choice by marsh wrens: the influence of male and territory quality. Anim. Behav. 36: 517-528.

LIGHTBODY, J. P., & P. J. WEATHERHEAD. 1988. Female settling pattern and polygyny: tests of a neutral-mate-choice hypothesis. Am. Nat. 132: 20-33.

LOMBARDO, M. P. 1988. Evidence of intraspecific brood parasitism in the tree swallow

Wilson Bull. 100: 126-128.

NORUSIS, M. J. 1986. SPSS/PC+ advanced statistics. Chicago, SPSS Inc.

ORIANS, G. H. 1969. On the evolution of mating systems in birds and mammals. Am. Nat. 103:589-603.

PLESZCSYNSKA, W., & R. I. HANSELL. 1980. Polygyny and decision theory: testing of a model in lark buntings (*Calamospiza melanocorys*). Am. Nat. 116: 821-830.

QUINNEY, T. E. 1983. Tree swallows cross a polygyny threshold. Auk 100:750-754.

-----------. 1986. Polygyny in tree swallows: Response to R. E. Simmons. Auk 103: 442-443.

ROBERTSON, R. J., & L. GIBBS. 1982. Superterritoriality in tree swallows: a re-examination. Condor 84: 313-316.

SEARCY, W. A. 1988. Do female red-winged blackbirds limit their own breeding density? Ecology 69: 85-95.

SOKAL, R. R., & F. J. ROHLF. 1981. Biometry. New York, W. H. Freeman.

STUTCHBERRY, B. J., & R. J. ROBERTSON. 1987. Signalling subordinate and female status: two hypotheses for the adaptive significance of subadult plumage in female tree swallows. Auk 104: 717-723.

VERNER, J. 1964. Evolution of polygamy in the long-billed marsh wren. Evol. 18: 252-261.

VERNER, J., & M. F. WILLSON. 1966. The influence of habitat on mating mating systems of North American passerines. Ecology 47: 143-147.

WEATHERHEAD, P. J., & R. J. ROBERTSON. 1979. Offspring quality and the polygyny threshold: "the sexy son hypothesis". Am. Nat. 113: 201-208.

WITTENBERGER, J. F. 1979. The evolution of mating systems in birds and mammals. Pp. 271-349 in Handbook of behavioral neurobiology, vol. 3, social behavior and communication (P. Marler and J. G. Vandenbergh Eds.). New York, Plenum Press.

-----------. 1980. Vegetation structure, food supply, and polygyny in bobolinks (Dolichonyx oryzivorus). Ecology 61: 140-150.

WITTENBERGER, J. F., & R. L. TILSON. 1980. The evolution of monogamy: hypotheses and evidence. Ann. Rev. Ecol. Syst. 11: 197-232.

WOOTTON, J. T., E. K. BOLLINGER, & C. J. HIBBARD. 1986. Mating systems in homogeneous habitats: the effects of female uncertainty, knowledge costs, and random settlement. Am. Nat. 128: 499-512.

YASUKAWA, K., & W. A. SEARCY. 1986. Simulation models of female choice in red-winged blackbirds. Am. Nat. 128: 307-318.

VI. GENERAL DISCUSSION

Monogamy is associated with relatively high levels of male parental care. However, this relationship does not necessarily indicate what factors maintain monogamy in bird populations. For example, in some species males and females may appear monogamous, but male parental care may not be necessary to reproduce successfully. In this case there may be other constraints on the breeding behavior of males that make it more advantageous to males to stay with their mate than to desert (Maynard Smith 1977). In this chapter I discuss the maintenance of monogamy in two species in which the importance of male parental care to reproductive success varies from a necessity in one species to no apparent effect in the other species.

This study indicated that male parental care was an absolute necessity for successful reproduction in black-billed magpies (Chapter II), but that male parental care had little or no effect on female reproductive success in tree swallows (Chapter III, IV). These results indicate that monogamy in magpies is obligatory, while in tree swallows monogamy is facultative (Murray 1984). Food abundance is thought to influence the importance of male parental care (Emlen and Oring 1977). If true, then food availability may be relatively lower for magpies than for swallows; however there are no comparable data on food availability to test this hypothesis between the two species. Within species, however, there are data from tree swallows that allow a preliminary examination of the food hypothesis. The observed variation in food abundance within my study sites in Alberta did not appear to influence the importance of male parental care. However, insect abundance appears to be much lower in southern Ontario, where Leffelaar and Robertson (1986) studied tree swallows, than at Beaverhill Lake (P. Dunn, unpubl. data). In contrast to swallows at Beaverhill Lake, unaided females in southern Ontario generally failed to raise any offspring (Leffelaar and Robertson 1986, Robertson unpubl. data). These results tend to support the hypothesis that food abundance influences the need for male parental care. In a more detailed comparison, I would predict that polygyny is costly to secondary females in Ontario and that the polygyny threshold model is more likely to be applicable to females there. A comparison of polygyny and food abundance in Ontario and Alberta would be a useful first test of the modified polygyny threshold model (Wootton et al. 1986) because it could indicate the relative importance of habitat quality versus other constraints on male mating behavior.

Bart and Tornes (1989) provided a list of conditions under which male parental care would likely be most and least important to reproductive success. They suggested that the strongest correlate of male value was male assistance with incubation and that feeding the female during incubation was less important (based on male removals in pied flycatchers and snow buntings). This conclusion is similar to the conclusion that I arrived at independently in Chapter II; however, my study of magpies indicates that male parental care can also be very important in species where the male feeds the female during incubation. The difference between my study of magpies and the studies of pied flycatchers and snow buntings may be because male magpies feed their mates to a greater degree. Further male removal studies on species in which the male incubates or feeds the female while she incubates would help resolve this question and increase our knowledge of the overall importance of male parental care to reproductive success (Fig. II-1). For comparative purposes, these studies should also estimate the relative extent of the contribution of males to each breeding activity (e.g., % time spent incubating by males).

Male parental care is likely to be least important to reproductive success when males only guard the nest and feed the young (Bart and Tornes 1989, Fig. II-1). In these situations a variety of factors could favor male parental care and monogamy. Bart and Tornes (1989) present three hypotheses for why males may remain with their mate and provide parental care, but two of these are probably only applicable to species that make two nesting attempts per year. The third hypothesis is that the benefits of male parental care (in terms of reproductive success) are greater than the costs, because assisting the female is relatively cheap for the male, especially during good conditions. This hypothesis may have some application in tree swallows, because, although male parental care does not measurably improve female fledging success (Chapter III), there do not appear to be any better alternatives for males during the nestling period (such a finding another mate), and assisting the female with feeding probably improves the condition of nestlings in larger broods (Chapter III). Nevertheless, in cases where the male has little or no effect on reproductive success there must be other constraints on male behavior, otherwise they should desert their mate after breeding and search for another female. These constraints could include few alternative mating opportunities (as above) and high predation rates such that remaining with one's mate facilitates renesting. These other constraints are the likely reasons why males of some species are monogamous even though male parental care is relatively unimportant.

Intrasexual competition and the maintenance of monogamy

The assumption that polygyny is costly to females is integral to most hypotheses for the maintenance of monogamy (e.g., polygyny threshold and female aggression). Alternative hypotheses have been proposed that assume polygyny is not costly (Wootton et al. 1986, Lightbody and Weatherhead 1987, 1988). These models attempt to explain why polygyny appears to occur randomly with respect to territory quality. "Neutral" models suggest that polygyny will occur randomly if territories are homogeneous (such that females cannot differentiate between higher and lower quality territories) and all territories are high quality (so there is no selection against inability to choose). Although this explanation may be suitable for explaining polygyny, it does not explain why many individuals are monogamous. That is, if all territories in a given area are similarly high in quality, then why is polygyny uncommon? Presumably, random settlement would result in more cases of polygyny and higher numbers of mates per male. In addition, one might expect females from lower quality habitats to attempt to settle on the higher quality areas and further increase the chance of polygyny.

A major factor limiting most males to monogamy may be intrasexual competition for access to resources needed for breeding (McLaren 1972, Murray 1984, Davies and Houston 1986, Lightbody and Weatherhead 1987, Arcese 1989). Competition among males for access to breeding resources could limit the territory size of most males and competition among females for a nest-site or exclusive access to male parental care could limit the settlement of secondary females. Assuming that females require a certain minimum area or a discrete resource for breeding within a male's territory, then males may only become polygynous if their territory is big enough that 1) there are sufficient resources to support a second female and 2) territoriality by the already-mated female does not preclude the use of this "extra" area by a second female (McLaren 1972, Stobo and McLaren 1975 Hannon 1984, Arcese 1989).

Examples of non-breeding subpopulations caused by intrasexual competition for breeding resources (e.g., nest-sites, display sites feeding areas) are common in birds (Brown 19[illegible], Rip[illegible] and Boag 1974, Hannon et al. 1982, Hannon 1983, Stutchberry and Robertson [illegible] [illegible] and Arcese 1989). However, there is little evidence that intrasexual competition maintains monogamy in situations where there are no other apparent constraints. Previous studies that have suggested that intrasexual competition influences mating behavior have also found that polygyny is costly to secondary females (Stobo and McLaren 1975, Askenmo 1984, Davies and Houston 1986, Arcese 1989, Wolf et al. 1989). In these cases it was not known if female choice or intrasexual competition was more important in influencing mating behavior. In the past, when most studies found that polygyny was disadvantageous to secondary females they concluded that monogamy was maintained because a polygyny threshold was rarely exceeded; they did not consider the role of female aggression or male-male competition in limiting the options of either sex. In cases where females do not incur a cost from polygyny, the role of intrasexual competition is not confounded by female choice (females should not be avoiding polygyny if it is not costly). To date, only studies of yellow-headed blackbirds (Lightbody and Weatherhead 1987, 1988), willow ptarmigan (Hannon 1984, Martin and Cooke 1987) and tree swallows (this study) suggest that: 1) polgyyny is not costly and 2) the relative size of male and female territories determines the mating behavior. In these cases, the relative ability of males and females to gain access to breeding resources is the major determinant of the mating system (rather than female choice). As Arcese (1989) recently pointed out, the roles of intrasexual competition and female choice in mating systems can best be understood by first determining if polygyny is costly and then assessing the potential for males and females to defend breeding resources. In cases where polygyny is costly to females, experimental manipulations of male and female competitive ability (Hannon 1984, Wingfield 1984) could allow one to estimate the relative importance of female choice versus intrasexual competition.

LITERATURE CITED

ARCESE, P. 1989. Intrasexual competition and the mating system in primarily monogamous birds: the case of the song sparrow. Anim. Behav. 38: 96-101.

ASKENMO, C. E. H. 1984. Polygyny and nest site selection in the pied flycatcher. Anim. Behav. 32: 972-980.

BART, J., & A. TORNES. 1989. Importance of monogamous male birds in determining reproductive success. Evidence for house wrens and a review of male-removal studies. Behav. Ecol. Sociobiol. 24: 109-116.

BROWN, J. L. 1969. Territorial behavior and population regulation in birds. A review and re-evaluation. Wilson Bull. 81: 293-329.

DAVIES, N. B., & A. I. HOUSTON. 1986. Reproductive success of dunnocks, *Prunella modularis*, in a variable mating system. II. Conflicts of interest among breeding adults. J. Anim. Ecol. 55: 139-154.

EMLEN, S. T., & L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223.

GREENLAW, J. S., & W. POST. 1985. Evolution of monogamy in seaside sparrows, *Ammodramus maritimus*: tests of hypotheses. Anim. Behav. 33:373-383.

HANNON, S. J., L. G. SOPUCK, & F. C. ZWICKEL. 1982. Spring movements of female blue grouse: evidence for socially induced delayed breeding in yearlings. Auk 99: 687-694.

HANNON, S. J. 1984. Factors limiting polygyny in the willow ptarmigan. Anim. Behav. 32:153-161.

LEFFELAAR, D., & R. J. ROBERTSON. 1986. Equality of feeding roles and the maintenance of monogamy in tree swallows. Behav. Ecol. Sociobiol. 18:199-206.

LIGHTBODY, J. P., & P. J. WEATHERHEAD. 1987. Polygyny in the yellow-headed blackbird: female choice versus male competition. Anim. Behav. 35: 1670-1684.

-----------. 1988. Female settling patterns and polygyny: tests of a neutral-mate-choice hypothesis. Am. Nat. 132: 20-33.

MARTIN, K., & F. COOKE. 1987. Bi-parental care in willow ptarmigan: a luxury? Anim. Behav. 35:369-379.

MAYNARD SMITH, J. 1977. Parental investment: a prospective analysis. Anim. Behav. 25: 1-9.

MCLAREN, I. A. 1972. Polygyny as the adaptive function of breeding territory in birds. Trans. Conn. Acad. Arts Sci. 44: 189-210.

MURRAY, B. G. Jr. 1984. A demographic theory on the evolution of mating systems as exemplified by birds. Evol. Biol. 18: 71-140.

RIPPIN, A. B., & D. A. BOAG. 1974. Recruitment to populations of male sharp-tailed grouse. J. Wildl. Manage. 38: 616-621.

SMITH, J. N. M., & P. ARCESE. 1989. How fit are floaters? Consequences of alternative territorial behaviors in a nonmigratory sparrow. Am. Nat. 133: 830-845.

SMITH, J. N. M., Y. T. YOM-TOV, & R. MOSES. 1982. Polygamy, male parental care and sex ratio in song sparrows: an experimental study. Auk 99:555-564.

STOBO, W. T., & I. A. MCLAREN. 1975. The ipswich sparrow. Nova Scotia Inst. Sci. Halifax, N.S.

STUTCHBERRY, B. J., & R. J. ROBERTSON. 1985. Floating populations of female tree swallows. Auk 102: 651-654.

WEATHERHEAD, P. J. 1979. Ecological correlates of monogamy in tundra-breeding savannah sparrows. Auk 96:391-401.

WINGFIELD, J. C. 1984. Androgens and mating systems: testosterone induced polygyny in normally monogamous birds. Auk 101: 665-671.

WOLF, L., E. D. KETTERSON, & V. NOLAN JR. 1988. Paternal influence on growth and survival of dark-eyed junco young: do parental males benefit? Anim. Behav. 36: 1601-1618.

WOOTTON, T. T., E. K. BOLLINGER, & C. J. HIBBARD. 1986. Mating systems in homogeneous habitats: the effects of female uncertainty, knowledgo costs, and random settlement. Am. Nat. 128: 499-512.