The Role of Parental Care in the Evolution and Maintenance of Monogamy in the Barn Swallow Hirundo rustica

Patricia Dawn Goley
B.S. (Hons.), University of North Carolina at Wilmington, 1983

A THESIS SUBMITTED IN PARTIAL FULFILLMENT

OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in the Department

of

Biology

ACCEPTED
FACULTY OF GRADUATE STUDIE
[redacted]
DEAN
DATE May 18, 1987

We accept this thesis as conforming to the required standard

[redacted]

Edward H. Miller, Ph.D.

[redacted]

Geraldine Allen, Ph.D.

[redacted]

Patrick Gregory, Ph.D.

[redacted]

Paul Baker, Ph.D.

[redacted]

William Munro, M.Sc.

UNIVERSITY OF VICTORIA

December 1986

DEDICATION

To my Grandparents ... for opening my eyes to the beauty and wonder of the world

To my Parents ... for constant support and encouragement in all of my endeavors

Supervisor: Edward H. Miller, Ph.D.

ABSTRACT

Breeding biology and parental care of the Barn Swallow (Hirundo rustica) were studied in order to assess the role of parental care in the maintenance and evolution of monogamy in this species. Data were analysed from a long-term study of Barn Swallow breeding biology carried out between 1975 and 1984 on the Qualicum National Wildlife Area, Qualicum Beach, British Columbia. Information from this study included time of arrival, clutch initiation dates, clutch size, brood size and number of fledglings for first and second broods. A detailed examination of parental behaviour of five pairs of Barn Swallows was carried out from 15 April to 1 September 1984.

Double-brooded, (and presumably older, mated) pairs initiated first clutches sooner, had a higher hatching and fledging success than single-brooded pairs, and fledged an average of 6.2 young per season compared to 2.2 for single-brooded birds. The advantages of monogamy in Barn Swallows may be reflected in the increased reproductive success of double-brooded birds, and in the overall high reproductive success of the species.

Males and females participated equally in nest-building and feeding nestlings, although females incubated and brooded more than males. Equal participation in nest-building activities may maintain or establish pair bonds, or may protect the male from cuckoldry. Biparental participation in feeding the nestlings is common

in altricial birds, and maximizes reproductive success by increasing the amount of food delivered to the young. Unequal parental participation in incubation and brooding may reflect the protected nature of the nesting situation. Equal participation during nest-building and feeding the nestlings may help maintain monogamy in this specis.

Most features of Barn Swallow breeding biology and social system structure have evolved in relation to their mode of feeding. Barn Swallows are able to nest in protected sites and have an overall high reproductive success. The nature of their food resource precludes territoriality and makes monopolization of the mate very difficult. This may be an underlying reason for the low level of polygamy in swallow species. Barn Swallows migrate long distances in order to feed where insects are abundant, which may lead to high adult mortality. The strength of the monogamous bond that is established or maintained during the nest building period and the efficient interactions of pair members throughout the rest of the breeding cycle allow individuals to maximize their reproductive success.

Examiners:

[redacted]
Edward H. Miller, Ph.D.

[redacted]
Geraldine Allen, Ph.D.

[redacted]
Patrick Gregory, Ph.D.

[redacted]
Paul Baker, Ph.D.

[redacted]
William Munro, M.Sc.

CONTENTS

TABLES

FIGURES

ACKNOWLEDGEMENTS

I thank my supervisor, Edward Miller for his support. I am grateful to the members of my committee, Gerry Allen, Pat Gregory, Paul Baker, and Bill Munro, for their comments and advice on the manuscript. Gerry Allen provided constructive critism and enthusiastic support throughout each stage of my Master's programme, and to her I am indebted.

I am very grateful to Neil Dawe for allowing access to the Qualicum National Wildlife Area and for his support and suggestions throughout the study. Without his help this study would not have been possible. I also wish to thank Megan Stone and Tom Broadley for invaluable field assistance.

I wish to express sincere thanks to Karen Dawe, Dan Farr, Guillermo Giannico, Karl Larsen, Jo Ann Lawrence, Mary Potyrella, and Gill Saxby for their stimulating conversations and encouragement. I am also grateful to Mike Keating and Laura Proctor for assistance with the computer.

Special thanks are extended to Brent Bisgrove, Neil Dawe, and Vilis Nams for commenting on various drafts of this thesis.

INTRODUCTION

The evolution of avian mating systems has received much attention (reviewed by Orians 1969, Wilson 1975, Emlen and Oring 1977, Wittenberger 1979, Oring 1982, Mock 1983). The majority of this research has focused on the evolution of polygyny (Verner 1964; Verner and Willson 1966; Carey and Nolan 1975; Pleszczynska 1978; Wiley 1974; Wittenberger 1976, 1979; Patterson et al. 1980; Altmann et al. 1979), and polyandry (Jenni 1974; Jenni and Collier 1972; Graul et al. 1977; Oring and Maxson 1978; Faaborg and Patterson 1980), although polygamous mating systems are present in less than 10% of all avian species (Lack 1968).

Mating systems have been defined by the genetic contribution to the offspring (Ralls 1977), by the ability to monopolize mates or resources (Emlen and Oring 1977), and by the nature of the pair bond between two individuals (Lack 1986). It is difficult, however, to group mating systems into discrete classes, since they form a continuum. In this context mating systems will be defined following Lack (1968) and Wittenberger and Tilson (1980). Polygyny and polyandry are the two basic forms of polygamy. In polygynous mating systems, a male forms pair bonds simultaneously or sequentially with more than one female, and in polyandrous systems, a female forms pair bonds simultaneously or sequentially with more than one male. Monogamous mating systems are characterized by an essentially exclusive pair bond between one male and one female. No definite pair bond is formed in promiscuous species; the two sexes meet solely for copulation, one male normally copulating with several females and one female probably copulating with several males. In polygynous and promiscuous species the female normally raises the brood unaided, whereas in polyandrous species the male does so. Monogamous systems normally have biparental care (Wittenberger and Tilson 1980).

The ways in which individuals of each sex maximize their reproductive success have shaped the evolution of mating systems. Each individual gains from having as many offspring as possible, but the best method to achieve this is not necessarily the same for both sexes (Trivers 1972). In most birds, females can be assumed to have a greater parental investment than males by the time the clutch is completed, because of the energetic costs of egg production in relation to sperm production (Trivers 1972). Female reproductive success is generally maximized by securing male parental care by mating polyandrously or monogamously (Davies, 1985). However, if one adult can successfully perform all postlaying parental duties, the female would be expected to be subject to desertion by the male. Given this, desertion is favoured if deserting males have a high probability of obtaining additional mates and thereby fathering more young than nondeserting males. In these conditions, male reproductive success is maximized by mating polygynously (Davies 1985). If the previous investment of the male would be wasted by inadequate effort or desertion, the male would not be expected to desert. However, even in monogamous systems males often seek extra-pair copulations to increase their reproductive success (Gladstone 1979, McKinney et al. 1984). Hence, there is a conflict of interest between the sexes.

Different mating systems represent the different outcomes of sexual conflict, with females benefiting most from polyandry and males benefiting most from polygyny. Monogamy and promiscuity may represent the mating combinations in which neither sex is able to gain an advantage in relation to the other. Life-history and behavioural parameters such as feeding habits, breeding success, nesting chronology, parental care patterns and ecological factors such as the abundance and distribution of resources and mates, predation pressures and the operational sex ratio set the evolutionary framework and the context in which the conflict is resolved.

The polygyny-threshold model (Verner 1964; Verner and Willson 1966; Orians 1969) suggests that polygyny should evolve when the differences in quality of male territories is great enough that the female can be more successful mating with already mated males in optimal habitat than with unmated males in poor habitats, despite the prospect of losing some or all of the male's assistance in provisioning her young. This model has been extended to explain the evolution of polyandry (Gowaty 1981). It is suggested that in poor-quality habitats it benefits a second male (beta male) to settle with an already mated female rather than an unpaired one because three adults (two males and a female) can rear proportionately more young than two when resources are scarce. The costs of shared paternity are more than offset by the better chick production of cooperative polyandry compared with monogamy (Davies 1985).

Emlen and Oring (1977) have presented a mating-system model defined in terms of resource monopolization. The fundamental difference between this and the polygyny-threshold model is the inclusion of potential mates as a resource equal in importance to habitat quality. The environmental potential for polygamy (EPP) depends on the degree to which multiple mates, or resources to attract multiple mates, are economically defendable.

In polygamous systems, a major component of an individual's ability to defend mates and resources is emancipation from parental care. Conversely, Lack (1968) suggests that the necessity of biparental care has resulted in the evolution of monogamy. The importance of biparental care is maximized by several factors, all of which may interact. Among these are the requirement for continuous attendance of eggs or young due to extremes of cold, heat or predation, and the nutritional demands of the young (Oring, 1982).

Since a mate's contribution to parental care in monogamous systems is important to reproductive success, the effect of deterioration of condition of the mate is substantial (Oring 1982). The cost of current reproductive effort may be offset by behaviour that enhances a mate's well-being (provisioning on the nest). The importance of mate condition to future success has been documented in some long-lived species with perennial pair bonds and in those species in which it is common for pairs to reunite year after year (Coulson 1966, Black-legged Kittiwake; Brooke 1978, Manx Shearwater; Finney and Cooke 1978, Snow Goose; Nelson 1966, Northern Gannet; DeSteven 1978, Tree Swallow). In these studies reproductive success generally increases with age and experience.

Oring (1982) attributes the prevalence of monogamy among birds to the inability of most species to take advantage of an environmental polygamy potential. As considerable parental care by both parents is often required for successful rearing of young, losses to an individual parent accrued by withholding care from one set of offspring while courting and mating with additional mates may be greater than the gains resulting from such behaviour.

Other factors that could affect the evolution of monogamy include: low environmental potential for polygyny, male defence of female, and aggression by mated females that prevents males from acquiring additional mates. Males may also reject second mates because polygyny lowers male reproductive success (Wittenberger and Tilson 1980).

Recent work on the evolution of monogamy has focused on male-removal experiments to test the effect of a skewed operational sex ratio and uniparental care on a monogamous system (Weatherhead 1979; Smith et al. 1982; Gowaty 1983; Hannon 1984; Post and Greenlaw 1982; and Greenlaw and Post 1985). Female Eastern Bluebirds (Gowaty 1983) and Willow Ptarmigan (Hannon 1984) raised young equally well with or without male assistance. In Song Sparrows (Smith et al. 1982), Savannah Sparrows (Weatherhead 1979), Bobolinks (Wittenberger 1982), and Seaside Sparrows (Post and Greenlaw 1982), unaided females raised fewer young than did females with male aid. These studies suggest that male care is not essential to the ability of the female of some species to raise some young, although it may be essential to maximize reproductive success.

The effects of uniparental care may be more complex than a reduction in female seasonal reproductive success. In monogamous birds, reproductive success is a consequence of the behavioural interaction of a male and female parent. To remove the male may affect not only the seasonal reproductive success but may also affect offspring growth, post-fledging success, future reproductive success of the young (Greenlaw and Post 1985; Smith et al. 1982), survival of the female

(Hannon 1984) and the lifetime reproductive success of the female. This is because the reproductive role of the male in many of these species consists not only of direct parental care (incubating, feeding the young) but also of indirect parental care (defence of territory from other males) which may involve considerable risk and expenditure of time and energy (Howe 1979). The effect of male parental care on female reproductive success could be more studied more usefully in a non-territorial monogamous bird. Understanding the parental care patterns of males and females in such a species should lead to a clearer understanding of the importance of male parental care.

The Barn Swallow, Hirundo rustica, is a monogamous, non-territorial species and its life history has been studied extensively throughout most of its range (Samuel 1969; Snapp 1973; McGinn and Clark 1978). It is a relatively short-lived aerial insectivore and nests either singly or in small colonies (Bent 1942). Two broods per year are common for older birds and individuals generally retain the same mate in successive years. Females and males share in all phases of the breeding cycle, although the female incubates and broods more than the male (Bent, 1942). Barn Swallows generally build mud nests in barns although some natural nesting sites such as caves and hollows in cliffs still exist (Speich et al. 1986). They are amenable to study as they can be approached with little disturbance of their behaviour.

This study analyses breeding biology and parental care in Barn Swallows in order to assess the role of parental care patterns in the evolution of monogamy in this species.

METHODS AND MATERIALS

Barn Swallows (Hirundo rustica) were observed from 15 April to 1 September 1984 at Qualicum Beach, on the Qualicum National Wildlife Area (QNWA) on Vancouver Island, British Columbia, Canada. QNWA consists of 125 acres of mixed forest and farmland adjacent to an estuary. Two open livestock sheds, a barn and the eaves of a log cabin on the area were sites for five nests during the 1984 breeding season. Those sites were monitored periodically following the spring arrival of swallows and the dates of breeding events were recorded. Data on clutch size, brood size, and number of fledglings in each nest were collected for first and second broods.

Eggs that failed to hatch were dissected to determine cause of failure. If no embryo was present eggs were considered to be infertile. Some eggs were preyed upon by Deer Mice (Peromyscus maniculatus). as indicated by droppings found in the nest area along with broken egg shells. A small amount of egg loss resulted from handling during inspection by the investigator. In those cases where eggs were missing and signs of predation were not apparent the cause of mortality was listed as unknown.

Nestlings were weighed daily between 0800 and 0900 hours to the nearest 0.1 gram on a triple-beam balance. Nestlings were marked daily with a permanent black marker on the inner or outer portion of the leg. A unique combination of markings was used to identify individual nestlings. When they were seven days old nestlings were banded with U.S. Fish and Wildlife Service aluminum bands. To avoid premature fledging, chicks older than 15 days were not handled (Samuel 1969).

Two species of blowfly parasitized the nestlings, *Protocalliphora hirudo* and an undescribed *Protocalliphora sp*. *Protocalliphora hirudo* larvae fed on the blood of the nestling subcutaneously. Evidence for internal parasitization was the presence of larvae under or emerging from the skin. Larvae of the undescribed *Protocalliphora* fed externally on the blood of the nestling and were detected during weighing attached to it. Evidence of parasitization was also gained from subsequent examination of the nest for *Protocalliphora* pupal cases. In parasitized nests, only those behavioural observations made when all chicks were alive were used.

Data on breeding biology from 1975 to 1983 were made available by Neil K. Dawe (Canadian Wildlife Service, Qualicum Beach). Measurements and observations as described above were taken by Dawe except that nestlings generally were weighed every two or three days during the first 15 days of life. Unless otherwise noted, breeding biology statistics are the grand mean by year (n=10).

Capture Methods

After nest building was complete adult birds were captured with mist nets that were placed at an entrance to the nesting area. Captured birds were banded with U.S. Fish and Wildlife Service aluminum bands and were sexed (Samuel 1971b). Body weight, chord length and outer rectrix length were recorded. The forehead and one outer rectrix of one individual of each breeding pair was marked with a spot of white enamel paint to aid in individual identification at the nest site.

Behavioural Observation Techniques

Parental behaviour was observed from blinds located behind a natural partition in the nesting area. Behaviours were observed with the unaided eye or with the use of 7 x 35 binoculars. At two nests that were difficult to observe directly, a video camera was positioned two m from the nest and connected to a monitor in the blind. Late-night observations were made with the aid of a 60-watt red light bulb placed 1 to 2 m from the nest. The light was left on for 24 hours a day to accustom the birds to its presence.

Observation Schedule

To sample behaviour during the daily cycle, six four-hour time blocks were used beginning at 0400 hrs. Observations were generally made for two hours of each four-hour period. An attempt was made to sample one entire daily cycle for each pair during each of the six stages of the breeding cycle:

Incubation

The incubation period began with the laying of the last egg and ended with the hatching of the first chick.

1. Early Incubation- first five days of the incubation period
2. Middle Incubation- second five days of the incubation period
3. Late Incubation- last five days of the incubation period or until chicks hatch

Nestling

The nestling period began with the hatching of the last chick and ends with the fledging of the first young.

4. Early Nestling- first seven days of the nestling period
5. Middle Nestling- second seven days of the nestling period
6. Late Nestling- last seven days of the nestling period or until first chick fledged.

A total of 320.4 hours of observation was recorded (Tables 1 and 2).

Table 1: The number of pairs observed and the total amount of observation time for each stage of the breeding cycle.

Breeding Stage	Number of Pairs Observed	Number of Observation Hours
Early Incubation	4	28.8
Middle Incubation	5	52.6
Late Incubation	5	66.8
Early Nestling	5	58.2
Middle Nestling	4	48.0
Late Nestling	2	66.0
Total	-	320.4

Table 2: The number of pairs observed and the total amount of observation time for each period of the daily period.

Period of Day	Number of Pairs Observed	Number of Observation Hours
1. 0400 - 0800	5	54.5
2. 0800 - 1200	5	74.3
3. 1200 - 1600	5	76.7
4. 1600 - 2000	5	77.3
5. 2000 - 2400	5	29.3
6. 2400 - 0400	2	8.3
Total	-	320.4

Behaviour

The behaviour of a pair was recorded continuously throughout a sample period. For both male and female each change in behaviour was recorded together with the starting time, and the distance of the bird from the nest and mate. The starting time was recorded with a manually operated stopwatch to the nearest second. Durations of different kinds of behaviour included those which were interrupted in minor ways, so some durations were for behavioural bouts. Data were collected for each of the following behavioural categories:

1. Attendance -- (ATT) when bird was in nesting area

2. Incubation -- (INC) period from when bird entered nest cup and settled on eggs to when it was off nest for more than 10 seconds. Three categories of incubation behaviour were recognized:

   incubate still -- (INCS) bird was settled in nest cup, eyes open or closed.

   incubate preen -- (INCP) any feather adjustment with the bill while on nest. Preening was generally done while still settled in nest cup.

   incubate move -- (INCM) any non-preening movement including: standing up in nest and placing bill in nest, standing up in nest and changing position, or adjusting nesting material with bill. INCM may function as direct parental care to the eggs or personal maintenance of the adult.

3. Perch -- (P) bird was perched while in attendance. Two categories of perching behaviour were recognized:

   perch still -- (PS) perched in nesting area, eyes open or closed.

perch preen -- (PP) any feather adjustment or maintenance behaviour while bird was perching.

4. Brood -- (BRO) period from when adult entered nest cup and covered nestlings to when adult was off nest for more than 10 seconds. Three categories of brooding behaviour were recognized:

brood still -- (BROS) adult settled over nestlings, eyes open or closed.

brood preen -- (BROP) any feather adjustment with bill while on nest.

brood move -- (BROM) any non-preening movement including: standing up in nest and placing bill in nest, standing up in nest and changing direction, and adjusting nest material with bill. While adult was brooding, nestlings moved beneath it, making reason for parental movements difficult to determine.

5. Feed -- (FEED) placing food into a nestling's mouth.

6. Locomotion -- (LCM) any flying movement in the nesting area. Three categories of locomotion were recognized:

Fly in -- (FI) bird flew into nest area either silently or vocalizing, with or without food.

Fly while in nesting area -- (FWIN) bird flew from one perch to another

Fly out -- (FO) bird flew out of nest area either silently or vocalizing, with or without fecal material

In subsequent analysis only ATT, INC, P, BRO, FEED, and their corresponding categories will be considered. Locomotion to and from the nest site was not considered because its duration in the nest-site vicinity was less than one second and its frequency corresponded directly to attendance bouts.

Statistical Analysis

The sample size within each behavioural category was the total number of adult swallows of each sex. The percentage of time spent in each behaviour for each bird was computed relative to total Attendance during an observation period. The frequency of occurrence of each behaviour was also calculated relative to Attendance time.

One-way analysis of variance (ANOVA) was used to analyze variation within each sex over the daily period or breeding cycle. T-tests were used to test for differences between sexes. Percentage and frequency data were analysed parametrically using ANOVAs and t-tests. Behavioural durations and other data that were non-normal were analyzed with corresponding non-parametric analyses (Wilcoxon sign-ranked tests and Mann-Whitney U tests). All mean values are reported with the standard error. Probabilities of 0.05 or less were considered significant. Because of the small sample size, results of both parametric and non-parametric tests are conservative tests. Data were analyzed using the Statistical Analysis System (SAS, SAS Institute Inc., 1985).

RESULTS - BREEDING BIOLOGY

Data collected by Neil K. Dawe (1975-1983), and those collected during the present study (1984) are pooled in reporting the results in this section.

Nesting Chronology

From 1975 to 1984 Barn Swallows first arrived at QNWA in mid to late April with a mean first arrival date of 20 April (Table 3). During this period 135 nests were observed on the area, including 85 first and 50 second clutches. The durations of the breeding stages for first and second broods of Barn Swallows are listed in Table 4.

Nest Building

Barn Swallow nests consist of a mud cup lined with grass and then feathers. Mud for the nests was gathered at the estuary 200 m away from the nesting area. Nest building occurred in the early morning and was carried out by both members of a pair. This period averaged 10.7 days.

Egg Laying

A single egg was laid in the early morning on successive days; thus the number of days in the egg-laying period was equal to the clutch size.

The egg-laying season began in late April and extended into early August with peaks in late May and mid July (Figure 1). Most eggs of first clutches were laid by early June (mean initiation date was 30 May). Second clutches were generally laid by mid July (mean initiation date was 10 July; Table 3). Double-brooded pairs initiated first clutches earlier than single-brooded pairs ($p=.0083$, t-test). An average of 8.5 first clutches and 5.2 second clutches were laid per year at QNWA. The interval from the laying of the first egg of the first clutch to that of the first egg of the second clutch of successful nests was 51.3 days (±0.7days) for 25 nests. Successful nests were considered to be those from which at least one young fledged.

Incubation

Sporadic incubation began after the first egg was laid, but constant incubation was not observed until the clutch was complete. Males and females shared in the incubation duties throughout the day and the female incubated throughout the night. In 42 nests the mean incubation period was 14.6 days.

Table 3: Data on Barn Swallow breeding biology on QNWA from 1975 - 1984. Each entry is mean (s.e.) (n=10).

	First Clutch	Second Clutch	Total
Clutch Size	4.5(0.2)	4.1(0.04)	4.3(0.1)
Number of Eggs to Hatch Per Nest	4.1(0.3)	3.9(0.1)	3.9(0.2)
% of Eggs to Hatch Per Nest	86.6(5.5)	95.1(2.5)	88.8(4.4)
Number of Fledglings Per Nest	2.5(0.3)	3.4(0.2)	2.7(0.3)
% of Eggs to Fledge Per Nest	51.7(7.5)	83.9(3.6)	60.6(5.9)
% of Nestlings to Fledge Per Nest	61.2(6.9)	87.9(3.4)	69.0(5.6)
Date of First Arrival	- -	- -	20 Apr(1.0)
Date of Clutch Initiation	30 May (2.0)	10 July (2.0)	- -

Table 4: Duration (in days) of breeding stages of Barn Swallows (1975 - 1984).

Breeding Stage	Mean(se)	Range	Number of Pairs
Nest Building	10.7 (0.9)	5 - 23	26
Egg Laying	4.3 (0.1)	1 - 6	135
Incubation	14.6 (0.2)	13 - 17	42
Nestling	19.5 (0.5)	14 - 25	12

Nestling

Nestlings were brooded during the day by both the male and the female with the female brooding throughout the night. Nestlings were fed by both parents. In 12 nests the mean nestling period was 19.5 days.

Clutch Size and Hatching Success

First clutches were significantly larger than second clutches (p=.0325; t-test) with five eggs the most common first clutch size, and four eggs the most common second clutch size. Size of first clutches ranged from one to six, whereas second clutches ranged from three to five eggs (Figure 2, Table 3).

Overall, 3.9 eggs per nest hatched; differences between sizes of first and second clutchs were not significant. In 13% of first nests all eggs failed to hatch, whereas in all second nests at least one egg hatched (Figure 3). The percentage of eggs that hatched per nest was slightly lower in first clutches than in second clutches, but the difference was not significant. All nests were included in the analysis. In most nests over 80% of the eggs hatched (Figure 3 a).

Figure 1: Frequency distribution of initiation dates of first and second clutches, 1975-1984.

Shaded portions refer to first cluch and unshaded portions refer to second clutch.

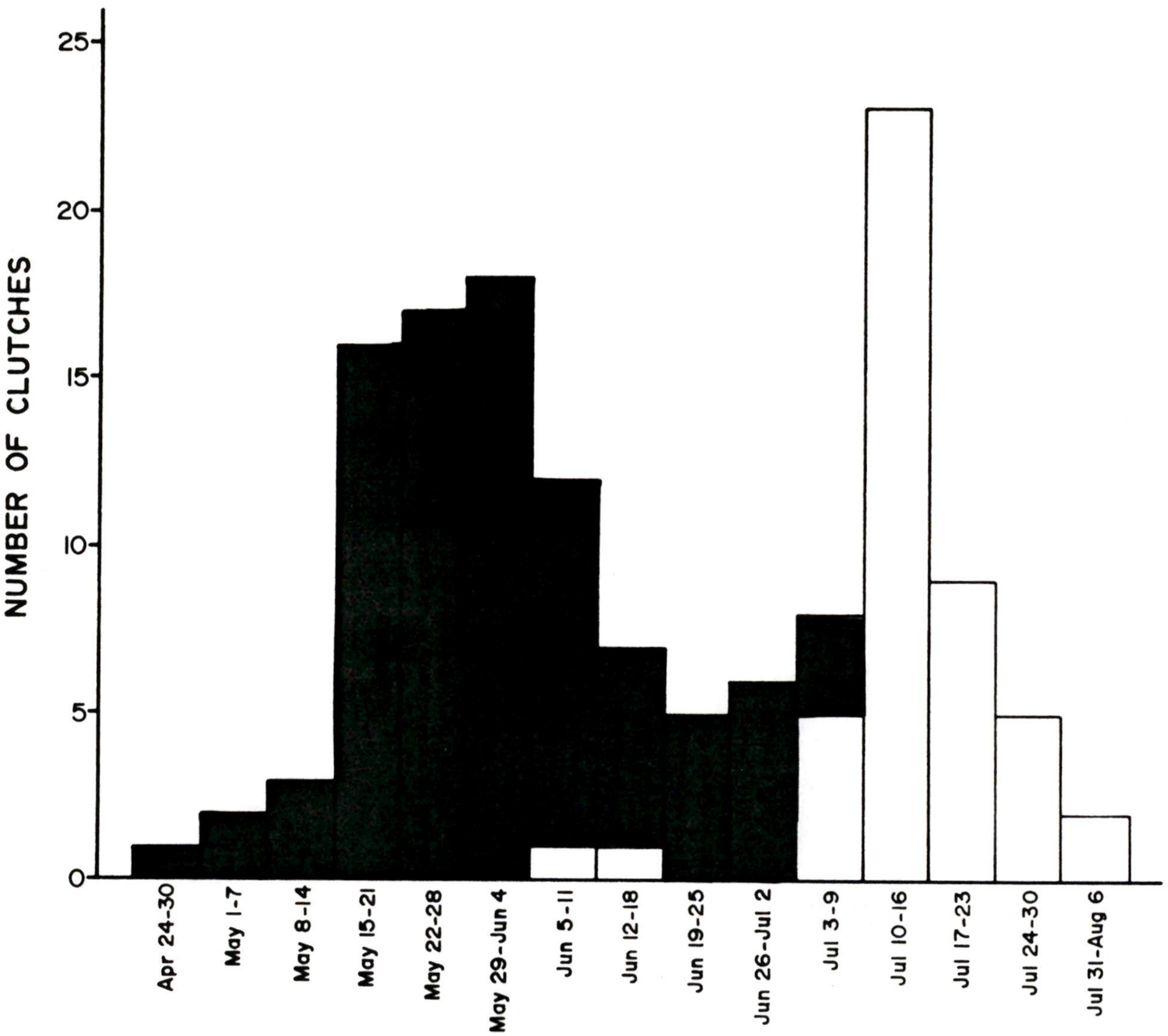

NUMBER OF CLUTCHES
0
5
10
15
20
25
Apr 24-30
May 1-7
May 8-14
May 15-21
May 22-28
May 29-Jun 4
Jun 5-11
Jun 12-18
Jun 19-25
Jun 26-Jul 2
Jul 3-9
Jul 10-16
Jul 17-23
Jul 24-30
Jul 31-Aug 6

Figure 2: Frequency distributions of (A) clutch size, (B) brood size, and (C) number of fledglings per nest, 1975-1984.

Shaded portions refer to first clutch and unshaded portions refer to second clutches. ▽ = no individuals

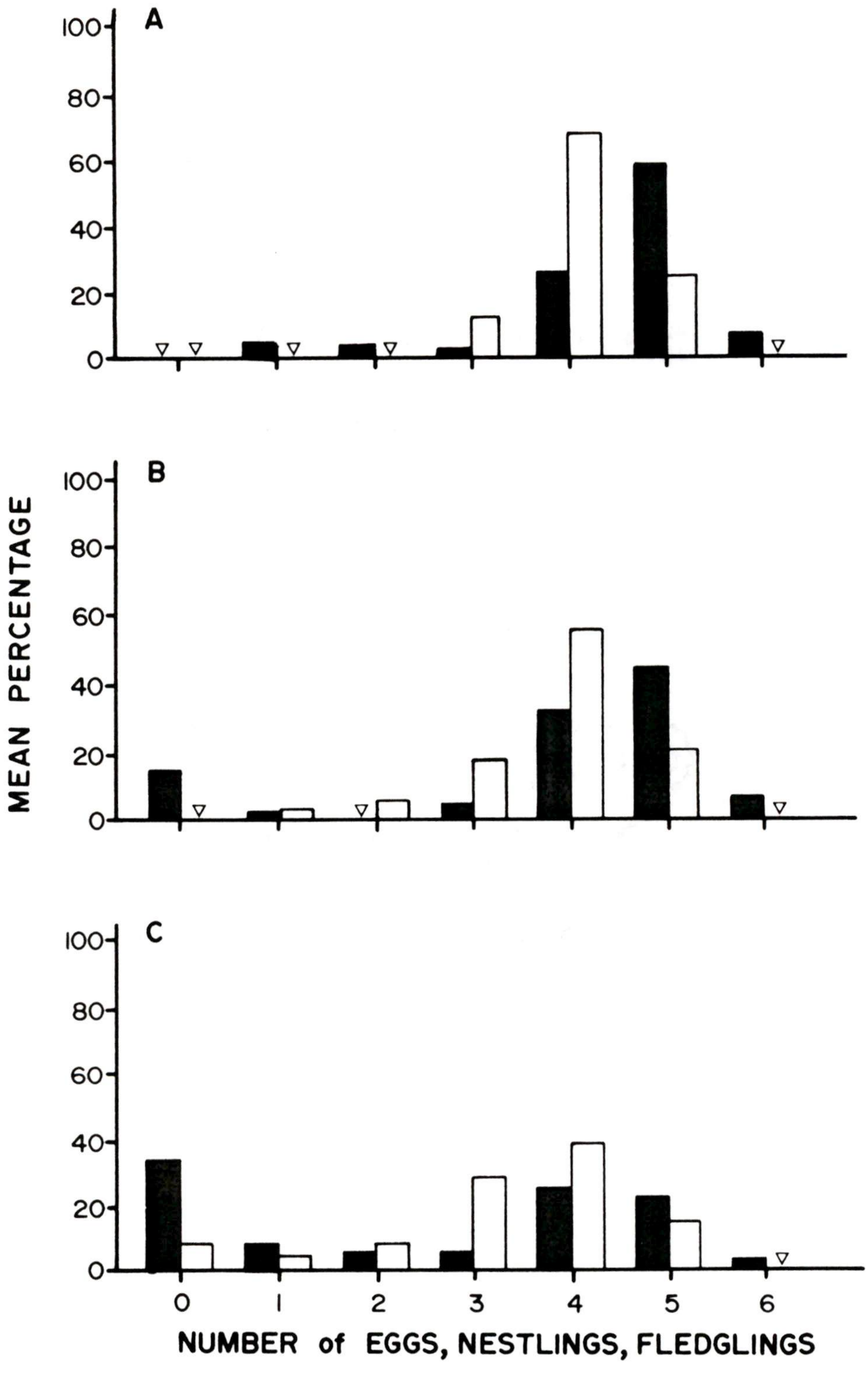
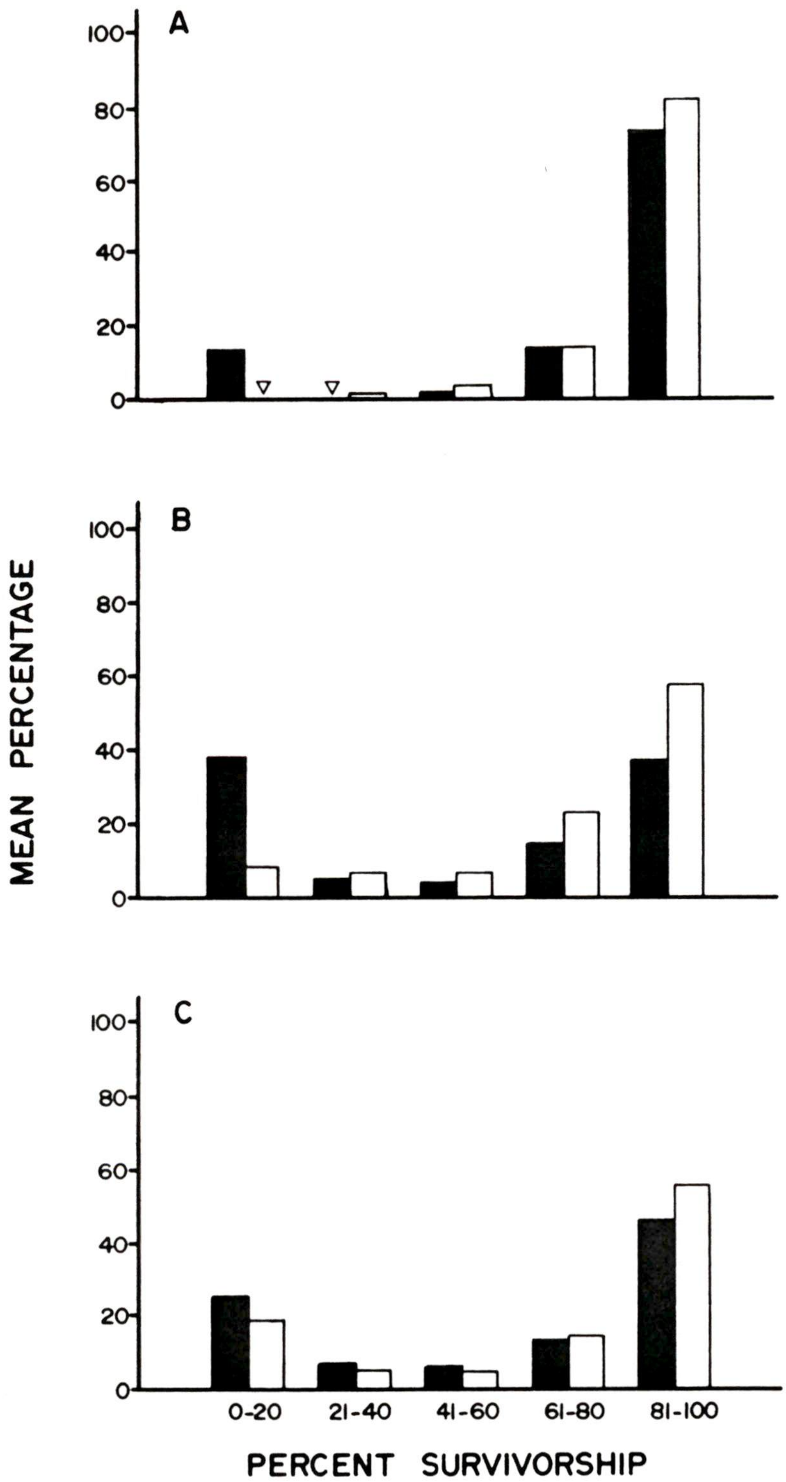

A
B
C
100
80
60
40
20
0
MEAN PERCENTAGE
0
1
2
3
4
5
6
NUMBER of EGGS, NESTLINGS, FLEDGLINGS

Figure 3: Frequency distribution of survivorship for (A) eggs to hatch, (B) eggs to fledge, and (C) nestlings to fledge, 1975-1984.

Shaded portions refer to first clutch and unshaded portions refer to second clutches. ∇ = no individuals


A
B
C
100
80
60
40
20
0
MEAN PERCENTAGE
0-20
21-40
41-60
61-80
81-100
PERCENT SURVIVORSHIP

Nestling Success

First nests had fewer fledglings per nest ($p=.0297$; t-test) and a lower fledging success ($p=.0011$; t-test) than second nests. An average of 2.5 chicks per first nest fledged, with an average success rate of 51.0% of eggs to fledge (61.2% of nestlings to fledge). Thirty-five percent of first nests but only 10% of second nests failed to fledge any chicks. An average of 3.4 chicks fledged per second nest with an average success rate of 82.8%. The overall average number of chicks that fledged per nest per year was 2.68 with 61.2% of eggs fledged (69.0% of nestlings to fledge, Table 3; Figures 2c, 3b, 3c). The number of fledged young produced per year was higher for double-brooded birds (mean 6.2) than for single-brooded birds (mean 2.2; $p=.0001$, t-test).

Causes of Mortality

Of 377 first-clutch eggs laid, 333 hatched (88.3%). Leading causes of failure were predation and infertility (Table 5). In two instances nests were abandoned. Of 208 eggs laid in second clutches, 196 hatched (94.2%). The leading cause of failure in second clutches was infertility and no eggs were lost due to predation or abandonment (Table 5).

Of 333 nestlings in first clutches, 212 fledged (63.7%). Of 196 nestlings in second clutches, 165 fledged (84.2%). The leading cause of mortality in both first and second clutches was *Protocalliphora* infestation (21.9%, Table 6). Of the nestlings studied in 1984, five out of nine nestlings infested with *Protocalliphora*

Table 5: Causes of failure of eggs to hatch 1975 - 1984. Entries are percentage of all eggs and (n).

Causes of Failure to Hatch	First Brood	Second Brood	All Broods
Infertile	3.2 (12)	4.3 (9)	3.6 (21)
Predation	3.7 (14)	0.0 (0)	2.4 (14)
Abandoned	0.5 (2)	0.0 (0)	0.4 (2)
Human	0.0 (0)	0.5 (1)	0.2 (1)
Unknown	4.2 (16)	1.0 (2)	3.1 (18)

Table 6: Causes of failure of chicks to fledge 1975 - 1984. Entries are percentage of all chicks and (n).

Causes of Failure to Fledge	First Brood	Second Brood	All Broods
Protocalliphora sp.	26.7 (89)	10.2 (20)	20.6 (109)
Predation	5.1 (17)	0.0 (0)	8.7 (17)
Adults Killed	1.2 (4)	0.0 (0)	0.8 (4)
Unknown	3.3 (11)	5.6 (11)	4.2 (22)

hirudo failed to fledge, whereas 10 out of 10 nestlings infested with the undescribed *Protocalliphora* failed to fledge.

Chick Growth

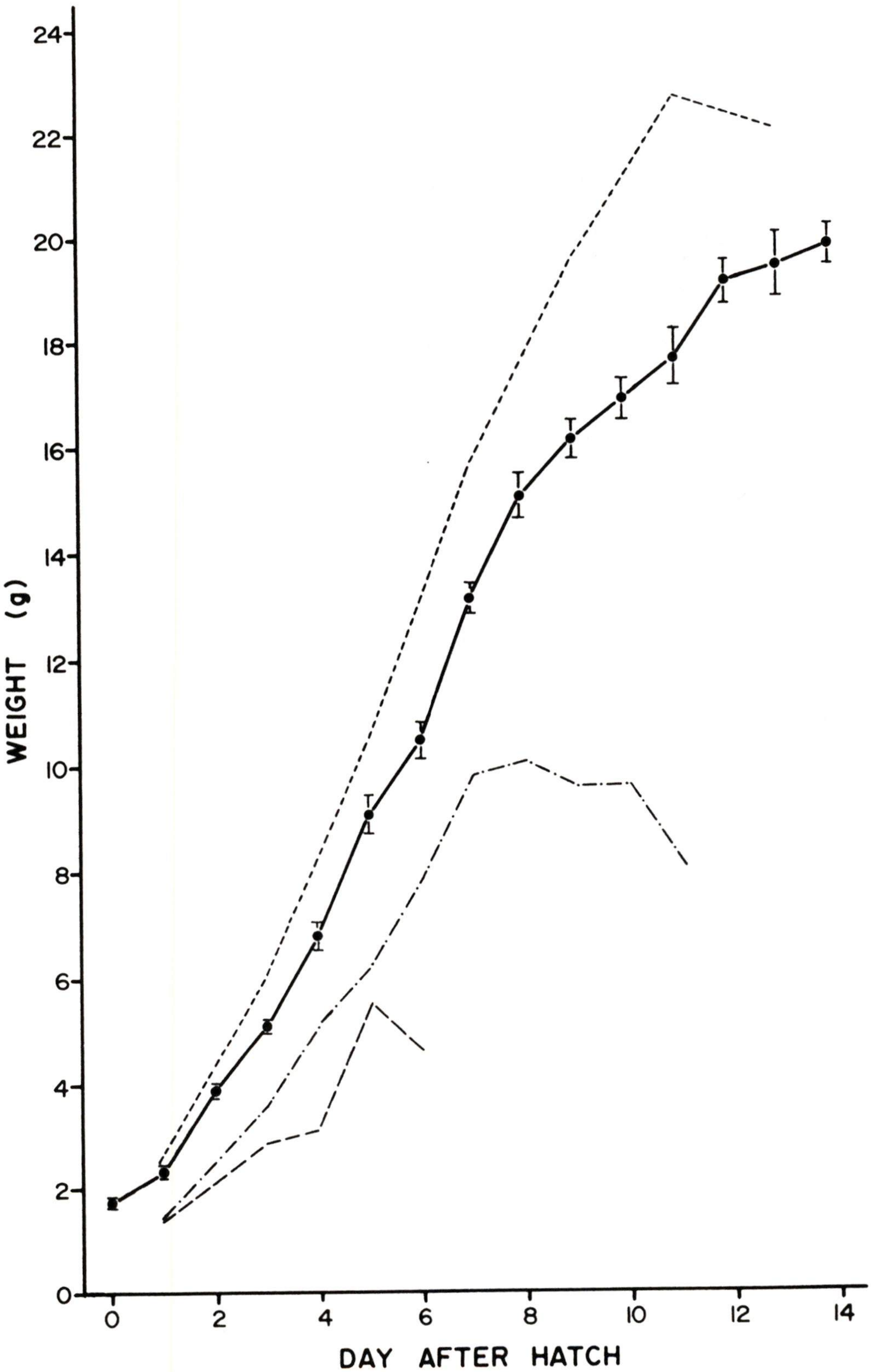
One hundred and fifty chicks were weighed during the first 14 days of life between 1975 and 1984. On the day of hatching, nestlings averaged 1.6 grams in weight (± .03 ,range 1.1 to 2.7g). Growth was rapid during the first nine days and nestlings gained between one and three grams in weight daily. Weight gain then increased more gradually to an average weight of 19.8 g for 14-day-old nestlings. This figure includes 'heavy' nestlings (heaviest chick in a clutch), 'runts' (lightest and generally youngest chick in a clutch) and parasitized nestlings. The generalized growth curve plus representative growth curves of a heavy nestling, a parasitized nestling, and a runt are shown in Figure 4.

Adult Recaptures

Twenty-nine adults were banded between 1977 and 1981. Fifty-eight percent of the birds were seen during one breeding season only. The remaining 42% were captured over 2, 3, 4 and 5 year periods. Two individuals (6.8%) were recaptured over a 5-year period and they were a mated pair. Thus the maximum age reported on the area was 6 years.

Figure 4: Nestling growth curve for all nestling weight measurements combined (——), a heavy nestling (----), an internally parasitized nestling (–·–), and a runt (– –).

Verticle bars represent (s.e.).



WEIGHT (g)
24
22
20
18
16
14
12
10
8
6
4
2
0
0
2
4
6
8
10
12
14
DAY AFTER HATCH

RESULTS - PARENTAL BEHAVIOUR - DAILY PERIOD

Incubation

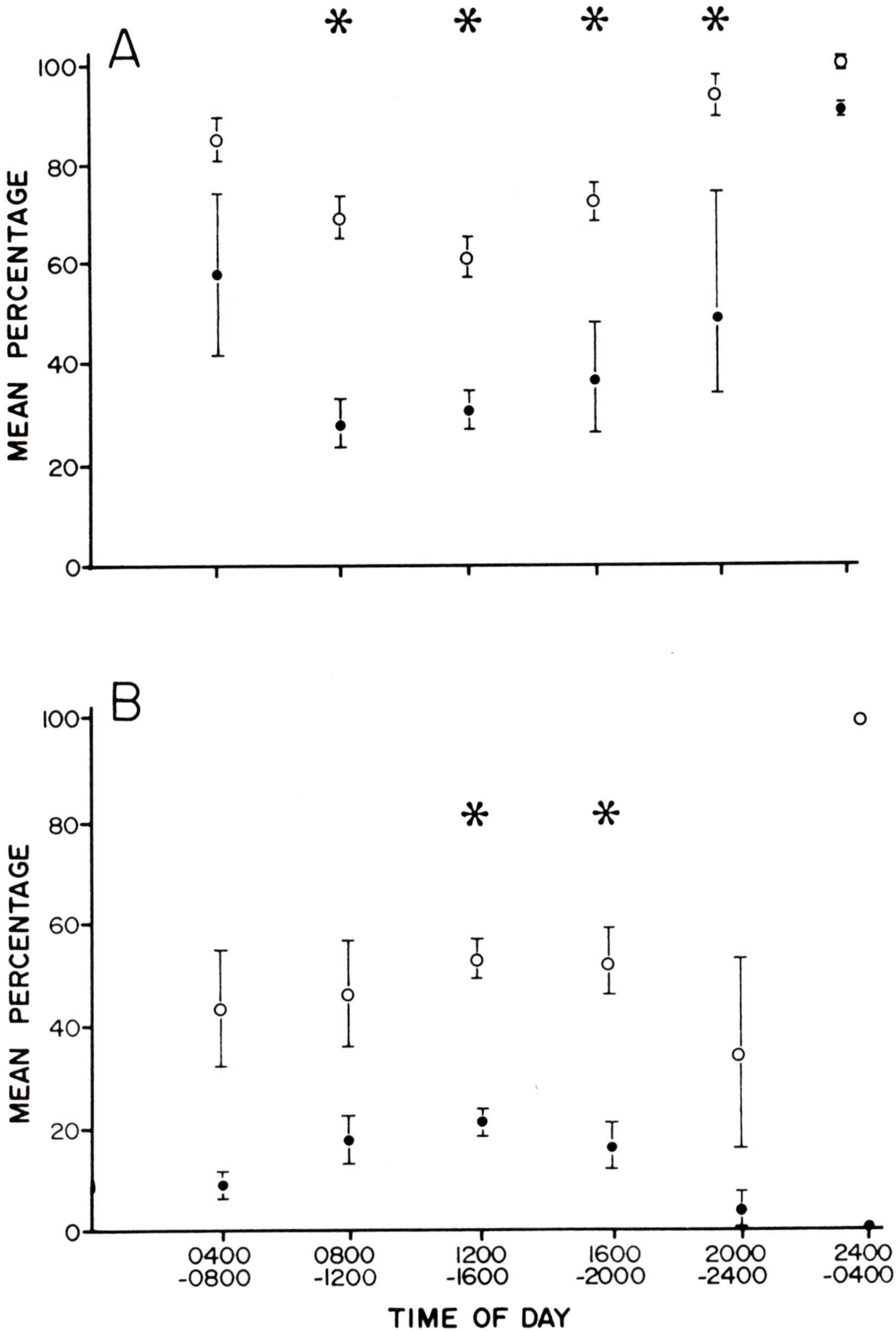
Attendance

The nesting area was attended by one or both parents for approximately 90% of each observation period. Females attended the nesting area for 75.6% of the time and males 39.4% (p=.0021,ANOVA). Both males and females attended the nest for a higher percentage of time in the morning and evening, although daily trends in attendance were not significant for either sex (Figure 5a). Females spent a larger percentage of time attended attending alone (49.6 ± .07) than did males (14.4 ± .03, p=.0021,t-test) (Figure 5b).

Periods of female attendance were longer than male (12.3 minutes, 7.3 minutes, p=.0283,t-test). Duration of attendance did not vary throughout the day for either sex. There was no difference in frequency of attendance between males (3 times per 100 minutes) and females (4 times per 100 minutes).

Figure 5: Mean percentage of the observation period spent by male and female Barn Swallows A) attending the nesting area and B) attending the nesting area without the mate during the Incubation period.

Open circles represent female values and shaded circles represent male values. Vertical bars represent ± standard error. Significant differences between the sexes for a period are indicated with an asterisk.


A
B
MEAN PERCENTAGE
0
20
40
60
80
100
*
0400
-0800
0800
-1200
1200
-1600
1600
-2000
2000
-2400
2400
-0400
TIME OF DAY

Incubation

Incubation was shared by the sexes although the female incubated for a greater percentage of the observation time, for longer periods of time, and more often than the male. The eggs were incubated for approximately 90% of the time. Females incubated an average of 74.3% of the observation time and the male incubated an average of 15.4%. The percent of time the female incubated varied over the daily period (p=.0007,ANOVA). The female spent a larger percentage of time incubating in the morning and evening than in mid-day (Figure 6a). Ninety percent of the time the male incubated, the female was not present in the nesting area. The female incubated 96.7% of her ATT whereas the male incubated 44.7% of his ATT (p=.0001,t-test, Figure 6b). The percentage of ATT the male incubated varied over the day (p=.0055, ANOVA). The male incubated more in mid-day.

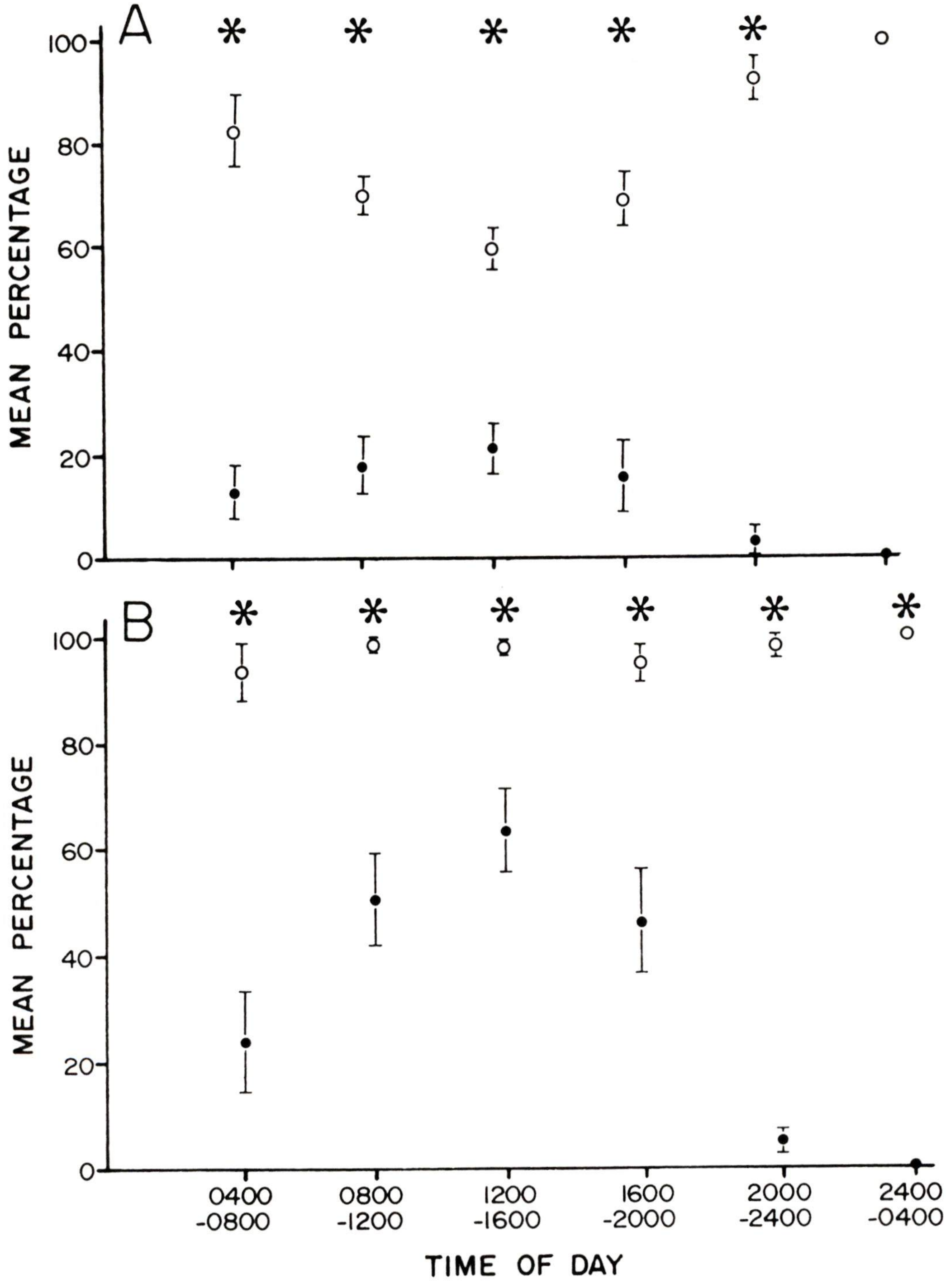
The durations of female incubation were longer (median 12.0, range 8.0 to 19.8) than male (median 5.2 range .10 to 6.3, p=.0037;Mann-Whitney-U), but there was no significant difference in the frequency of incubation bouts between sexes. There was no difference in frequency over daily period for either sex.

Behaviour

The percentage of attendance time that males and females spent in INCS, INCP, PS, PP were different (p<.05,t-test). The percentage of attendance time spent in INCM was not different between sexes (Table 7).

Figure 6: A) Mean percentage of observation period that male and female Barn Swallows incubated and B) Mean percentage of attendance period that male and female incubated.

Open circles represent females values and shaded circles represent male values. Vertical bars represent ± standard error. Significant differences between the sexes for a period are indicated with an asterisk.


A
B
MEAN PERCENTAGE
100
80
60
40
20
0
0400 -0800
0800 -1200
1200 -1600
1600 -2000
2000 -2400
2400 -0400
TIME OF DAY

When all preening behaviours were combined into the category Maintenance (MTN), the percentage of attendance time spent in MTN was different for males (24.8 % ± 3.3) and females (10.2 % ± 2.5, p=.0079,ANOVA).

The percentage of ATT that males and females spent in each of the described behaviours is illustrated in Figure 7, and summarized in Appendix A. Females allotted over 70% of their time to INCS with most of the remaining time spent on MNT. Males divided their time more evenly between INCS, MNT, and PS. The percentage of time that males spent in INCS and PS was different over the day. Males performed INCS more at mid-day and PS more in the morning and evening. The percentage of time that females spent in INCM was different over day with a greater percentage of time spent INCM in the morning.

Nestling

Attendance

The nest area was attended by one or both parents for approximately 50% of the nestling period. Females attended the nest area on average of 30.7% and the males 18.8% of the time, but the difference was not significant. There was no difference in the percentage of time males and females attended the nest area alone (15.9% and 23.3% respectively). The percentage of observation time the female attended was slightly greater in the morning and evening than at mid-day, but the daily trend was not significant (Figure 8).

The length of attendance bouts (median) was not different for males (3.6 sec range 15.1 to 1.0) and females (6.0 sec, range 57.4 to 1.0). There was no significant difference in the median duration of attendance bouts over the daily period for males and females.

Males and females each attended the nest approximately 20 times every 100 minutes. There was no difference in frequency of attendance between sexes or over the daily period. Males and females attended slightly more in the morning and evening, but the trends were not significant.

Brooding

Brooding duties were shared by the sexes, with the female brooding for a slightly larger percentage of the observation period. The female brooded alone constantly through the night. Females brooded an average of 22.7% of the observation period and males brooded 5.7%; however due to variability, the differences were not significant. The female spent 41.1% of the time she was in attendance brooding whereas the males spent 20.1%, although the difference was not significant. The percentage of ATT spent brooding by males and females varied significantly over the day (p=.0102 and p=.0258 respectively,ANOVA). The female brooded for a greater percentage of ATT in the morning and evening than at mid-day. The male brooded more in the morning than in other daily periods (Figure 9).

Table 7: Percentage of attendance time of male and female Barn Swallow behaviours during the incubation stage (n=5). Entries are mean (s.e.).

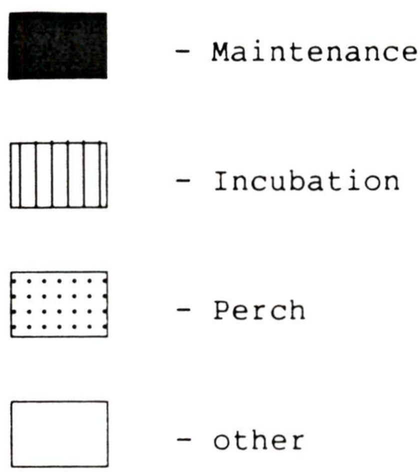
Behaviour	Male	Female	Difference over Day	
			male	female
Incubate Still*	40.1 (7.6)	72.9 (6.4)	p=.012	ns
Incubate Preen*	2.4 (0.6)	8.8 (2.0)	ns	ns
Incubate Move	2.7 (0.8)	3.1 (0.4)	ns	p=.0199
Perch Still*	24.5 (3.7)	1.4 (0.5)	p=.0011	ns
Perch Preen*	21.5 (3.4)	5.1 (2.3)	ns	ns
Maintenance*	24.8 (3.3)	10.2 (2.5)	ns	ns

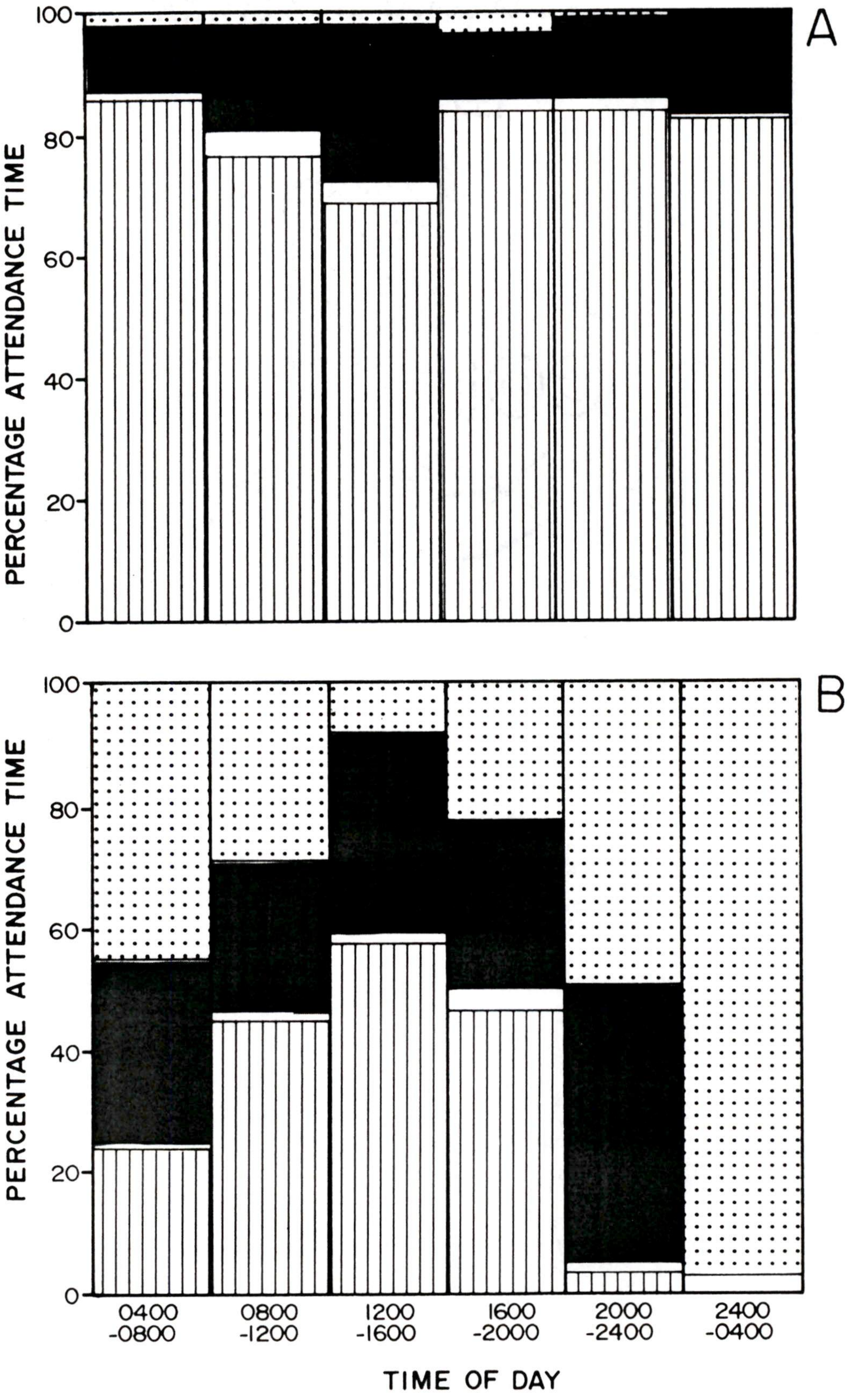
* significant ($p < .05$) difference between sexes

Median durations of brooding did not differ significantly between males (2.2 min, range 3.6 to 1.0) and females (1.7 min, range 3.6 to 0.8). There was no difference in median brooding bout duration over the daily period for either sex.

The frequency of brooding bouts was not significantly different between males and females (1.6 per 100 minutes and 5.2 per 100 minutes respectively), yet the female brooded slightly more often. Females brooded slightly more often in morning and evening than at mid-day but differences were not significant.

Figure 7: Daily time budget of a) female and b) male Barn Swallows during the incubation stage.





A
B
100
80
60
40
20
0
PERCENTAGE ATTENDANCE TIME
0400 -0800
0800 -1200
1200 -1600
1600 -2000
2000 -2400
2400 -0400
TIME OF DAY

Figure 8: Mean percentage of the observation period spent by male and female Barn Swallows A) attending the nesting area and B) attending the nesting area without the mate during the Nestling period.

Open circles represent female values and shaded circles represent male values. Vertical bars represent ± standard error.

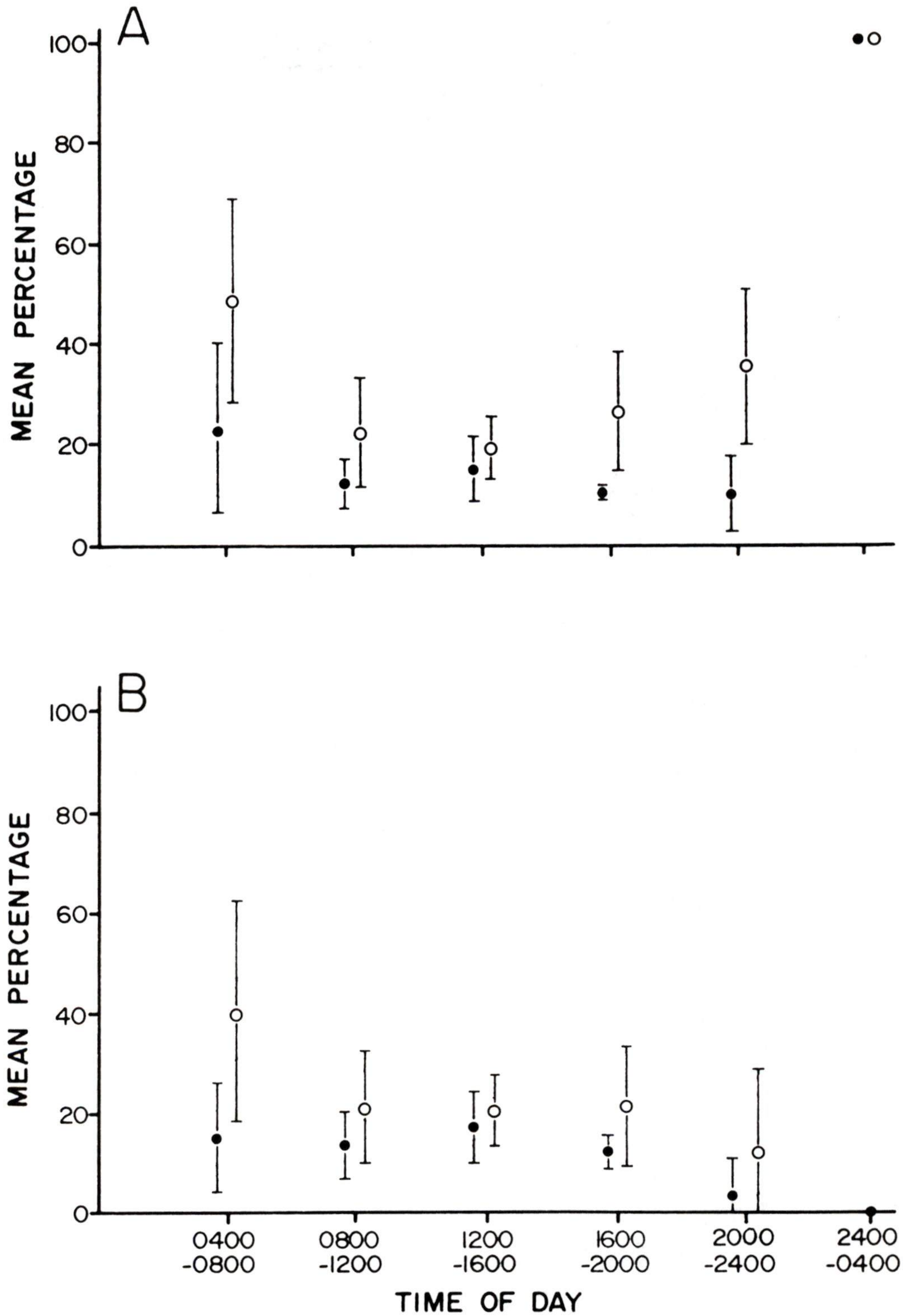

A
B
100
80
60
40
20
0
MEAN PERCENTAGE
0400 -0800
0800 -1200
1200 -1600
1600 -2000
2000 -2400
2400 -0400
TIME OF DAY

Figure 9: A) Mean percentage of observation period that male and female Barn Swallows brooded and B) Mean percentage of attendance period that male and female brooded.

Open circles represent female values and Shaded circles represent male values. Vertical bars represent ± standard error.

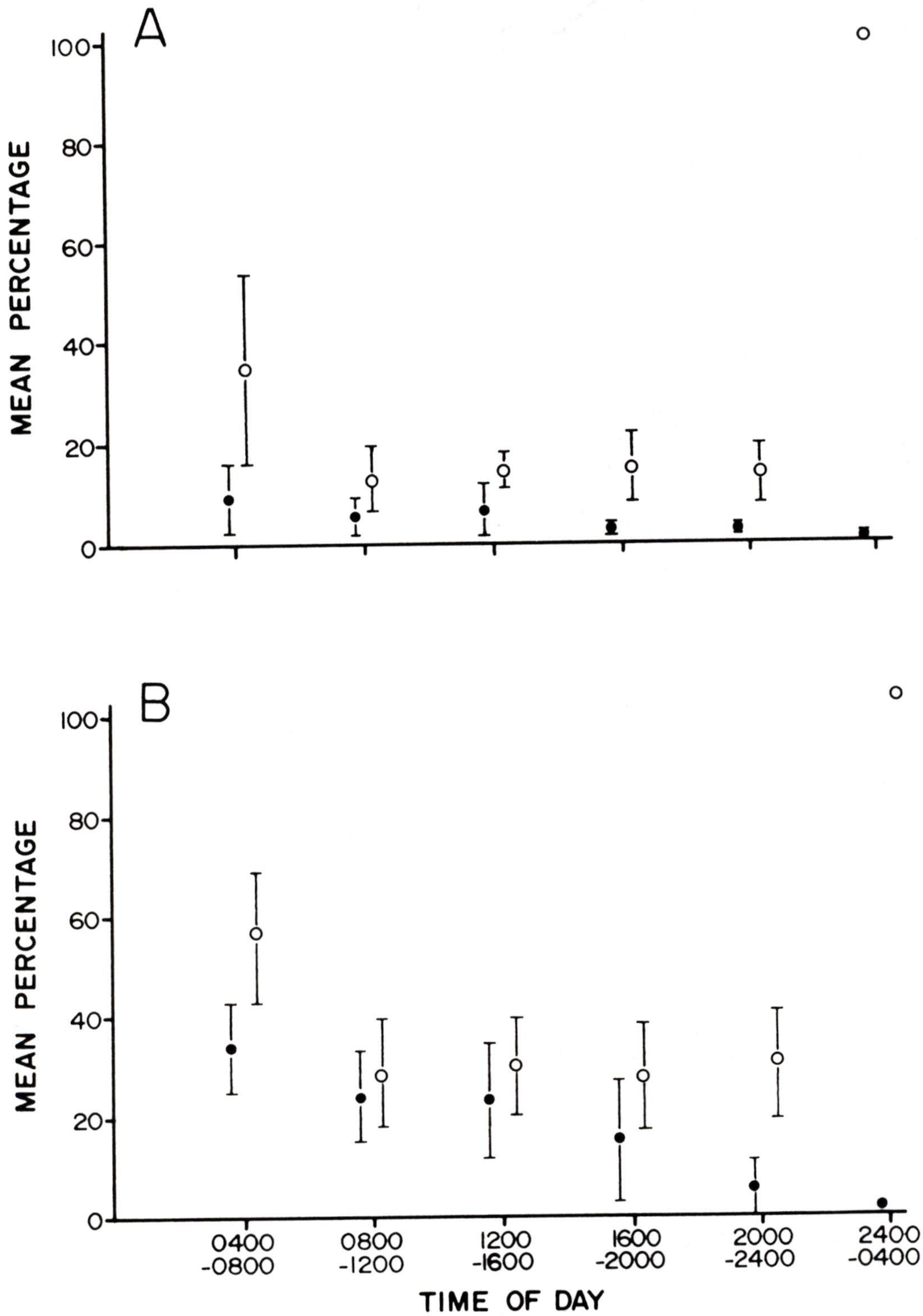

A
B
MEAN PERCENTAGE
0
20
40
60
80
100
0400
-0800
0800
-1200
1200
-1600
1600
-2000
2000
-2400
2400
-0400
TIME OF DAY

Table 8: Percentage of attendance time spent by male and female Barn Swallow in different behaviours during the Nestling stage (n=5). There were no significant differences in behaviour over the day. Entries are mean (s.e.).

Behaviour	Male	Female
Brood Still	20.3 (5.3)	38.0 (7.0)
Brood Move	7.3 (3.6)	11.0 (1.4)
Perch Still	28.6 (7.9)	27.4 (8.0)
Perch Still (nest rim)	17.7 (3.8)	20.6 (6.8)
Maintenance	8.5 (5.1)	3.5 (1.9)
Feed Nestlings	37.5 (10.8)	23.9 (9.2)

Behaviour

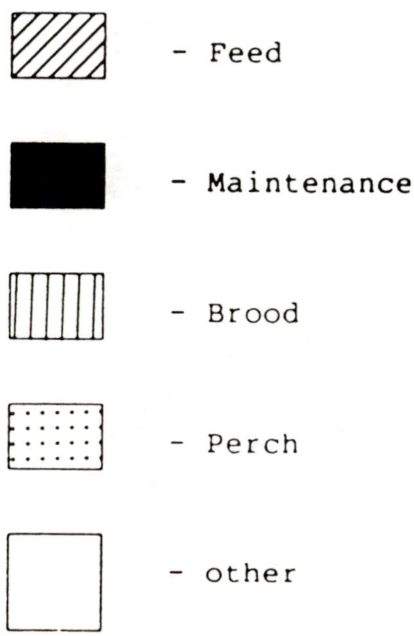
The percentage of attendance time spent in each of the nestling behaviours was not significantly different between males and females. No daily trends were present in any behaviour for either sex (Table 8). The amount of time males and females spent in each of the behaviours during the nestling period is illustrated in Figure 10.

Feeding

The percentage of attendance time spent feeding the nestlings was not different for males and females (37.5 ±0.1 and 23.9 ±0.1 respectively). The percentage of attendance time spent in feeding for both sexes increased slightly from mid-day to evening but this increase was not significant (Figure 11a).

Frequency of feeding visits was equal for males and females (18 visits per 100 minutes). There was an increase in the frequency of feeding visits in the morning and a slight increase in the evening but the trends were not significant (Figure 11b).

Figure 10: Daily time budget of a) female and b) male Barn Swallows during the Nestling stage.



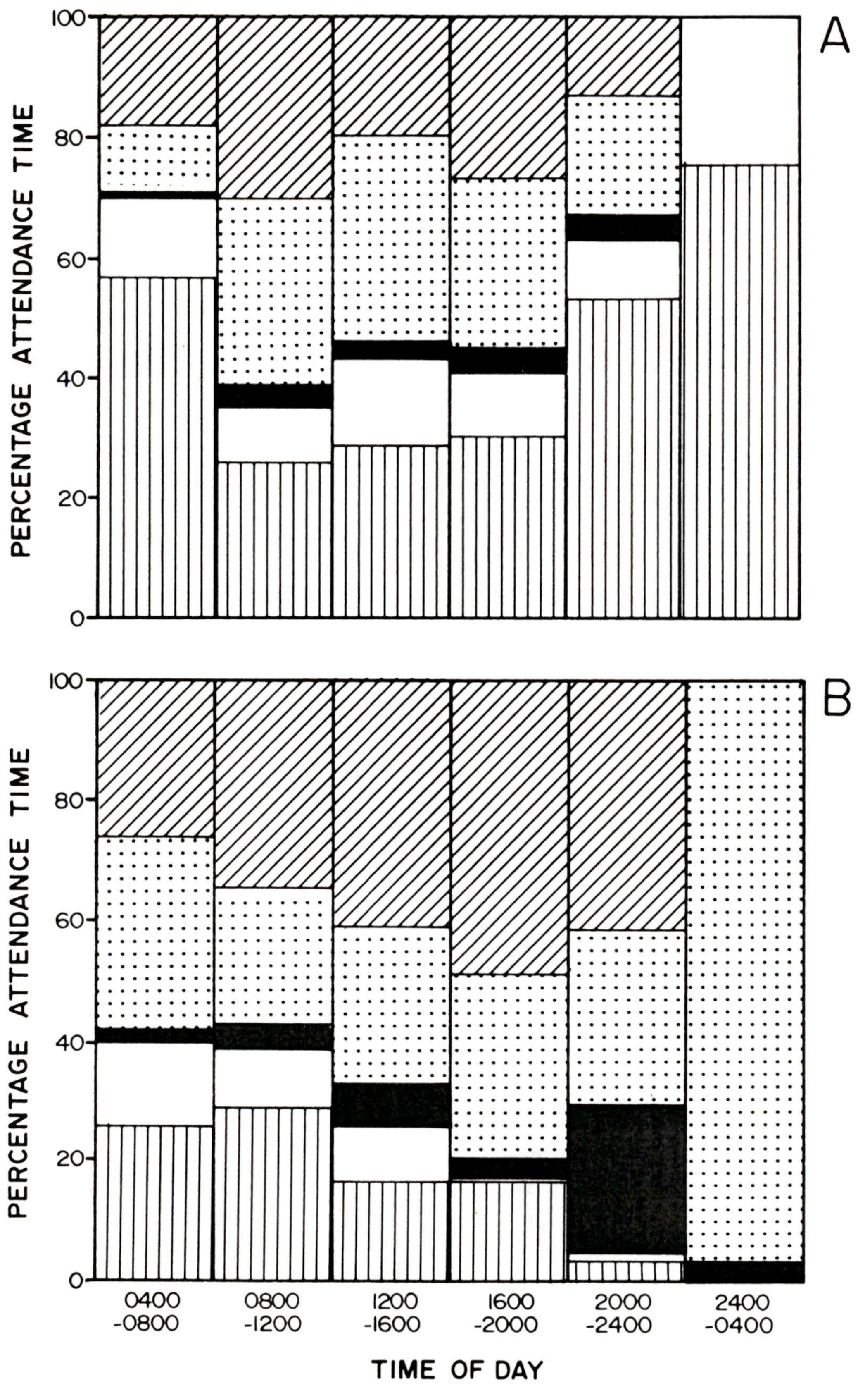
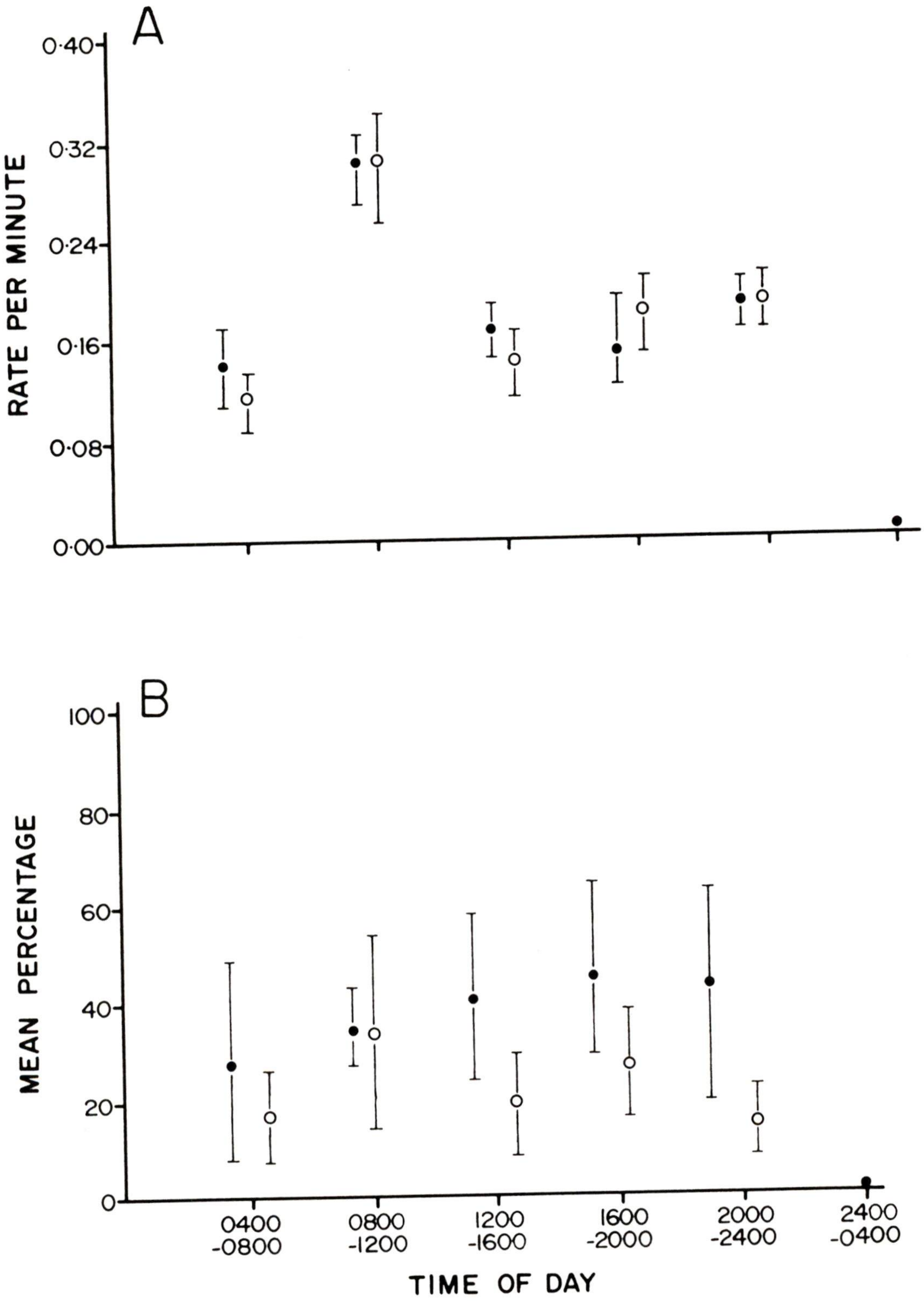

A
B
PERCENTAGE ATTENDANCE TIME
100
80
60
40
20
0
0400 -0800
0800 -1200
1200 -1600
1600 -2000
2000 -2400
2400 -0400
TIME OF DAY

Figure 11: A) Mean frequency of feeding visits of male and female Barn Swallows during the daily period and B) Mean percentage of observation time that male and female Barn Swallows spent feeding nestlings.

Open circles represent female values and shaded circles represent male values. Vertical bars represent ± standard error.


A
RATE PER MINUTE
0·40
0·32
0·24
0·16
0·08
0·00
B
MEAN PERCENTAGE
100
80
60
40
20
0
0400 -0800
0800 -1200
1200 -1600
1600 -2000
2000 -2400
2400 -0400
TIME OF DAY

Breeding Stage

Attendance

Both sexes attended the nesting area a greater percentage of the time during incubation than during nestling stages. The percentage of observation time attended differed between sexes in breeding stages 1 to 4 (Figure 12). Females spent a greater percentage of time than males attending the nesting area alone during incubation. There was no difference in the time spent attending alone between the sexes in the nestling period.

The median durations of attendance bouts were longer during the incubation stage than in the nestling stage for both sexes. There were no differences between sexes in the median duration of attendance bouts in any stage of the breeding cycle. The nesting area was attended more frequently during the the nestling stage (20 times per 100 minutes) than during the incubation stage (3 times per 100 minutes, p=.0230,ANOVA). There was no difference in frequency of attendance bouts between sexes in any stage of the breeding cycle.

Incubation/Brooding

Females incubated for a larger percentage of the observation period during the incubation period than they brooded during the nestling period (p=.0103,ANOVA). The percentage of observation time spent incubating differed between sexes in breeding stages 1 to 4 (Figure 13a). The percentage of observation time spent incubating decreased to less than 10 % in breeding stage 6 for both sexes. The trend is more apparent in males when percentage of time is calculated relative to attendance time (Figure 13b).

Figure 12: Mean percentage of the observation period spent by male and female Barn Swallows A) attending the nesting area and B) attending the nesting area without the mate over the breeding cycle.

Open circles represent female values and shaded circles represent male values. Vertical bars represent ± standard error. Significant differences between the sexes for a period are indicated with an asterisk.

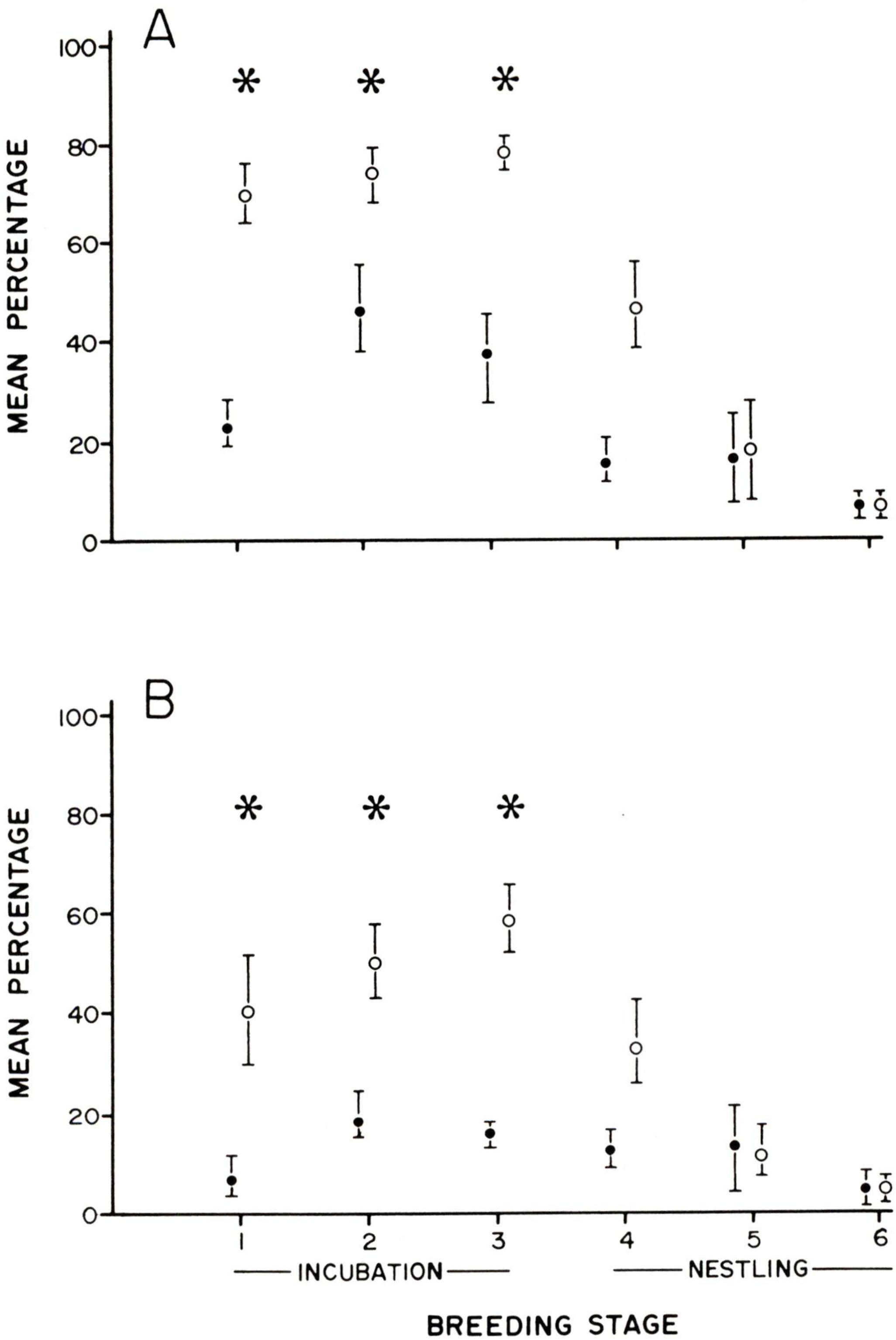
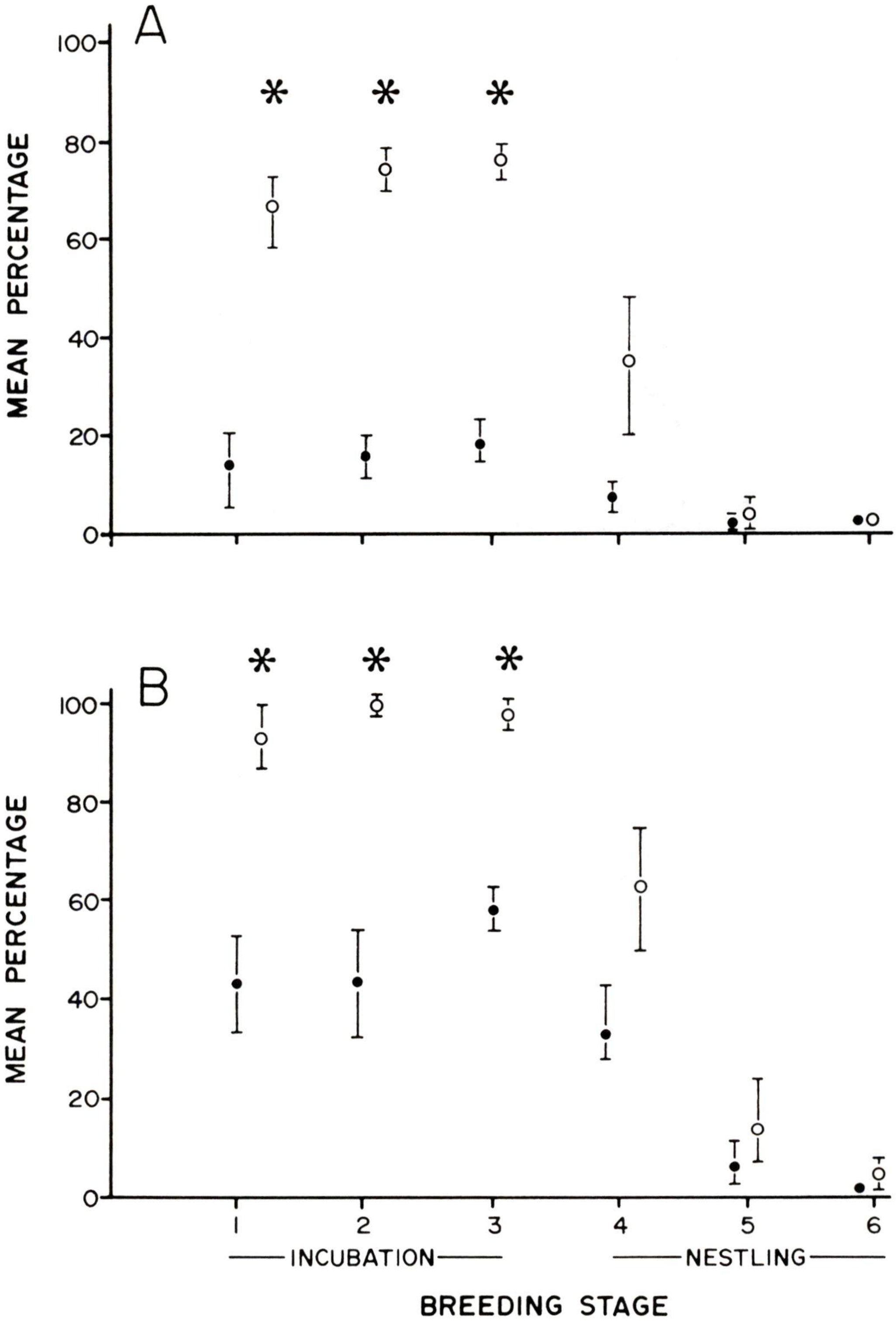

A
B
*
MEAN PERCENTAGE
0
20
40
60
80
100
1
2
3
4
5
6
INCUBATION
NESTLING
BREEDING STAGE

Figure 13: A) Mean percentage of observation period that male and female Barn Swallows incubated/brooded and B) Mean percentage of attendance period that male and female incubated/brooded.

Open circles represent female values and shaded circles represent male values. Vertical bars represent ± standard error. Significant differences between the sexes for a period are indicated with an asterisk.


A
B
MEAN PERCENTAGE
MEAN PERCENTAGE
100
80
60
40
20
0
*
1
2
3
4
5
6
INCUBATION
NESTLING
BREEDING STAGE

The median duration of incubation/brooding bouts was longer during the incubation stage than in the nestling stage for both sexes. There was no difference in median bout duration between sexes in any stage of the cycle.

The chicks were brooded less frequently during the nestling period than they were incubated during the incubation period. There was no difference in frequency of brooding or incubation bouts between sexes in any stage of the breeding cycle.

Behaviour

To analyze trends in behaviours across the breeding cycle, INCS and BROS were combined to form NS, INCM and BROM were combined to form NM,and INCP, BROP,and PP were combined to form MTN.

The percentage of attendance time spent in NS, PS, and MTN differed significantly between sexes ($P<.05$;t-test), but that spent in NM and FEED did not (Table 9).

The percentage of attendance time spent in each of the described behaviours is illustrated in Figure 14. Significant differences in the percentage of attendance time spent in each behaviour over the breeding stage are listed in Table 9.

Females performed NS for a larger percentage of attendance time during the incubation periods than in periods 5 and 6. Females performed NM more during the nestling stage than in the incubation stage. Females performed PS for a larger percentage of attendance in the nestling stage. This increase in perching time was associated with perching on the nest rim to deliver food to the chicks. Approximately 75% of the time allocated to PS is associated with a feeding visit.

Table 9: Percentage of attendance time spent by male and female Barn Swallows in different behaviours over the breeding cycle (n=5). Entries are mean (s.e.).

Behaviour	Male	Female	Difference over Day	
			male	female
Nest Still*	32.0 (4.8)	57.7 (5.5)	p=.0360	p=.0001
Nest Move	4.3 (1.6)	7.3 (1.2)	ns	p=.0001
Perch Still*	28.4 (3.7)	13.9 (4.2)	ns	p=.0001
Maintenance*	10.7 (2.5)	4.4 (0.9)	ns	p=.0276
Feed	32.0 (8.4)	22.0 (7.2)	ns	ns

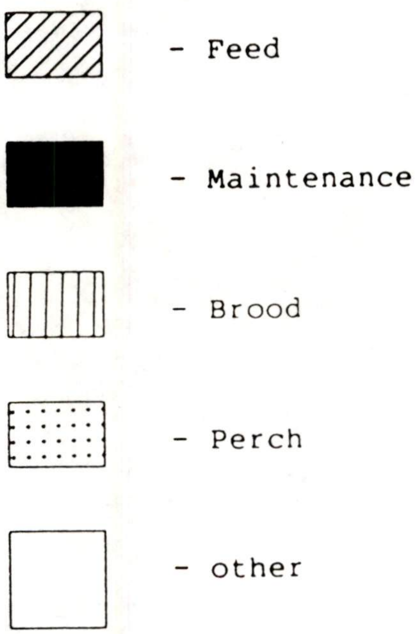
* significant (p<.05) difference between sex

Females spent an average of 10% of the attendance time in maintenance behaviours during the incubation stages. After the eggs hatched females performed maintenance behaviours less than 5 % of the attendance time. The percentage of time gradually increased to 12 % in stage 6. A similar trend was seen in the percentage of attendance time spent in maintenance behaviours of the male.

Males performed NS behaviours for a larger percentage of attendance time in stages 1 to 4 than in other stages.

The percentage of attendance time spent feeding the chicks was not different between males and females. As the breeding stage progressed males and females spent a larger percentage of the attendance time feeding the chicks. The rate of feeding the chicks was not different between the sexes or over breeding stage (Figure 15).

Figure 14: Time budget of A) female and B) male Barn Swallows during the breeding cycle.



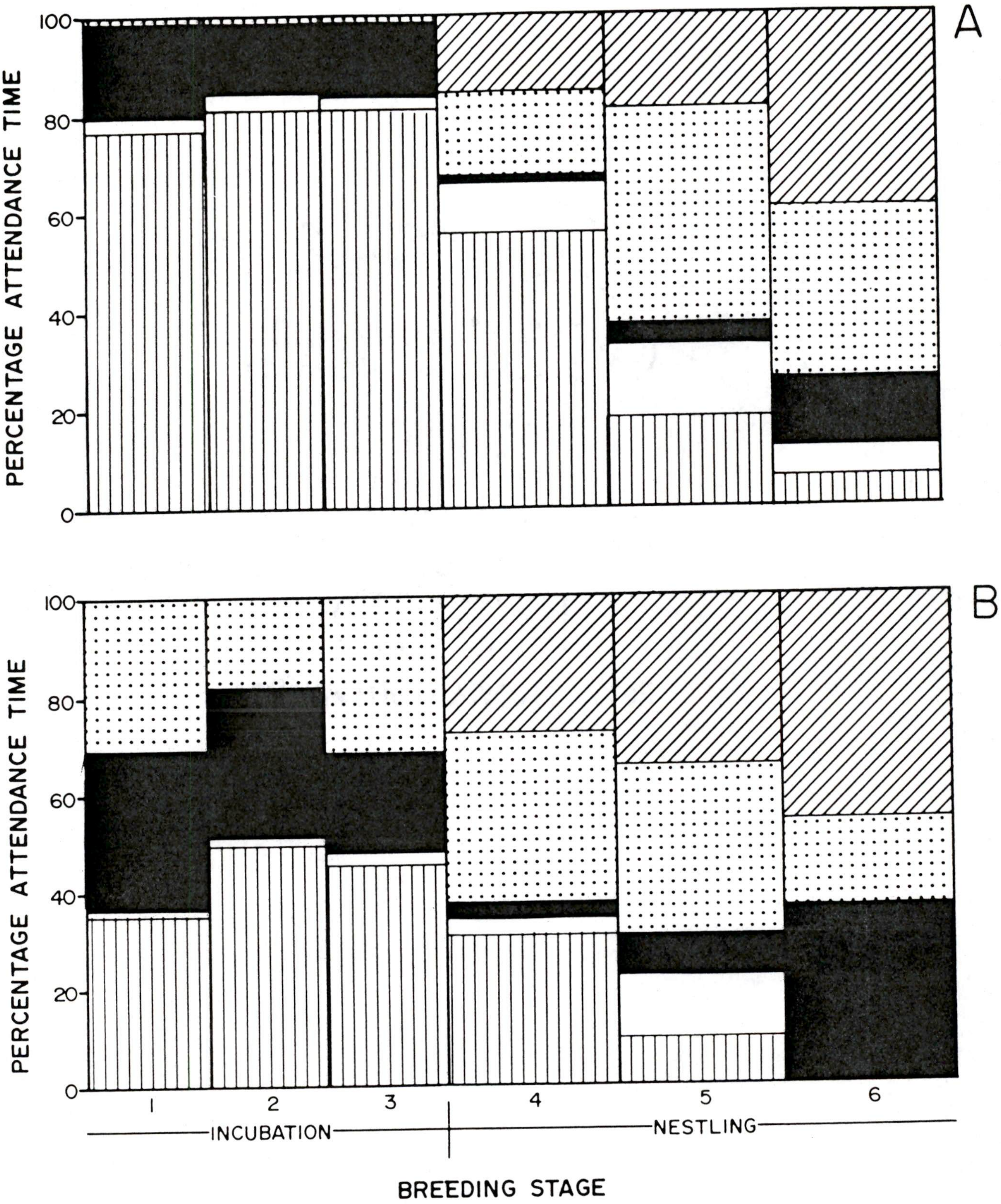
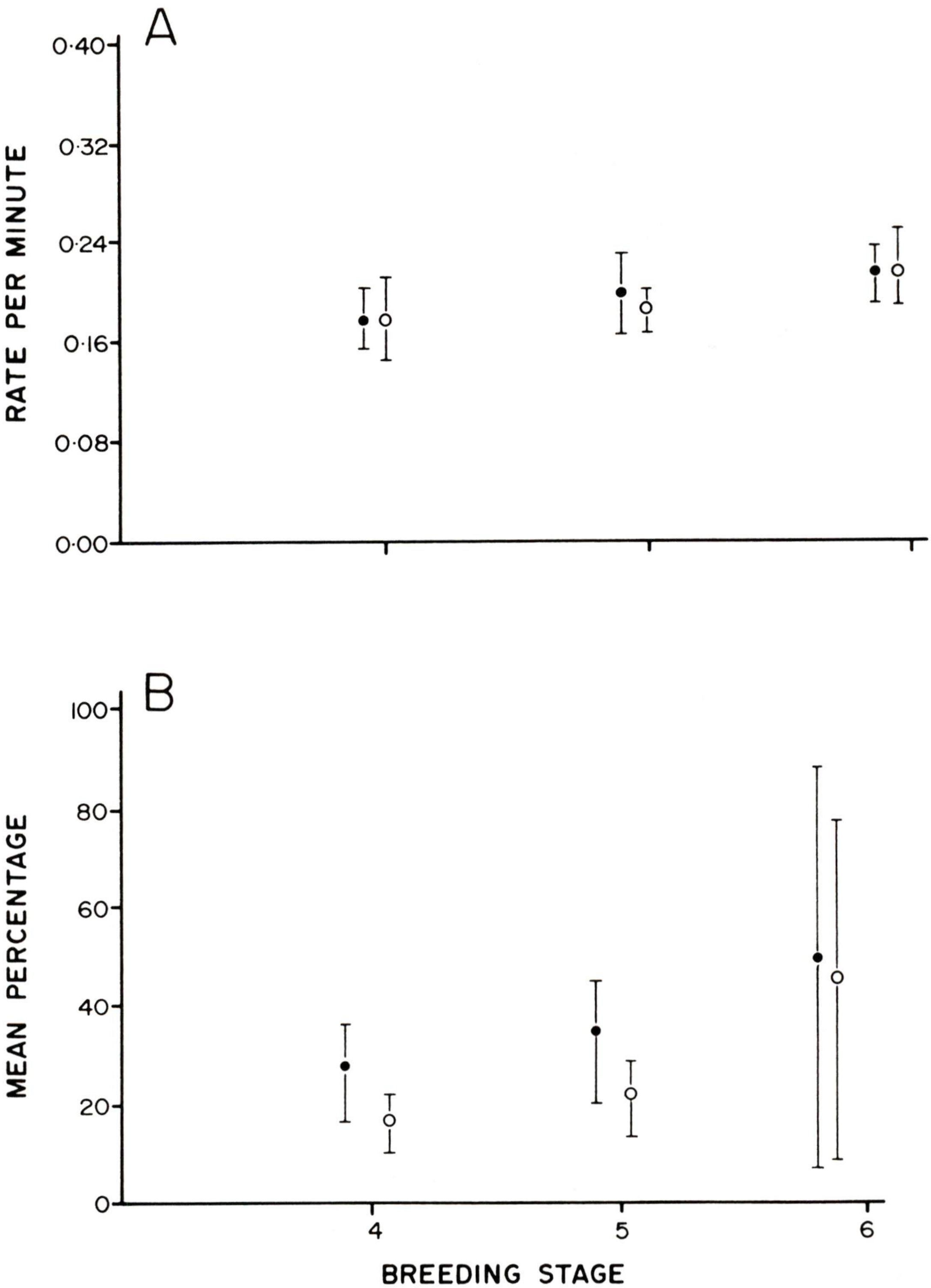

A
100
80
60
40
20
0
PERCENTAGE ATTENDANCE TIME
B
100
80
60
40
20
0
PERCENTAGE ATTENDANCE TIME
1
2
3
4
5
6
INCUBATION
NESTLING
BREEDING STAGE

Figure 15: A) Mean frequency of feeding visits of male and female Barn Swallows during the nestling period and B) Mean percentage of observation time that male and female Barn Swallows spent feeding nestlings.

Vertical bars represent ± standard error.


A
0·40
0·32
0·24
0·16
0·08
0·00
RATE PER MINUTE
B
100
80
60
40
20
0
4
5
6
MEAN PERCENTAGE
BREEDING STAGE

DISCUSSION - BREEDING BIOLOGY

The American subspecies of Barn Swallow (Hirundo rustica erythrogaster, Boddaert) migrates from its winter range in South America to North America, through the West Indies and the Bahamas to Florida, and to more western points through Central America and Mexico (A.O.U. 1957). Extensive studies on Barn Swallow breeding biology have been done in Virginia (Samuel 1969), Washington state (Moody 1968), and New York (Snapp 1973). Similar studies of the breeding biology of the European subspecies H.r.rustica L., also have been done in England (Hosking and Newberg 1946), Bavaria (Purchon 1948), and Scotland (McGinn and Clark 1978).

As the Barn Swallow has such an extensive breeding range, comparisons of life history traits were made to determine how the breeding biology of the Qualicum National Wildlife Area population compared with that of other populations throughout the range. Generally, populations of Barn Swallow were similar in many aspects studied. The patterns of parental care observed in Barn Swallows were generally similar to those found throughout the Hirundinidae, yet there are some important differences. From that information some inferences about the evolution of monogamy in Barn Swallows in particular and the family Hirundinidae in general can be made.

Many aspects of Barn Swallow breeding biology may be adaptations for hunting insects on the wing. Lack (1968) suggested that this frees swallows from nesting in close proximity to the food source. They are then able to nest in relatively safe sites. Males do not defend a territory with resources for young and mates from other males; thus the role of the male is less complex. Nest sites are protected from weather and predators, and therefore parental care duties in the nesting area (incubation, brooding) are potentially less stressful to the parent than in other passerine species. An examination of the role of male and female parental care in combination with other aspects of the ecology and behaviour of these swallows allows a better understanding of the role of parental care in the evolution of monogamy in the Barn Swallow and other aerial insectivores.

Arrival

In this study, Barn Swallows arrived from mid to late April. Other studies carried out in northwestern North America reported similar arrival dates (Bent 1942, Moody 1968, Evenden 1969). Arrival in other swallow species such as Purple Martins (Allen and Nice 1952) and Bank Swallows (Petersen 1955) generally follows a warm period, as swallows are dependent on aerial insects for food and these generally are associated with warmer weather. Møller (1982) found that the first birds that arrive in spring are primarily older, experienced birds that settle down to use the most favourable nests and nest sites.

Nest Building

The nest building phase lasts from 5 to 14 days in Barn Swallows , and both sexes participate in the building (Table 10). The duration of this phase varies with weather conditions (Kuzniak 1967) and breeding experience of the pair (Mason 1953, Emlen 1954). In wet or colder conditions nesting material may be difficult to obtain and the nest will not dry quickly; therefore the nest building period will be prolonged.

Within the Hirundinidae, nests are generally built by both sexes (Table 11). Male and female participation may create and/or maintain a pair bond (Emlen 1954, Petersen 1955), allow the partners to assess the parental care abilities of one another in newly formed pairs and/or may prevent the male from being cuckolded (Beecher and Beecher 1979).

Extra-pair copulations (Samuel 1971a) and instances of hybridization with Cliff Swallows (Martin 1980) have been reported for Barn Swallows. By guarding the female during her receptive period the male can ensure that the young he will eventually raise are his own. Extra-pair copulations and mate guarding are common throughout the Hirundinidae (Beecher and Beecher 1979 and Petersen 1955, Bank Swallow; Emlen 1954 and Butler 1982, Cliff Swallow; Allen and Nice 1957 and Brown 1978, Purple Martin; DeSteven 1978, Tree Swallow).

Table 10: Comparison of duration and parental participation for each period of the breeding cycle from the present study with those from other studies on the Barn Swallow.

Breeding Period	Duration (days)	Participation	Source
Nest Building	11	m = f	this study
	10	m = f	Smith 1933
	6	m = f	Samuel 1971
	5 - 14	-	Kuzniak 1967
	7 - 10	m = f	Hosking et al. 1946
	-	m = f	Purchon 1948
Incubation	15	m < f	this study
	15	m < f	Smith 1933
	15	m < f	Samuel 1971
	15	f	Kuzniak 1967
	14 - 15	m < f	Hosking et al. 1946
	15	m < f	Tate 1981
Nestling (brooding)	20	m < f	this study
	18	-	Smith 1933
	21	f	Samuel 1971
	19 - 23	-	Kuzniak 1967
	21	f	Hosking et al. 1946
	17 - 24	f	Tate 1981
(feeding)		m = f	this study
		m = f	Samuel 1971
		m = f	Kuzniak 1967
		m = f	Hosking et al. 1946
		m = f	Tate 1981
		m = f	Purchon 1948

Egg laying

In this study laying for the first clutch occured from the last week in April to early July with a peak from mid-May to early June. Similarly, the number of renests and second nests peaked in mid-July. These findings are similar to findings reported by Bent (1942), and Hosking and Newberg (1946).

In this study, Barn Swallow pairs that raised two broods initiated egg-laying earlier in the spring than single-brooded pairs. Barn Swallows raising two clutches are generally older and have previously ben mated to the same individual (Davies 1977). Thus, in this study, the pairs that initiated clutches earlier are probably more experienced. Those individuals breeding earlier will have a greater probability of raising two broods when insect abundance is adequate, although they also take a greater risk of loss due to unpredictable weather conditions in early spring (Bryant 1979). Greater experience in parental care and foraging may counteract these risks (Bryant 1979; DeSteven 1978). To elucidate these details, descriptions of individual breeding activities extending over several breeding seasons would be of value.

The range in clutch-initiation dates in other species may be caused by the age and mated status of the birds (Mason 1953; Bryant 1979, Coulson 1966; Crawford 1977; DeSteven 1978) and/or variation in weather (Turner 1982, Bryant 1975). Larger and older House Martins start to breed earlier than smaller and younger ones (Bryant 1979). The formation of a pair bond also may have an effect; Kittiwake pairs that have mated in successive years nest earlier than new pairs of the same age (Coulson 1966). Turner (1982) suggests that the main factors

Table 11: Comparison of parental care patterns amoung several species of Swallows measured as a percentage of total time.

Swallow Species	Nest Building	Incubation	Brooding	Feeding	Source
Barn	m = f	m < f	m < f	m = f	Table 10
Wire-Tailed	-	f	f	m = f	M
Bank	m = f	m = f	m = f	m = f	PMSBBe
Cliff	m = f	m = f	m < f	m = f	EBeSa
Amer. Rough Winged	m = f	f	f	m = f	L
Blue and White	m = f	-	-	m = f	SK
Pacific	m = f	f	f	m = f	H
Violet-Green	m < f	f	f	m = f	CE
Tree	m < f	f	f	m = f	K
Mangrove	-	-	-	m = f	RD
Purple Martin	m = f	f	-	m = f	BeADSFG
House Martin	m = f	m = f	-	m = f	M

*A=(Allen and Nice 1952),Be=(Bent 1942), B=(Beyer 1938), C=(Combellack 1955) Ds=(DeSteven 1980), D=(Drycz 1984), E=(Emlen 1943 and 1954), F=(Finlay 1971) G=(Gaunt 1979), H=(Hails 1984), K=(Kuerzi 1941), L=(Lunk 1962), M=(Moreau and Moreau 1940), P=(Petersen 1955), Q=(Quinney 1986), R=(Ricklefs 1971), Sa=(Samuel 1969), Sk=(Skutch 1952), S=(Stoner 1945) determining the laying date in hirundines are the level, stability, and predictability of the food supply either during egglaying or at later stages. Experienced adults, known to return to the same site in successive years (Boyd 1936), arrive back at their breeding sites ahead of less experienced birds and not only lay earlier, but also lay larger clutches than younger birds (McGinn and Clark 1978).

Incubation

The duration of the incubation period of Barn Swallows is about 15 days (Table 11). Both sexes incubate but the female incubates for a greater percentage of the time than the male. Lone female incubation has been reported more commonly in the European subspecies *H. r. rustica* (Kuzniak 1967).

Within the Hirundinidae, species are about equally divided with respect to whether or not the male incubates (Table 11). This variability in parental care patterns may be a consequence of the nesting habits (Lack 1968). As the nests are relatively secluded and protected from high levels of predation, the incubating adult is not subject to high risks of predation or undue thermal stress (Walsberg and King 1978). Therefore biparental care in this portion of the breeding cycle may not be as important as at other stages; this gives rise to the different roles for the sexes among the hirundines.

Nestling

The duration of the nestling period has been reported as lasting from 17 to 21 days (Table 10). In this study this period lasted an average of 19.5 days. Because swallows are aerial insectivores, when young swallows are ready to fledge they must be physically well advanced, thus, the subsequent period of parental care is brief.

In this study, both sexes brooded the young, however this trend is not consistent in all studies of Barn Swallows (Table 10) or throughout the hirundines (Table 11). Brooding is no more stressful a parental duty than incubation and biparental care in this phase may not be very important.

In Barn Swallows and other swallows, both parents appear to feed the young equally (Table 11). The equitable allocation of food-provisioning duties by the sexes is consistent with the hypothesis that male assistance in brood rearing is substantial in monogamous species raising altricial young (Trivers 1972;Emlen and Oring 1977; Wittenberger 1979).

Clutch size

First clutches were larger than second clutches for Barn Swallows (Table 12). The general reduction in Barn Swallow clutch size as the season advances may be related to hours of light increasing until mid-June and decreasing thereafter

(McGinn and Clark 1982; Bryant 1975). The time available for feeding decreases after mid-June, as presumably would the amount of food supplied per brood of nestlings. Therefore, selection favors smaller second clutches (McGinn and Clark 1978;Lack 1968).

Breeding Success

Although first clutches were larger, a smaller percentage of young tended to hatch from them. This trend is commonly reported for Barn Swallows (Table 12). This may be due to unpredictable weather early in the spring, affecting aerial insect abundance, in combination with less experienced adults attempting to rear the young (McGinn and Clark 1978). Overall, the success of hatching were still high (76.3%).

In this study, first nests had fewer fledglings per nest and a lower fledging success than second nests. This is not consistent with patterns observed in other studies (Table 12). This is possibly due to a larger number of young pairs breeding, poor weather conditions or the high level of parasitization of the young.

Nestling mortality was largely due to parasitization by *Protocalliphora* Parasites of this genus have been reported as destructive to nestling Purple Martins(Allen and Nice 1952), Bank Swallows (Lincoln 1931), Barn Swallows (Lincoln 1931), and Tree Swallows (Johnson 1932).

Table 12: Comparison of data on the breeding biology from the present study with those from other studies.

Feature		this study	Snapp (1973)	Samuel (1969)	Adam (1984)	Kuzniak (1967)
Clutch	1	4.5	4.8	4.6	4.8	4.8
	2	4.1	4.5	4.1	4.7	4.1
Number of Eggs to Hatch	1	4.1	4.2	3.8	-	4.5
	2	3.9	4.0	3.5	-	3.8
% of eggs to hatch	1	84.9	87.1	83.3	90.5	90.5
	2	95.1	89.5	85.8	-	87.0
number of eggs to fledge	1	2.5	3.8	3.7	3.8	4.0
	2	3.4	3.5	3.5	4.6	3.5
% of eggs to fledge	1	51.0	83.3	81.2	71.9	80.5
	2	82.0	85.8	85.0	-	74.5
Peak Weight		19.8	21.6	-	-	22.9

In this study, the overall breeding success (as measured by the number of young fledged as a percentage of eggs laid), was found to be 76.3%, which is similar to that reported in other studies (Table 12), despite the heavy infestation of Protocalliphora. Such a high level of success is common in aerially insectivorous species which nest in man-made shelters or caves (typical sites chosen by swallows and swifts). In temperate zones, nests in such situations have a success of about 70% (Hails 1984) and in tropical habitats the White-Rumped Swift Apus caffer has an reproductive success of 76% (Moreau 1939a), the Chestnut Collared Swift Cypseloides rutilis 63% (Snow 1962), and Swiftlets of Niah Cave in Sarawak, 58% (Medway 1962). Probably the inaccessibility of these sites to predators makes them less subject to predation and thermal stress than nests in vegetation. In contrast, the breeding success of the Chestnut Collared Swift in accessible sites is only 36% (Collins 1968).

Chick Growth

Chicks studied at the QNWA from 1975-1984 attained a peak weight of 19.8 g. This is somewhat smaller than those reported in other studies (Table 12), possibly because of the high incidence of parasitization. Deleterious effects of parasitization on chick growth also were reported by Edson (1943). These results may also be caused by some aspect of insect abundance (Turner 1982; Bryant 1975; Quinney et al. 1986), a factor which was not measured in this study.

Although the peak weight is lower than in other studies, the pattern of growth is the same. The hirundine pattern of growth is characterized by a rapid increase in weight during the first half of the nestling period followed by a sharp decrease in weight before the nestlings fledge. This has been shown previously by Stoner (1935) in Hirundo rustica. Ricklefs (1968) has considered this phenomenon of weight recession in the species as being related to changes in the water content of the tissues of nestlings during their development. Accounts of nestling development in the following species, showing the same general trends, have also been reported: Bank Swallows (Beyer 1938; Petersen 1955), European Swallows (Georg and Al-Rawy 1970), Cliff Swallows (Stoner 1945), Tree Swallows (Paynter 1954), Violet-Green Swallows (Edson 1943) and Purple Martins (Allen and Nice 1952).

Conclusions

Some variability in incubation and brooding participation is common throughout the Hirundinidae. The habit of nesting in protected areas may allow the female to incubate and brood more than the male, with little or no added stress to the female, although both parents are needed to feed the chicks. The main factors affecting participation are probably the availability of food for the attending parent and the absence of the need to engage in other activity that may restrict the amount of time spent incubating (e.g. nest defense).

The aerial insectivorous mode of feeding has affected many aspects of the breeding biology of the Barn Swallow and the Hirundinidae. Feeding on the wing may require more experience for a bird to forage efficiently enough for itself as well as for offspring (Finlay 1971). Similarly, the newly established pair bond may prolong the prenesting period and may make other aspects of the breeding cycle less efficient (DeSteven 1978). Therefore, older experienced pairs may have a higher reproductive success than younger birds that have a newly formed pair bond. A more detailed description of individual breeding activities is necessary to confirm that hypothesis in the Barn Swallow.

Barn Swallows show little variation in characteristics of breeding biology throughout a very wide breeding range. In many species of birds, variability in the breeding biology may be a result of differences in ecological factors between populations. These ecological factors may be related to food sources, breeding sites, and mate availability. As feeding on aerial insects allows the Barn Swallow to nest in protected areas away from the food resource, there is little variability in nesting habitat and thus lower variability in breeding biology.

DISCUSSION - PARENTAL BEHAVIOUR

Parental roles in feeding are often considered to be the most important aspects of the role of parental care in mating systems, because of the large time and energy investment in parental feeding behaviours. Although feeding the young is an important aspect of parental care, especially in altricial species, this behaviour fulfills only the nutritional needs of the young. Parental interactions relating to incubation and brooding are also important. Performance of these behaviours in relation to environmental circumstances determines the success of the reproductive effort. A more detailed examination of all parental care patterns during the breeding cycle is reported here yielding a more complete assessment of the role of parental care in the evolution of monogamy in the Barn Swallow.

Incubation Period

Daily attendance patterns during the incubation period were similar for both sexes; attendance was higher in the morning periods than in the afternoon. Although activities outside the nesting area were not directly observed in this study, the observed attendance patterns may reflect increased foraging abilities in the afternoon as aerial insect abundance probably increases with the increasing levels of light and temperature (Finlay 1971).

The sexes differed in their behaviours while attending nests. Females spent most of their time incubating while they attended nests. Males incubated more in the afternoon, and generally while alone. In other words, when females attended nests, they incubated, and males only incubated when females left the nesting area completely. The female brood patch is more developed than that of the male, therefore the female would be the more efficient incubator (Ball 1983), especially during cooler mornings. In the afternoon, when temperatures are higher, males can relieve females to allow them to forage.

Male investment in incubation is slight, but it is very important. Since males attend the nest even when not performing parental care duties, and since there is so much variability in incubation patterns, the male has the potential to and is available to relieve the female in times of stress. Male attendance while not performing direct parental care duties also may serve to reinforce or maintain the pair bond. This pattern of attendance also may be interpreted as indirect parental care, in that the male is available to incubate if the female requires relief.

The evolution of the inequality in male and female attendance and incubation patterns can be interpreted in various ways. Trivers (1972) suggests that the initially larger investment of the female in the offspring burdens her with a subsequently higher investment, as the female stands to lose more. Dawkins and Carlisle (1969) suggest that prospects of future investment, instead of past investment, affect behaviour. The end result is the same in both cases: females should invest slightly more than males during the breeding season.

Although parental investment theory seems to account for this inequality in behaviour patterns, it may be that even though female swallows spend more time during the incubation period, they actually invest less and take a lower risk in breeding than do males. Because swallows nest in an area that is protected from weather conditions and predators, parental care (incubation) duties could be less expensive and risky than non-parental care duties. This points out the main difficulty with Parental Investment theory - the quantification of investment (Knapton 1984).

Possibly the most straightforward way to interpret these behaviours is by invoking individual selection. Females have put forth the resources to produce eggs. If these eggs fail to hatch because of lack of care, the female will need to lay more or not reproduce that season. The female has a well developed brood patch, incubates in a protected area, and lives in an area where food is generally easily accessible and abundant. Thus, the reproductive success of the female would be maximized by incubating as often as possible.

The reproductive success of the male may be maximized in two ways. Maintaining the pair bond and participating in parental care activities may ensure that the female can forage and maintain her condition, so that she will be able to assist in future parental care activities. By attending the nest only a portion of the day during the incubation period the male retains the opportunity of seeking extra-pair copulations (Beecher and Beecher 1979). Thus, the male may maximize his reproductive success during the incubation period by attending the nesting area and incubating when necessary, and seeking extra-pair copulations at other times.

Nestling Period

Parental care of nestlings includes brooding, feeding and foraging for the young. Male and female behaviour during the nestling period is therefore influenced not only by parental needs, but also by the increasing demands of the young. Parents are equally able to provide care during this period therefore trends in male and female behaviour are more similar than during the incubation phase.

In contrast to the incubation period, the only daily trend in behaviour was in brooding. Males and females brooded more in the morning than in other periods of the day, probably because lower temperatures in the early morning made it necessary to provide warmth to the chicks. Parents must make trade-offs between brooding nestlings, feeding nestlings and self-maintenance during the nestling period. Since all these behaviours occur throughout the day, daily trends in behaviour are minimal.

Male and female Barn Swallows appear to be filling similar roles in the feeding of young. In other studies of Hirundinidae, similar feeding rates are common (Moreau 1939a,b, 1940; Allen and Nice 1952; Lefellar and Robertson 1986; Quinney 1986). Equal rates and time allocated to feeding activities suggest that monogamy is maintained, at least in part, by the need for both members of the pair to provide food for the nestlings. This conclusion is supported by Quinney's (1983) findings that Tree Swallows are monogamous except in areas of very high food abundance, where polygyny sometimes occurs.

General Conclusions

The majority of studies of the evolution of monogamy focus on male removal studies, designed to assess the importance of male parental care in a monogamous system. The effects of male removal and therefore uniparental care have been measured by the seasonal reproductive success of the unaided female, the physical fitness of the unaided female and young, and the number of feeding visits of the unaided female in comparison to an aided female. Results have varied from little or no effect to a large affect on female performance. Aside from the lack of information on lifetime reproductive success in most studies, and the unknown effect of manipulation to the system, these studies fail to examine natural parental care patterns and their effects.

Much of Barn Swallow breeding biology and mating system structure is tied to their mode of feeding (Lack 1968). As a consequence of feeding on aerial insects, Barn Swallows are able to nest in protected sites, which allows female domination of incubation and brooding duties, and the male possibilities for extra-pair copulations, as well as a high breeding success. The nature of their food resource precludes territoriality and makes monopolization of the mate very difficult - ultimately affecting the low level of polygamy in swallow species. Barn Swallows migrate long distances in order to feed where insects are abundant, which may lead to high adult mortality.

Analysed in light of the life history and behavioural ecology of an organism, comparisons of the behaviour and health of assisted and unassisted individuals as well as the growth and survival of their offspring may help us understand the evolution of monogamy. Information on how different tasks in the nesting cycle are allotted between the sexes can provide insight into role of parental care in maintenance of this mating system.

Although it is possible that one parent could raise some young unaided, the cost to those young and that parent may be too large for a non-monogamous system to evolve. Barn Swallows have a high breeding success compared to other passerines (Lack, 1968), but also high juvenile and adult mortality. If a single parent must raise young unaided, the consequences may include: 1) even lower probability of survival for the adult, 2) lower quality offspring, 3) lower chance of reproductive success in subsequent years, and 4) altered behaviour patterns. From the results reported here on breeding biology and parental care patterns of the Barn Swallow, I would expect uniparental care in the Barn Swallow, especially during the nestling period, to lower present and future reproductive success of individuals.

In this study I have characterized the mating system of the Barn Swallow in terms of breeding biology and parental behaviour, to understand the role of parental care in the evolution of monogamy in this species. Evidence for the advantage of monogamy to the species is the increased reproductive success of double-brooded and presumably older and previously mated pairs. The strength of the monogamous bond which is established or maintained during the nest building period and the efficient interactions of pair members throughout the rest of the breeding cycle allow individuals to maximize their reproductive success.

LITERATURE CITED

Adam, R.G. 1984. A study of Swallows in Orkney during 1984. Orkney Bird Report 1984: 64-67.

Allen, R.W., and M.M. Nice. 1952. A study of the breeding biology of the Purple Martin (Progne subis). Amer. Midl. Natur. 47: 606-665.

Altmann, S.A., S.S. Wagner, and S. Lenington. 1979. Two models for the evolution of polygyny. Behav. Ecol. Sociobiol. 2: 397-410.

A.O.U. 1957. Checklist of North American Birds Port City Press, Inc. Baltimore Md., U.S.A. 691 pp.

Ball, G.F. 1983. Functional incubation in male Barn Swallows. Auk 100: 98-100.

Beecher, I.M. and M.D. Beecher. 1979. Sociobiology of Bank Swallows: reproductive strategy of the male. Science 205: 1282-1285.

Bent, A.C. 1942. Life Histories of North American Flycatchers, Larks, Swallows, and Their Allies. U.S. Natl. Mus. Bull. 179. 538 pp.

Beyer, L.K. 1938. Nest life of the Bank Swallow. Wilson Bull. 50: 122-137.

Boyd, A.W. 1936. Report on the Swallow Enquiry, 1935. Brit. Birds 30: 98-116.

Brooke, M. de L. 1978. Some factors affecting laying date, incubation and breeding success of the Manx Shearwater (Puffinus puffinus Brunnich). J. Anim. Ecol. 47: 477-495.

Brown, C.R. 1978. Sexual chase in Purple Martins. Wilson Bull. 91: 583-591.

Bryant, D.M. 1975. Breeding biology of House Martins, Delichon urbica, in relation to aerial insect abundance. Ibis 117: 180-216.

Bryant, D.M. 1979. Reproductive costs in the House Martin Delichon urbica J. Anim. Ecol. 48: 655-675.

Butler, R.W. 1982. Wing fluttering by mud-gathering Cliff Swallows; Avoidance of 'rape' attempts. Auk 99: 758-761.

Carey, M. and V. Nolan Jr. 1979. Population dynamics of Indigo Buntings and the evolution of avian polyandry. Evolution 33: 1180-1192.

Collins, C.T. 1968. The comparative biology of two species of swifts in Trinidad, West Indies. Bull. Florida State Mus. 11: 257-320.

Coulson, J.C. 1966. The influence of the pair-bond and age on the breeding biology of the Kittiwake Gull, Rissa tridactyla. J. Anim. Ecol. 35: 269-279.

Crawford, R.D. 1977. The breeding biology of year-old and older female Red-winged and Yellow-headed Blackbirds. Wilson Bull. 89: 73-80.

Davies, C.E. 1977. Dispersion and nest-site fidelity in breeding Swallows (Hirundo rustica). Ibis 118: 470.

Davies, C.E. 1985. Cooperation and conflict among Dunnocks, Prunella modularis, a variable mating system. Anim. Behav. 33: 628-648.

Dawkins, R. and T.R. Carlisle. 1976. Parental investment and mate desertion: a fallacy. Nature, Lond. 262: 131-133.

De Steven, D. 1978. The influence of age on the breeding biology of the Tree Swallow, Iridoprocne bicolor. Ibis 120: 516-523.

Dyrcz, A. 1984. Breeding biology of the Mangrove Swallow, Tachycineta albilinea and the Greybreasted Martin, Progne chalybea at Barrow Colorado Island, Panama. Ibis 126: 59-66.

Edson, J.M. 1943. A study of the Violet-Green Swallow. Auk 60: 396-403.

Emlen, J.T. 1954. Territory, nest-building and pair formation in the Cliff Swallow. Auk 71: 16-35.

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

Evenden, F.G. 1969. Nesting of the Barn Swallow in western Oregon. Murrelet 30: 17-18.

Faaborg, J. and C.B. Patterson. 1981. The characteristics and occurrence of cooperative polyandry. Ibis 123: 477-484.

Finlay, J.C. 1971. Breeding biology of Purple Martins at the northern limit of their range. Wilson Bull. 86: 255-269.

Finney, G.H. and F. Cooke. 1978. Reproductive habits in the Snow Goose: The influence of female age. Condor 80: 147-158.

Georg, P.V. and M. Al-Rawy. 1970. Growth studies of the common Swallow. Bull. Iraq Nat. Hist. Mus. 4: 3-20.

Gladstone, D.E. 1979. Promiscuity in monogamous colonial birds. Am. Nat. 114: 545-557.

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

Gowaty, P.A. 1983. Male parental care and apparent monogamy among Eastern Bluebirds. Am. Nat. 121: 149-157.

Graul, W.D., S.R. Derrickson, and D.W. Mock. 1977. The evolution of polyandry. Am. Nat. 111: 812-816.

Greenlaw, J.S. and W. Post. 1985. Evolution of monogamy in seaside sparrows. (Ammodramus maritimus); tests of hypotheses. Anim. Behav. 33: 373-383.

Hails, C.J. 1984. The breeding biology of the Pacific Swallow (Hirundo tahitica) in Malaysia. Ibis 126: 198-212.

Hannon, S.J. 1984. Factors limiting polygyny in the Willow Ptarmigan. Anim. Behav. 32: 153-161.

Hosking, E. and C. Newberg. 1946. The Swallow. Collins, London. 59 pp.

Howe, H.F. 1979. Evolutionary aspects of parental care in the Common Grackle (Quiscalus quiscula L.). Evolution 33:41-51.

Jenni, D.A. 1974. Evolution of polyandry in birds. Amer. Zool. 14: 129-144.

Jenni, D.A. and G. Collier. 1972. Polyandry in the American Jacana (Jacana spinosa). Auk 89: 98-110.

Johnson, C.W. 1932. Notes on Protocalliphora during the summer of 1931. Bird-banding 3: 26-29.

Knapton, R.W. 1984. Parental Investment: the problem of currency. Can. J. Zool. 62: 2673-2674.

Kuerzi, R.G. 1941. Life history studies of the Tree Swallow. Proc. Linn. Soc. N.Y. 52: 1-52.

Kuzniak, S. 1967. Observations on the breeding biology of swallows, Hirundo rustica L.. Acta. Orn. 10: 177-211.

Lack, D. 1968. Ecological Adaptations for Breeding in Birds. London. Methuen. 409 p.

Leffelaar, D. and R.J. Robertson. 1986. Equality of feeding roles and the maintenance of monogamy in Tree Swallows. Behav. Ecol. Sociobiol. 18: 199-206.

Lincoln, F.C. 1931. Protocalliphora infestation of Barn and Cliff Swallows. Bird-banding 2: 33-34.

Lunk, W.A. 1962. The Rough-Winged Swallow: a study based on its breeding biology in Michigan. Publ. Nuttal. Orn. Club 4: 1-155.

Martin, R.F. 1980. Analysis of hybridization between the hirundinid genera Hirundo and Petrochelidon in Texas. Auk 97: 148-159.

Mason, E.A. 1953. Barn Swallow life history data based on banding records. Bird-banding 24: 91-100.

McGinn, D.B., and H. Clark. 1978. Some measurements of Swallow breeding biology in lowland Scotland. Bird Study 25: 109-118.

McKinney, F., K.M. Chong, and D.J. Bruggers. 1984. Sperm competition in apparently monogamous birds. Pp. 523-545 in Sperm Competition and the Evolution of Animal Mating Systems (R.L. Smith ed.). Academic Press, N.Y.

Medway, L. 1962. The swiftlets (Collocalia) of Niah Cave, Sarawak. I. Breeding Biology. Ibis 104: 45-66.

Mock, D.W. 1983. On the study of Avian Mating Systems Pp. 55-84. in Perspectives in Ornithology (A.H. Bush and G.A. Clark Jr. eds.). Cambridge University Press, Cambridge.

Møller, A.P. 1982. Clutch size in relation to nest size in the swallow Hirundo rustica. Ibis 124: 339-343.

Moody, D.T. 1968. Niche differentiating mechanisms in two sympatric species of swallows. Unpubl. M.S. Thesis, Central Washington State College, Ellensburg.

Moreau, R.E. 1939a. Parental care by some African Swallows and Swifts. British Ornithologists Club Bulletin 59: 145-149.

Moreau, R.E. 1939b. Numerical data on African birds' behaviour at the nest; Hirundo s. smithii Leach, the Wire-Tailed Swallow. Proc. Zool. Soc. Lond. 109: 109-125.

Moreau, R.E. and Moreau. 1940. Observations of Swallows and House Martins at the nest. British Birds 33: 146-151.

Nelson, J.B. 1966. The breeding biology of the Gannet, Sula bassana, on the Bass Rock, Scotland. Ibis 108: 584-624.

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

Oring, L.W. 1982. Avian mating systems. Pp. 1-79 in Avian Biology Vol VI (eds. Farner, D.S., J.R. King and K.C. Parkes), Academic Press, San Diego.

Oring, L.W. and S.J. Maxson. 1978. Instances of simultaneous polyandry by a Spotted Sandpiper, Actitis macularia. Ibis 120: 349-353.

Patterson, C.B., W.J. Mann and G.H. Orians. 1980. An experimental study of parental investment and polygyny in male blackbirds. Am. Nat. 116: 757-769.

Paynter, R.A. Jr. 1954. Interrelations between clutch-size, brood-size, prefledging survival and weight in Kent Island Tree Swallows. Bird-banding 25: 35-38, 102-110, 136-148.

Petersen, A.J. 1955. The breeding cycle in the Bank Swallow. Wilson Bull. 67: 235-286.

Pleszczynska, W.K. 1978. Microgeographic prediction of polygyny in Lark Bunting. Science 201: 935-937.

Post, W. and J.S. Greenlaw. 1982. Comparative costs of promiscuity and monogamy: a test of reproductive effort theory. Behav. Ecol. Sociobiol. 10: 101-107.

Purchon, R.D. 1948. The nesting activity of the swallow. Proc. Zool. Soc. London 118: 146-170.

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

Quinney, T.E. 1986. Male and female parental care in Tree Swallows. Wilson Bull. 98: 147-150.

Quinney, T.E. D.J.T. Hussel, and C. Davison Ankney. 1986. Sources of variation in growth of Tree Swallows. Auk 103: 389-400.

Ralls, K. 1977. Sexual dimorphism in mammals: Avian models and unanswered questions. Am. Nat. 111:917-938.

Ricklefs, R.E. 1968. Weight recession in nestling birds. Auk 85: 30-35;

Ricklefs, R.E. 1971. Foraging behaviour of Mangrove Swallows at Barrow Colorado Island. Auk 88: 635-651.

Samuel, D.E. 1969. The ecology, behavior and vocalizations of sympatric Barn and Cliff Swallows in West Virginia. Unpublished PhD dissertation, West Virginia University.

Samuel, D.E. 1971a. The breeding biology of Barn and Cliff Swallows in West Virginia. Wilson Bull. 83: 284-301.

Samuel, D.E. 1971b. Field methods for determining sex in Barn Swallows (Hirundo rustica). Ohio J. Sci. 71: 125-128.

SAS Institute Inc. 1985. SAS User's Guide: Statistics, Version 5 Edition. SAS Institute Inc, Cary, N.C.

Skutch, A.F. 1952. Life history of the Blue and White Swallow. Auk 69: 392-406.

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

Smith, W.P. 1933. Some observations of the nesting habits of the Barn Swallow. Auk 50: 414-419.

Snapp, B.D. 1973. The occurrence of colonial breeding in the Barn Swallow (Hirundo rustica) and its adaptive significance. Unpub. Ph.D. thesis. Cornell Univ.

Snapp, B.D. 1976. Colonial breeding in the Barn Swallow Hirundo rustica and its adaptive significance. Condor 78: 471-480.

Snow, D.W. 1962. Notes on the biology of some Trinidad Swifts. Zoologica, N.Y. 47: 129-139.

Speich, S.M., H.L. Jones and E.M. Benedict. 1986. Review of natural nesting of the Barn Swallow in North America. Amer. Midl. Natur. 115: 248-254.

Stoner, D. 1935. Temperature and growth studies on the Barn Swallow. Auk 52: 400-407.

Stoner, D. 1945. Temperature and growth studies of the Northern Cliff Swallow. Auk 62: 207-216.

Tate, P. 1981. Swallows H.F. and G. Witherby Ltd., London. 96 pp.

Trivers, R.L. 1972. Parental investment and sexual selection. Pp. 135-179 in Sexual Selection and the Descent of Man (B. Campbell ed.). Aldine, Chicago.

Turner, A.K. 1982. Timing of laying by Swallows (Hirundo rustica) and Sand Martins (Riparia riparia). J. Anim. Ecol. 51: 29-46.

Verner, J. 1964. Evolution of polygamy in the Long-billed Marsh Wren. Evolution 18: 252-261.

Verner, J. and M.F. Willson. 1966. The influence of habitats on mating systems of North American passerine birds. Ecology 47: 143-147.

Walsberg, G.E., and J.R. King. 1978. The energetic consequences of incubation for two passerine species. Auk 95: 644-655.

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

Wiley, R.H. 1974. Evolution of social organization and life-history patterns among grouse. Q. Rev. Biol. 49: 201-227.

Wilson, E.O. 1975. Sociobiology Harvard Univ. Press, Cambridge, Massachusetts.

Wittenberger, J.F. 1976. The ecological factors selecting for polygyny in altricial birds. Am. Nat. 110: 779-799.

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

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. Vandenbergh, eds.). Plenum, New York.

Wittenberger, J.F. 1982. Factors affecting how male and female bobolink apportion parental investment. Condor 84: 22-39.

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

Appendix A: Summary of mean percentage of ATT spent by A) females and B) males in behaviours during the breeding season.

A. Female

Period	Feed	Maintenance	Incubate/ Brood	Perch	Other
1	--	19.0	76.4	1.2	3.4
2	--	14.6	79.7	1.3	4.2
3	--	15.5	80.0	1.8	2.7
4	16.1	2.4	55.2	16.2	10.1
5	19.6	4.5	17.8	43.1	15.0
6	40.8	12.6	6.2	34.2	6.2

B. Male

Period	Feed	Maintenance	Incubate/ Brood	Perch	Other
1	--	33.0	34.6	30.2	2.2
2	--	30.5	48.2	18.2	3.1
3	--	20.6	45.7	30.7	3.0
4	25.4	3.2	31.6	35.5	4.3
5	34.2	8.3	31.6	36.1	12.4
6	46.1	36.5	--	17.4	--

VITA

Surname: Goley

Given Names: Patricia Dawn

Place of Birth: Mt. Holly, New Jersey

Date of Birth: September 17, 1961

Educational Institutions Attended, with Dates of Entering and Leaving:

University of North Carolina, Wilmington 1979 to 1983

University of Victoria 1983 to 1986

Degrees, Diplomas, Etc., Awarded, with Dates and Names of Institutions:

Bachelor of Science 1983 University of North Carolina, Wilmington

Master of Science 1986 University of Victoria

Honours and Awards:

King/Platt Memorial Scholarship

Lewis J. Clark Scholarship

University of Victoria Graduate Fellowship

Who's Who Among American Colleges and Universities

Phi Kappa Phi - National Honor Society

Phi Eta Sigma - National Freshman Honor Society

Publications:

Goley, P.D., and D.W. Webster. 1983. Seasonality in cetacean strandings along the coast of North Carolina (abstract). Journal of Elisha Mitchell Scientific Society 99(4): 171-172.

Webster, D.W., and P.D. Goley. (in press). Seasonality of cetacean strandings along the North Carolina Coast with annotated check list of the marine mammals of North Carolina. Brimleyana.