

**A COMPARISON OF THE PATERNITY DEFENSE  
STRATEGIES OF VIOLET-GREEN SWALLOWS AND  
TREE SWALLOWS**

by

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THESIS SUBMITTED IN PARTIAL FULFILLMENT OF  
THE REQUIREMENTS FOR THE DEGREE OF  
Doctor of Philosophy

in the Department  
of  
Biological Sciences

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SIMON FRASER UNIVERSITY

December 1994

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DEGREE: DOCTOR OF PHILOSOPHY

TITLE OF THESIS:

**A COMPARISON OF THE PATERNITY DEFENSE STRATEGIES OF VIOLET  
GREEN SWALLOWS AND TREE SWALLOWS**

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A comparison of the paternity defense strategies of violet-green

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## Abstract

I compared the paternity defense behaviour of males in two congeners, violet-green swallows *Tachycineta thalassina* and tree swallows *Tachycineta bicolor*. I showed that male violet-green swallows associated with their mates in temporal and spatial patterns characteristic of mate guarding. In contrast, male tree swallows did not guard their mates, instead they copulated frequently with their mates at times that indicated they were defending their paternity by either devaluing or displacing the sperm of potential competitors. The different paternity defense strategies of these congeners were correlated to the relative levels of competition for nest sites and female mates that each experienced. Male removal experiments demonstrated that absent male violet-green swallows suffered higher risks of mate loss than nest loss because male intruders tried to gain direct access to the female and ignored the nest site. Absent male tree swallows suffered high risks of both nest loss and mate loss because male intruders tried to usurp nests and gain access to the female who was guarding the nest. Once males were released tree swallows copulated frequently with their mates, whereas violet-green swallows did not. Female removal experiments demonstrated that absent female violet-green swallows were not replaced, whereas absent female tree swallows were usually replaced by female floaters.

I tested whether increased competition for nest sites would reduce time and energy allocated to mate guarding by male violet-green swallows by presenting a conspecific male model at nests. Male violet-green swallows increased time spent guarding nests while models were present, and did not follow their mates as closely as during controls, however males were able to continue guarding

their mates because females assisted by flying nearby. I did not show any change in copulation frequency between pairs of violet-green swallows after long periods of absence or after models of male intruders were present.

I expected that the temporary male removals would serve to reduce the male's perception of paternity in violet-green swallows but not tree swallows. I found no reduction in male parental care as a result of temporary male removals for either species.

## Acknowledgments

I thank my supervisory committee, Nico Verbeek, Dolph Schluter and Bernie Roitberg, for their advice throughout the planning and writing stages of the thesis. Nico Verbeek provided financial support with his NSERC operating grant and additional funding was provided by an NSERC post-graduate award and a J.K. Cooper award to me.

I appreciate the time and effort expended by Susan Hannon and Ian Jones in examining my thesis and I am especially grateful to Susan Hannon for the plethora of suggestions scribbled on her copy. Aside from sending me "to the board" during my defense I thank Bernie Roitberg for forcing me to re-examine the essence of my thesis and strengthen my arguments.

Early chapter improvements were heartily recommended by Guy Beauchamps, Elsie Krebs, Rob MacGregor and Wally Rendall. I give special thanks to Guy Martel for the comic strip, to Karen Wiebe for her taxidermic wizardry, and to Vic Bourne for his reassuring guidance at the photo-stand.

I was assisted in the field by many pairs of eyes. Sue Holroyd, Uli Bergmann, Kerry Dawson, Gail MacCrimmon and Grant MacHutchon dedicated hours and hours of their "sleeping-in" time to behavioural observations. Lawrence L.W. Schalla helped me with every logistical problem that arose (and they did tend to add up) including the construction of 100 nest boxes and a few less than 100 vehicular dilemmas.

The Creston Valley Wildlife Management Area was a good headquarters for research and the staff knew how to make a good thing even better. I am very grateful to the residents of West Creston who let me to hammer nest boxes onto their barns, etc., and peer around their yards in the wee hours of the morning. I

especially thank Bob Frandle, Adam Doerner, the Locheads, the Hopcrafts, the Albrechts, the entire Lawrence family, and Marg Berg, even though her cow ate one of my mist nets.

My lab/field mates provided much support and comic relief over the years. Dave Wiggins introduced me to swallows in the Creston Valley with an acrobatic leap into the marsh. Joanne Siderius helped me catch birds, rebuild nest boxes, persevere through stormy weather (literally and figuratively) and expand my literary range. Steve Wilson let me stay in his home even after the 5-berry jam episode. Wally Rendall shared his enthusiasm for swallows and smarties. Robin Gutsell shared her ideas about female mating strategies.

I have enjoyed the stimulation and support that came from being a part of the Behavioural Ecology Research Group at SFU. I have been inspired and encouraged by Ron Ydenberg as a teacher, contagiously enthused by Rob Houtman as a co-TA and boosted by Karen Price as a public speaking coach.

I have shared living accommodations with many interesting and supportive people namely Marilyn, Annabelle, Bob + Dave, Ian, Rebecca, Dave's dog Dave, Stef, Lourdes, Grant, Margriet, Tracy and Steve.

I thank all the friends who have helped me relax and have fun during the course of this degree, especially Grant MacHutchon. Grant stood by me through many moments of stress and despair without flinching. I thank him for being a steady source of support and encouragement.

I have benefited greatly from the companionship and good humour of sweet old Katie-dog. Kate has enjoyed her stay at SFU but we can't figure out why she hasn't earned a degree yet.

Finally I thank my parents for supporting my education and making so many wonderful things possible.

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## Chapter 1

### General Introduction

The mating systems of approximately 90 percent of all bird species are considered "monogamous" (Lack 1968) which means that one male and one female form a "pair bond" that may extend through one or more nesting events. With the advent of improved techniques for genetic analyses in the 1980s, (i.e., DNA fingerprinting) much attention has been focused on the parentage of offspring reared by "monogamous" pairs. Investigators have demonstrated that clutches with mixed parentage (containing offspring of more than one female, more than one male, or both) occur fairly frequently (Burke et al. 1989; Morton et al. 1990; Gowaty and Bridges 1991; Lifjeld et al. 1993). These findings indicate that "monogamy" in birds is part of a mixed reproductive strategy (Trivers 1972) in which matings occur outside the primary pair bond, but both members of the pair contribute substantially to the care and feeding of young from their own nest.

The discovery of mixed reproductive strategies has led to questions about the tactics used by males to defend their paternity. Mate guarding, which is "the close following of females by their mates during the female's fertile period" (Birkhead 1979), has been documented in many "monogamous" species (Beecher and Beecher 1979; Møller 1985; Birkhead et al. 1989; Lambrecht 1989). But recently, other methods of paternity defense, such as cloacal pecking (Davies 1983) and frequent pair copulations (Birkhead et al. 1987), have been recognized in birds. The evolution of these different paternity defense options remains largely unexplored.

It has long been accepted that time allocated to mate guarding may be constrained by time spent in the acquisition of extra-pair copulations (Parker 1974) and Leffelaar and Robertson (1984) and Birkhead et al. (1987) suggested that other ecological constraints, such as the need to defend nest sites or territories, may prevent or reduce the intensity and/or duration of mate guarding. Comparative work shows that males prevented from guarding mates use other forms of paternity defense, such as frequent intra-pair copulations, to achieve reproductive success (Birkhead et al. 1987; Møller and Birkhead 1991).

The goal of my thesis is to identify ecological factors involved in determining (1) the tradeoff between guarding mates and guarding nests and (2) the use of alternative paternity defenses. To do so, I explore the relationship between the paternity defense strategies and the breeding ecologies of two congeners, the tree swallow *Tachycineta bicolor* and the violet-green swallow *Tachycineta thalassina*. The tree swallow was one of the first species shown to guard nests rather than mates. Leffelaar and Robertson (1984) postulated that the lack of mate guarding exhibited by male tree swallows was due to a combination of factors including a scarcity of nest sites and a female-biased sex ratio. They suggested that closely related species with similar breeding ecologies should be studied to see whether they lacked mate guarding as well. I chose to study violet-green swallows because, like tree swallows, they nest in secondary cavities and they forage as aerial insectivores away from their nest sites. These two factors implied that violet-green swallows could be prone to nest competition and males would have to leave nests undefended to follow their mates on foraging trips. The breeding behaviour of violet-green swallows had never been documented before my study except in brief anecdotal reports on a few pairs (Shirling 1935; Bent 1942; Edson 1943; Franzeb 1976; Brown 1983).

Chapter 2 of the thesis shows that, unlike tree swallows, male violet-green swallows guard their mates rather than their nests and do not copulate frequently with their mates. Chapters 3 and 4 attempt to discover how the availability of nest sites and the operational sex ratio of the populations of violet-green and tree swallows are correlated to the tradeoff between guarding mates and nests in each species.

From the adaptationist's perspective, selection is an iterative and competitive process that eventually produces outcomes (behavioural phenotypes) that represent the best achievable balance of costs and benefits (Krebs and Kacelnik 1991). To understand what led to the evolution of different paternity defense strategies of tree and violet-green swallows, I tried to assess the fitness costs and benefits of guarding mates versus nest sites in each species (Chapter 3). I performed temporary removals of males and asked whether absent males faced higher risk of nest loss or paternity loss. Then I determined whether the risk of paternity loss could be alleviated by alternate forms of paternity defense (i.e., frequent pair copulations) after mates were released.

As the risk of mate loss depends to some extent on the abundance of unmated females relative to males, I temporarily removed resident females in both species and determined whether they were replaced (Chapter 4). The female removal also enabled me to assess the influence of female absence on their male mate's promiscuity and to check again whether alternate forms of paternity defense were used when females were released after extended periods of mate separation.

The temporary removal experiments suggested a correlation between the paternity defense strategies of each species and the risk of nest loss. To test for cause and effect I experimentally increased the risk of nest loss by presenting

model intruders at nest sites of violet-green swallows. Then I tested whether an increased demand to guard nests from conspecific male intruders would reduce the time that male violet-green swallows spent guarding mates (Chapter 5).

Many studies have tried to correlate variation in intensity or duration of paternity defense with variation in the amount of parental care contributed by the male (Craig and Jamieson 1985; Møller 1988; Burke et al. 1989; Westneat 1988; Whittingham et al. 1993). Males who spend less time or effort defending their paternity are predicted to have lower confidence in their paternity and therefore invest less in parental care (Trivers 1972). I took advantage of the male removal experiments (Chapter 3) as a means of lowering the paternity defense, hence, the confidence of paternity, in a group of treatment males. Then I tested whether the treatment males provided less parental care than a set of control males (Chapter 6). By contrasting the results for tree and violet-green swallows I tried to determine whether the form of paternity defense (i.e., mate guarding versus frequent pair copulations) alters the tendency to reduce parental care in response to lowered paternity assurance.

The final chapter summarizes the results from the previous chapters and discusses them in the context of the main goal of the thesis. By asking what ecological factors influence the tradeoff between guarding mates and guarding nests I hope to better understand why alternative paternity defense strategies evolved and how their evolution has influenced other aspects of the reproductive behaviour of monogamous birds.

## References

- Beecher, M.D, and Beecher, I.M. 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.
- Birkhead, T.R. 1979. Mate guarding in the magpie *Pica pica*. *Anim. Behav.* 27: 866-874.
- Birkhead, T.R., Atkin, L., and Møller, A.P. 1987. Copulation behaviour of birds. *Behaviour* 101: 101-138.
- Birkhead, T.R., Hunter, F.M. and Pellat, J.E. 1989. Sperm competition in the zebra finch, *Taeniopygia guttata*. *Anim. Behav.* 38: 935-950.
- Birkhead, T.R. and Møller, A.P. 1992. *Sperm Competition in Birds*. London: Academic Press.
- Brown, C.R. 1983. Vocalizations and behavior of Violet-green Swallows in the Chiricahua Mountains, Arizona. *Wilson Bull.* 95: 142-145.
- Burke, T., Davies, N.B., Bruford, M.W. and Hatchwell, B.J. 1989. Parental care and mating behaviour of polyandrous dunnocks *Prunella modularis* related to paternity by DNA fingerprinting. *Nature* 338: 249-251.
- Craig, J.L. and Jamieson, I.G. 1985. The relationship between presumed gamete contribution and parental investment in a communally breeding bird. *Behav. Ecol. Sociobiol.* 17: 207-211.
- Davies, N.B. 1983. Polyandry, cloaca-pecking and sperm competition in dunnocks. *Nature* 302: 334-336.
- Edson, J.M. 1943. A study of the Violet-green Swallow. *Auk* 60: 396-403.
- Franzeb, K.E. 1976. Nest site competition between Mountain Chickadees and Violet-green Swallows. *Auk* 93: 836-837.

- Gowaty, P.A. and Bridges, W.C. 1991. Nest box availability affects extra-pair fertilizations and conspecific nest parasitism in eastern bluebirds, *Sialia sialis*. *Anim. Behav.* 41: 661-676.
- Krebs J.K. and Kacelnik, A. 1991. Decision-making. In: *Behavioural Ecology* 3rd ed. (Ed. by Krebs J.R. and Davies, N.B.), pp.105-136. Oxford: Blackwell Scientific Publications.
- Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. London: Chapman and Hall.
- Lambrecht, J. 1989. Mate guarding in geese: awaiting female receptivity, protection of paternity or support of female feeding? In: *The Sociobiology of Sexual and Reproductive Strategies*. (Ed. by Rasa, A.E., Vogel, C., and Voland, E.), pp. 48-60. London: Chapman and Hall.
- Leffelaar, D. and Robertson, R.J. 1984. Do male tree swallows guard their mates? *Behav. Ecol. Sociobiol.* 16: 73-79.
- Lifjeld, J.T., Dunn, P.O., Robertson, R.J. and Boag, P.T. 1993. Extra-pair paternity in monogamous tree swallows. *Anim. Behav.* 45: 213-229.
- Møller, A. P. 1985. Mixed reproductive strategy and mate guarding in a semi-colonial passerine, the swallow *Hirundo rustica*. *Behav. Ecol. Sociobiol.* 17: 401-408.
- Møller, A.P. 1988. Paternity and paternal care in the swallow, *Hirundo rustica*. *Anim. Behav.* 36: 996-1005.
- Møller, A.P. and Birkhead, T.R. 1991. Frequent copulations and mate guarding as alternative paternity guards in birds - a comparative study. *Behaviour* 118: 170-186.
- Morton, E.S., Forman, L., and Braun, M. 1990. Extrapair fertilizations and the evolution of colonial breeding in Purple Martins. *Auk* 107: 275-283.

- Parker, G.A. 1974. Courtship persistence and female guarding as male time investment strategies. *Behaviour* 48: 157-184.
- Shirling, A.E. 1935. Observations on the Violet-green Swallow. *Wilson Bull.* 47: 192-194.
- Trivers, R.L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man, 1871-1971*. (Ed. by Campbell, B.), pp. 136-179. Chicago: Aldine-Atherton.
- Westneat, D.F. 1988. Male parental care and extrapair copulations in the Indigo Bunting. *Auk* 105: 149-160.
- Whittingham, L.A., Dunn, P.O., and Robertson, R.J. 1993. Confidence of paternity and male parental care: an experimental study in tree swallows. *Anim. Behav.* 46: 139-147.

## Chapter 2

### Males on guard: a comparison of the paternity defenses used by violet-green swallows and tree swallows

#### Abstract

I showed that, unlike the closely related tree swallow *Tachycineta bicolor*, male violet-green swallows *Tachycineta thalassina* attempted to ensure their paternity by mate guarding rather than by using frequent pair copulations. Male violet-green swallows followed females more often than the reverse and males followed their mates most frequently during the female's fertile period ( $64\pm 5\%$  of all female flights were followed between 6 days before egg laying until the day of the penultimate egg), and shortly after eggs were laid in the morning ( $78\pm 8\%$  of all female flights were followed between 0800-0900 hours). Pair copulations by violet-green swallows were rarely observed ( $0.13\pm 0.06$  copulation attempts per 30 min during the fertile period). In contrast, male tree swallows did not follow their mates more than the reverse and the occurrence of mate following did not peak during the fertile period (only  $23\pm 6\%$  of all female flights) nor after egg laying in the morning ( $37\pm 4\%$  of all female flights between 0800-0900 hours). Instead, the rate of pair copulations by tree swallows peaked during the fertile period ( $2.71\pm 0.64$  copulation attempts per 30 min) and between 0500-0600 hours during the egg laying stage ( $19.98\pm 9.81$  copulation attempts per 30 min). Violet-green swallows left their nests unguarded for a greater proportion of time during the fertile period ( $59\pm 4\%$ ) compared to tree swallows ( $35\pm 4\%$ ). The alternative paternity defenses used by these closely related species were discussed in light of differences in the degree of competition for nest sites and mates that each species experienced.



## Introduction

Sexual selection favours males that are best able to acquire mates and ensure fertilizations. Mate guarding has been recognized as a tactic used by males to (1) monopolize a female until she becomes available for insemination and (2) reduce the chances of sperm competition after insemination (Parker 1974). But not all males use mate guarding to achieve these goals. As an alternative, males monopolize females by acquiring and defending territories that incorporate parts of, or the entire home range of a female (Davies 1991). If the territory holds all the resources necessary for the female, defense of the territory and mate can be mutually inclusive, however, if the territory contains only a portion of the resources necessary for breeding, e.g., a nest site, the male faces the problem of being unable to simultaneously guard his territory and mate when she leaves to forage. Males of species facing this dilemma (or other constraints on time for mate guarding) use frequent pair copulations as an alternative to mate guarding (Birkhead et al. 1987; Møller and Birkhead 1991; Birkhead and Møller 1992).

The violet-green swallow *Tachycineta thalassina* is a close congener of the tree swallow *Tachycineta bicolor*. Both species nest in secondary cavities and forage as aerial insectivores away from their nest sites. Intense competition for nest cavities makes nest guarding a priority for tree swallows (Holroyd 1975; Leffelaar and Robertson 1985; Lombardo 1986). Male tree swallows are known to guard nests rather than mates (Leffelaar and Robertson 1984), and to use frequent pair copulations to defend their paternity (Venier and Robertson 1991). When I set out to document the paternity defense tactics of male violet-green swallows little was known about their breeding ecology. One study had documented intense competition for nest sites within a breeding population of

violet-green swallows in Arizona (Brawn and Balda 1988). Thus, I assumed that violet-green swallows would experience competition for nest sites.

Consequently, I predicted that nest guarding would restrict mate guarding and male violet-green swallows would use frequent pair copulations to defend their paternity. The results reported in this paper show that the behaviour of male violet-green swallows did not meet my expectations. Male violet-green swallows allocated more time to mate guarding than nest defense and copulated with their mates relatively infrequently. Here I document the paternity defense strategies of each species and discuss differences between them in light of what they may indicate about the relative levels of competition for nest sites versus mates in each species.

### **Predictions**

As mate guarding can be used for other purposes besides ensuring paternity, e.g., to enhance foraging success of females (Lumpkin 1983; Lambrecht 1989), I looked for characteristics that would indicate that mate guarding served a paternity assurance function (see Birkhead and Møller 1992 for a review). These characteristics were (1) that males would follow females rather than the reverse (Birkhead 1982); (2) that mate following and mate association would be greatest when females were most likely to be fertilized, i.e., during the female's fertile period (Beecher and Beecher 1979; Birkhead 1979) and in the morning soon after eggs were laid during the "insemination window" (Cheng et al. 1983); and (3) that mate following and mate association would be greatest when females were most susceptible to extra-pair fertilizations, i.e., when male intruders were present during the fertile period (Davies 1985; Møller 1985). If frequent pair copulations serve as a paternity defense then they should be related to female fertility and the risk of extra-pair fertilizations in the same way

as mate guarding (Birkhead and Møller 1992). Therefore, I predicted that pair copulation attempts would be most frequent (1) when females were most likely to be fertilized and (2) when females were most susceptible to extra-pair fertilizations.

### **General Ecology of the Study Species**

Violet-green swallows breed in western North America from Alaska to the Mexican highlands, rarely occurring east of the Rocky Mountains. They winter from Mexico south to Guatemala (Brown et al. 1992). Tree swallows breed throughout central and North America. Northern breeders winter primarily in Florida and along the Gulf of Mexico (Robertson et al. 1992).

Both species nest in holes found in decaying limbs, snags, and fenceposts, cavities excavated by other birds and artificial nest boxes. In addition, violet-green swallows nest in rock crevices and holes in dirt banks. The two species can be found in the same breeding habitat but violet-green swallows are more common in dry open woodlands and around settlements whereas tree swallows usually nest near water, e.g., marshes, shorelines and wooded swamps. As aerial insectivores, both species forage low over open fields and water but violet-green swallows often circle at higher altitudes.

Violet-green and tree swallows arrive on the breeding grounds in mid-March or early April. Males usually arrive and defend a nest cavity several days before females arrive. Nest spacing depends partly on the spacing of cavities but each pair of tree swallows typically defends an area within a radius of 10 to 15 m surrounding their nest site even if that includes more than one cavity (Robertson and Rendell 1990). Little is known about the territorial behaviour of violet-green swallows but colonies of closely spaced nests have been documented (Bailey 1928; Nichols 1938; Burleigh 1972; Morrison in Bent 1942).

Tree swallows begin laying eggs during the first week of May, approximately two weeks before violet-green swallows begin laying. Tree swallows lay 4 to 7 eggs and violet-green swallows lay 4 to 6 eggs. Eggs are incubated solely by the females of each species for 14 to 15 days. Young tree swallows leave the nest 18 to 22 days after hatching and young violet-green swallows leave after 23 to 24 days. Both parents of each species participate in feeding nestlings. Violet-green and tree swallows leave the breeding grounds by mid-August.

The average lifespan for a tree swallow is 2.7 year with a maximum of 8 years and little evidence of biases in annual survival due to age or sex (Butler 1988). There is no information about the lifespan or survivorship of violet-green swallows. Both sexes of tree swallow breed as yearlings if they can obtain nest sites (Stutchbury and Robertson 1985). I expect the same would be true of violet-green swallows and I have records of yearling females breeding in west Creston. The average body mass of violet-green swallows (16 g) is smaller than the average body mass of tree swallows (21 g) but the average size (18.7 x 13.1 mm) and average mass (1.9 g) of their eggs are similar (Brown et al. 1992; Robertson et al. 1992).

## **Methods**

### **Study Area and Subjects**

The study was conducted at the Creston Valley Wildlife Management Area in southeastern British Columbia (49°05'N, 116°35'W). Data for violet-green swallows were collected between April and June of 1988 and data for tree swallows were collected between April and June of 1990.

Violet-green swallows nested in boxes mounted 15 to 30 m apart on the walls of cabins, barns and garages on hillsides adjacent to marshland. Tree swallows nested in boxes mounted on poles approximately 30 m apart along

several dikes around marshland. No pair of either species defended more than one nest box at a time. Contents of nest boxes were checked every third day before laying and every day throughout the laying period to determine the first and last day of laying.

I captured birds with mist nets in April and marked each with colored leg bands and streaks of acrylic paint on the wing, tail and breast feathers in specific color patterns for individual identification. Violet-green swallows could be sexed easily by plumage, but the sex of male and older female (after second year) tree swallows was difficult to determine (Hussell 1983) so subsequent behaviour during copulation attempts was used to confirm the sex of marked individuals (Cohen 1984).

### **Behavioural Observations**

Marked pairs were observed for 30 min periods every third to fifth day from the beginning of nest building to the end of incubation. I observed 15 pairs of violet-green swallows and 14 pairs of tree swallows. Most observations were conducted between 0500 and 1300 hours and some were conducted late in the afternoon or early evening.

During all observation periods I watched the nest site and surrounding area. I continuously observed the pair when they were in sight and any intruders that landed within 10 m of the nest box or pair. I recorded the time of all arrivals and departures, the frequencies of chases, and attempted copulation mounts (both successful and unsuccessful) by mates and extra-pair males. A single copulation attempt was scored each time a male hovered over a female or attempted to make cloacal contact.

I calculated (1) the proportion of flights away and overhead by the female that were followed by the male within 1 min and vice versa, (2) the time when mates

were together as a proportion of the total time that either or both were present, (3) the proportion of the watch when females were unguarded (i.e., the sum of the time during which the female and the male were present separately divided by total observation time) and (4) the proportion of the watch when nest sites were left unguarded.

The nesting season was divided into 3 periods with respect to female fertility. The pre-fertile period lasted from 22 days to 7 days before the first egg was laid. The fertile period included the 6th day before egg laying to the day when the penultimate egg was laid. The post-fertile period began on the last day of egg laying and ended 14 days later. Data collected during watches in each of these periods were averaged for each marked pair. Mean ( $\pm$ SE) date, day with respect to the first day of egg laying, and duration of observations for nests watched in each of these periods were summarized in Table 2.1.

Within the fertile period, I grouped watches according to whether an extra-pair male had intruded or not. My criterion for the occurrence of an intrusion was either of the following: (1) that an extra-pair male had been perched within 10 m of the pair for at least 5 s or (2) that an extra-pair male had swooped at, chased, or attempted to copulate with the female at least once during the watch. I compared the average values of data collected during watches when intrusions occurred to those when they did not for each nest that had experienced both during the fertile period.

### **Statistical Analyses**

I examined whether there was a tendency for each male to follow his female more than the reverse using  $X^2$  tests. I evaluated the significance of each  $X^2$  test at a table-wide level of 0.05 using a sequential Bonferroni test (Rice 1989). I compared the fertile period to the pre- and post-fertile periods with respect to

Table 2.1. Mean ( $\pm$  SE) date (day 1 = April 1), mean day with respect to egg laying (day 0 = day when first egg was layed) and mean duration (h) of observation time per pair of violet-green swallows and tree swallows during the pre-fertile, fertile, and post-fertile periods. N=total number of pairs observed.

Variable	Violet-green swallows			Tree swallows		
	pre-fertile N=15	fertile N=15	post-fertile N=15	pre-fertile N=14	fertile N=14	post-fertile N=14
Date	55.0 $\pm$ 3.3	65.3 $\pm$ 3.4	77.1 $\pm$ 3.0	39.5 $\pm$ 1.8	52.6 $\pm$ 2.6	63.3 $\pm$ 2.1
Day	-11.9 $\pm$ 0.8	-1.7 $\pm$ 0.6	10.1 $\pm$ 0.7	-13.4 $\pm$ 0.9	-0.3 $\pm$ 0.5	10.6 $\pm$ 1.0
Duration	1.6 $\pm$ 0.2	2.3 $\pm$ 0.3	2.8 $\pm$ 0.4	2.7 $\pm$ 0.5	2.0 $\pm$ 0.3	1.2 $\pm$ 0.5

mate guarding and the rate of pair copulation attempts using Friedman tests ( $\chi^2$ ) (Siegel 1956) followed by orthogonal comparisons of the fertile period with each of the other periods (Hollander and Wolfe 1973). I used Wilcoxon paired-sample tests to compare mate guarding and copulation frequencies between watches with male intruders and watches without male intruders (Siegel 1956). Comparisons within species were one-tailed. I used two-sample Komogorov-Smirnov tests to compare the distributions of data for mate association, nest guarding and rates of pair copulation between violet-green swallows and tree swallows (Siegel 1956). Comparisons between species were two-tailed. Statistics were computed with the SYSTAT statistical package (SYSTAT, Inc. 1986; Wilkinson 1986). Statistical significance was accepted at  $p < 0.05$ . Unless otherwise stated, non-significant results must be considered inconclusive because small samples did not produce sufficient power ( $1-\beta$ ) to detect differences. The power values of my tests were estimated by calculating 90% of the power of equivalent parametric tests (Cohen 1977). Numbers reported in the text are means  $\pm$  standard errors unless otherwise stated.

## **Results**

### **Violet-green swallows**

Male violet-green swallows can be classified as mate guarders on the basis of their high frequency of mate following (Table 2.2). Their guarding behaviour fit several of the criteria that characterize paternity defense. Males followed females more often than the reverse (Table 2.2) and males followed their mates on a higher proportion of flights during the fertile period than either the pre- or post-fertile periods (Table 2.3). Mates spent a greater proportion of the time present together during the fertile period than the post-fertile period and the proportion of all observation time when females were unguarded was



Table 2.2. The frequency of flights made by mates within 1 min of each other are compared to determine whether males followed females (MFF) more often than females followed males (FFM). All flights that occurred during observations in the fertile period of 10 pairs of violet-green swallows and 7 pairs of tree swallows were included. Only pairs for which expected frequencies were at least 5 were used (Siegel 1956). One-tailed probabilities are shown for each test. \* indicates significance at a table-wide level of 0.05 for each species using a sequential Bonferroni correction.

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Violet-green swallows					Tree swallows				
Pair	MFF	FFM	$\chi^2$	P	Pair	MFF	FFM	$\chi^2$	P
BW	10	5	1.67	.05<P<.1	T205	7	3	1.60	.2<P<.3
PAL	16	1	13.24	P<.001*	T206	3	8	2.27	.1<P<.2
V10	29	7	13.44	P<.001*	T207	6	5	0.09	.7<P<.8
V107	26	2	20.57	P<.001*	T209	17	7	4.17	P<.05
V121	26	12	5.16	P<.03	T212	8	11	0.47	.3<P<.5
V17	13	4	4.76	P<.03	T215	7	4	0.82	.3<P<.5
V2	45	11	20.64	P<.001*	T216	10	7	0.53	.3<P<.5
V48	10	0	10.00	P<.01*					
V49	51	12	24.10	P<.001*					
V5	26	3	18.20	P<.001*					

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Table 2.3. Means ( $\pm$ SE) of the proportion of female flights that were followed by mates within 1 min, the proportion of time that mates spent perched in sight together, the proportion of time that the female was unguarded by her mate (proportion of watch when the female was perched alone plus the proportion of watch when the male was perched alone) and the frequency of pair copulation attempts per 30 min during the pre-fertile, fertile and post-fertile periods.

Variable		Pre-Fertile	Fertile	Post-Fertile	$\chi_r^2$	P
Violet-green swallow N=15	proportion of female flights followed	0.29 $\pm 0.06$	* 0.64 $\pm 0.05$	* 0.26 $\pm 0.04$	12.54	.002
	proportion of time mates together	0.48 $\pm 0.07$	0.60 $\pm 0.06$	* 0.39 $\pm 0.06$	6.14	.046
	proportion of time female unguarded	0.22 $\pm 0.04$	0.17 $\pm 0.04$	* 0.37 $\pm 0.05$	10.53	.005
	frequency of pair copulations	0.01 $\pm 0.01$	0.13 $\pm 0.06$	0.05 $\pm 0.02$	1.23	.540
Tree swallow N=14	proportion of female flights followed	0.20 $\pm 0.03$	0.23 $\pm 0.06$	0.22 $\pm 0.08$	0.88	.646
	proportion of time mates were together	0.42 $\pm 0.04$	0.39 $\pm 0.06$	* 0.24 $\pm 0.04$	11.58	.003
	proportion of time female unguarded	0.28 $\pm 0.03$	0.38 $\pm 0.04$	* 0.59 $\pm 0.04$	17.71	.001
	frequency of pair copulations	1.91 $\pm 0.74$	2.71 $\pm 0.64$	* 0.92 $\pm 0.92$	7.00	.030

\* Values of the fertile period were significantly different from values in the adjacent period.

significantly lower during the fertile period than the post-fertile period (Table 2.3).

No precise measure of egg laying time was obtained but the evidence available from occasional early morning nest checks indicated that eggs were usually laid between 0530 and 0730. In domesticated birds fertilization generally occurs within 30 min of ovulation, which in turn occurs usually within 2 h of laying the previous egg (Howarth 1974; Sturkie 1976). Therefore, female violet-green swallows likely would have been fertilized sometime between 0600 and 0930. Although equally high proportions of female flights were followed between 0600 and 0700, 0800 and 0900, and 1000 and 1100, the variation around the peak between 0800 and 0900 was lower than the variation at these other times (Figure 2.1). Thus, a consistently high proportion of flights were followed within the range of time when fertilization was probable.

There was no significant difference in the number of intrusions, chases or extra-pair copulation attempts by male intruders with respect to fertility but intruder presence tended to decline from high levels during the pre-fertile and fertile periods to low levels during the post-fertile period (Figure 2.2). There was a peak in the number of intrusions between 0800 and 0900 hours during egg laying (Figure 2.3) which coincided with the most consistent peak in the proportion of female flights that were followed by males (Figure 2.1) and the range of time when fertilization was probable. Within the fertile period there was no significant effect of the presence of male intruders on mate following, the proportion of time mates spent together or the proportion of time when females were unguarded, but the power values of my tests were low (Table 2.4).

The rate of observed pair copulations by violet-green swallows was very low and did not follow a pattern with respect to the fertile period ( $1-\beta \sim 0.40$ ; Table

Figure 2.1. Mean proportion of female flights that were followed by her mate within 1 min during observations of nests at each hour of the morning during the egg laying period (i.e., from the first day of egg laying until and including the day when the penultimate egg was laid). Bars indicate standard errors. The mean  $\pm$  SE number of female flights per pair of swallows and the number of pairs that were observed are shown above each bar.

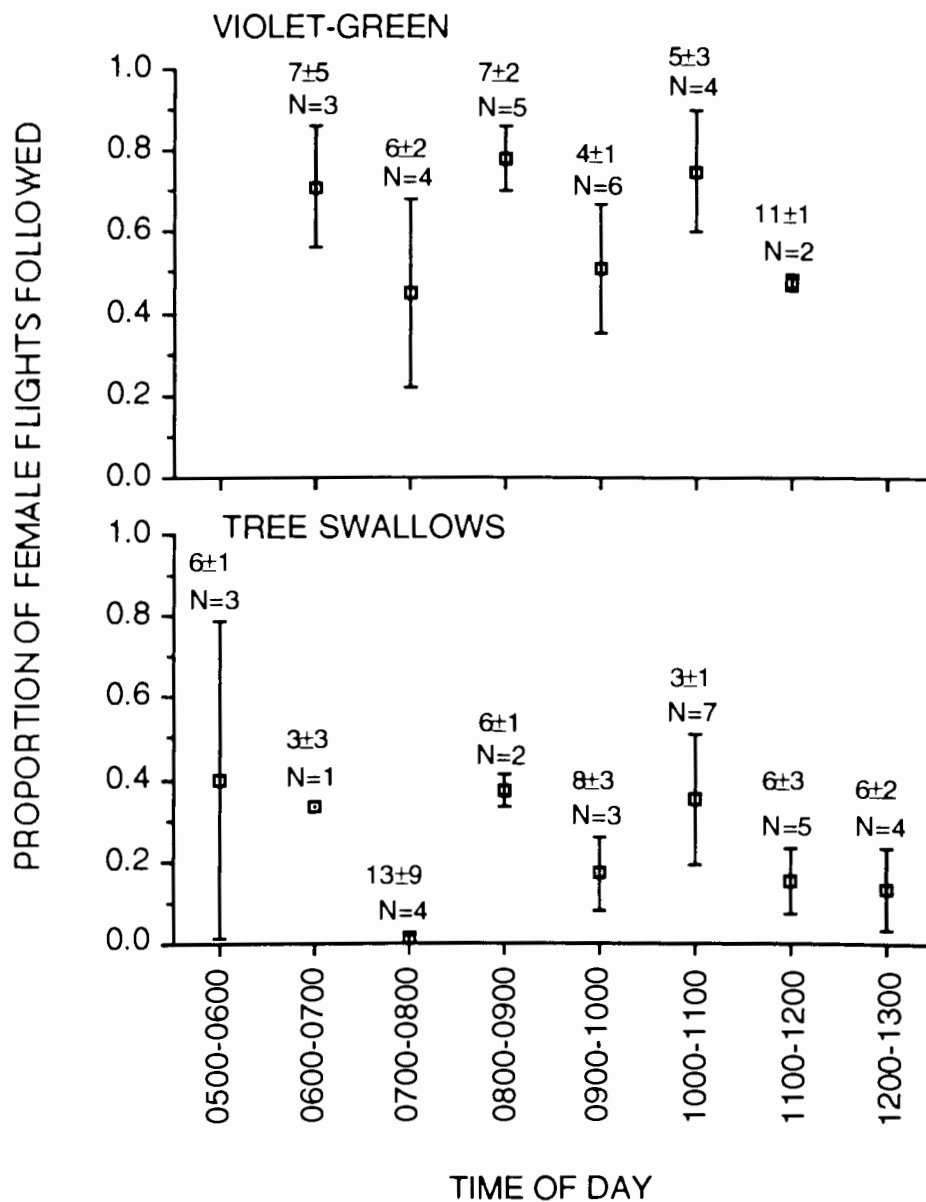


Figure 2.2. Mean frequency of intrusions by extra-pair males during the pre-fertile, fertile and post-fertile periods. Intrusions occurred when an extra-pair male landed within 10 m of the pair for at least 5 s (LANDINGS), swooped at or chased the resident female (CHASES) and attempted to copulate with the resident female (EPC ATTEMPTS). (N=15 for violet-green swallows; N=14 for tree swallows). Frequencies were calculated per 30 min of observation time. Bars indicate standard errors.

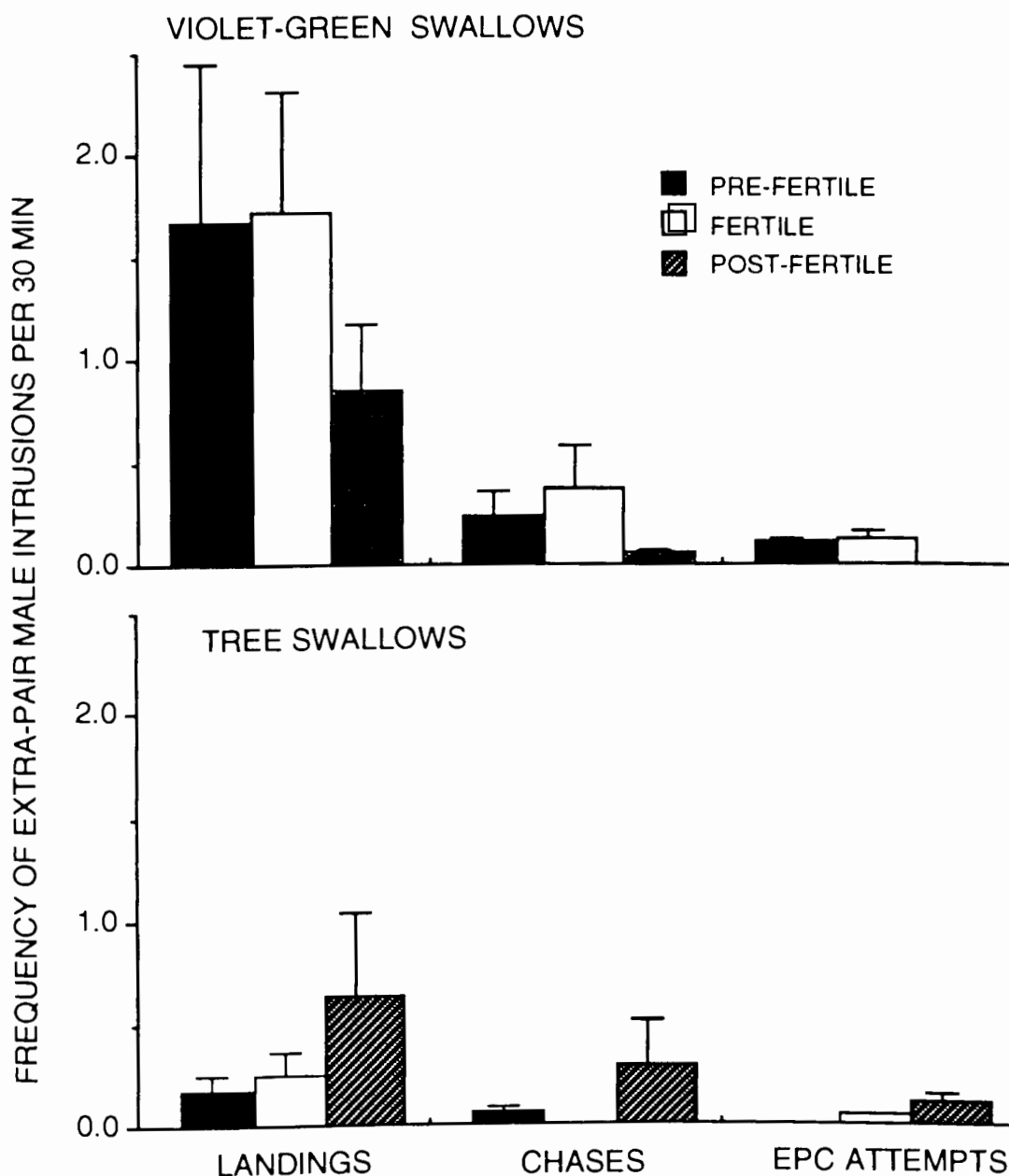


Figure 2.3. Mean frequency of male intruder landings within 10 m of the pair or nest at each hour of the morning during the fertile period (from the first day of egg laying until and including the day when the penultimate egg was layed). Frequencies were calculated per 30 min of observation time. Bars indicate standard errors and the number of observed pairs are shown above each bar.

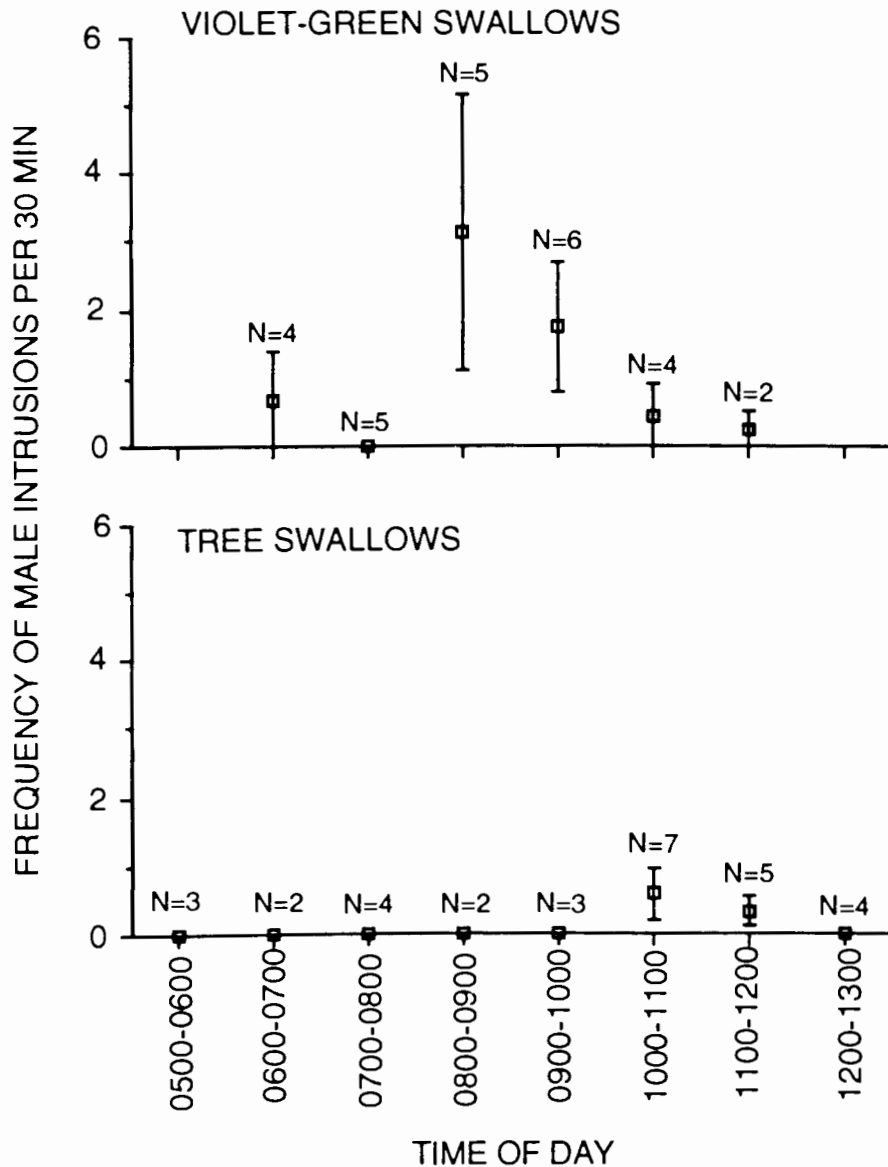


Table 2.4. Means ( $\pm$ SE) of the proportion of female flights that were followed by mates, the proportion of time that mates spent perched together, the proportion of time that the female was unguarded by her mate (proportion of watch when the female was perched alone plus the proportion of watch when the male was perched alone) and the frequency of pair copulation attempts per 30 min during the fertile period when a male intruder had been present or absent.

	Variable	Male Intruder Present	Male Intruder Absent	P	1- $\beta$
Violet-green swallows N=8	proportion of female flights followed	0.64 $\pm$ 0.09	0.47 $\pm$ 0.09	.173	.34
	proportion of time mates spent together	0.70 $\pm$ 0.10	0.55 $\pm$ 0.10	.132	.23
	proportion of time female unguarded	0.57 $\pm$ 0.08	0.20 $\pm$ 0.07	.155	.06
	frequency of pair copulations	0.36 $\pm$ 0.17	0.06 $\pm$ 0.06	.034	
Tree Swallows N=7	proportion of female flights followed	0.26 $\pm$ 0.11	0.21 $\pm$ 0.06	.368	.12
	proportion of time mates spent together	0.23 $\pm$ 0.07	0.34 $\pm$ 0.07	.155	.23
	proportion of time female unguarded	0.45 $\pm$ 0.07	0.42 $\pm$ 0.05	.400	.09
	frequency of pair copulations	1.63 $\pm$ 1.17	1.80 $\pm$ 0.65	.343	.07

2.3). There were too few observed pair copulations during egg laying to see any pattern with respect to time of day (Figure 2.4). There was, however, a significantly higher frequency of pair copulations when male intruders were present than when they were absent, despite the small number that were observed (Table 2.4).

### **Tree swallows**

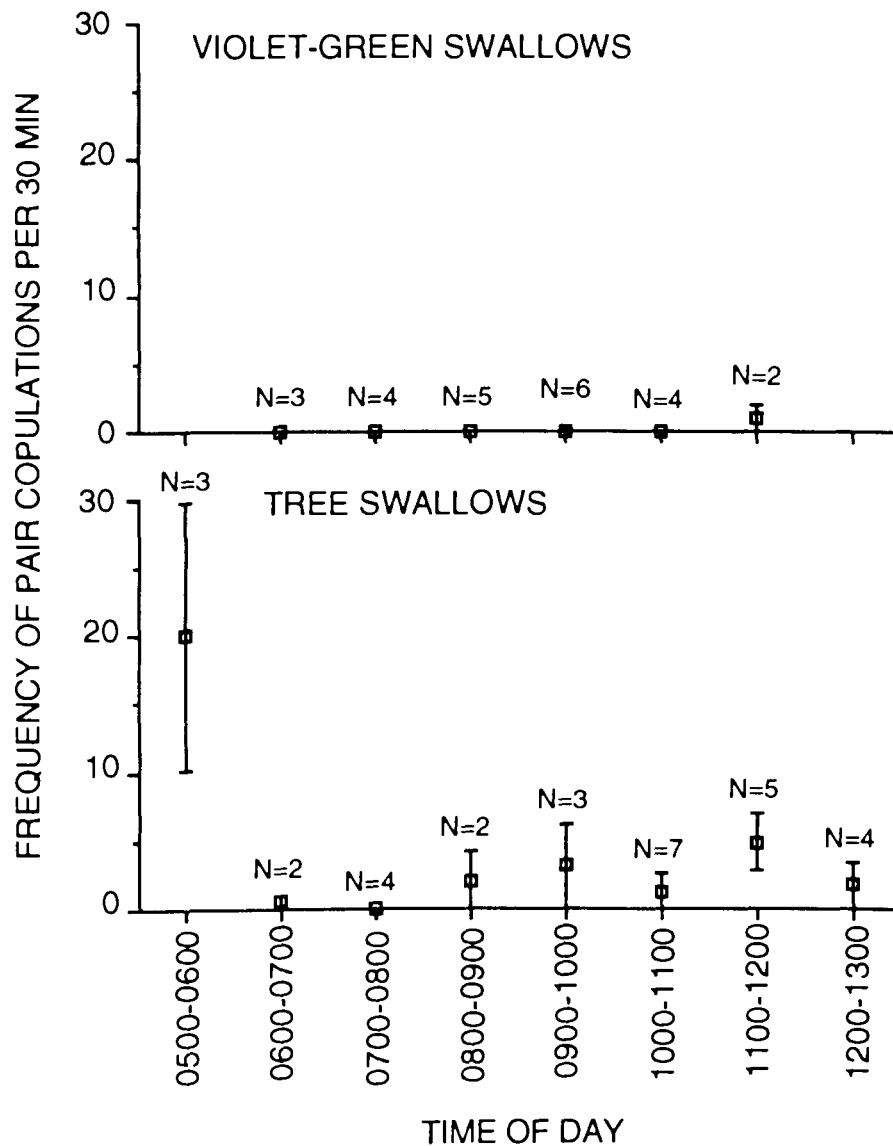
Unlike violet-green swallows, male tree swallows were not more likely to follow females than the reverse (Table 2.2) and the proportion of female flights that were followed by mates did not increase during the fertile period (Table 2.3). Mates spent less time together and females were unguarded a greater proportion of the time than their congeners (Kolmogorov-Smirnov tests:  $P=0.04, P=0.001$ , respectively). However, like violet-green swallows, mates were together a greater proportion of the time during the fertile period than during the post-fertile period (Table 2.3). There was no clear pattern in the proportion of female flights followed by mates with respect to time of day during egg laying except that almost no flights were followed between 0700 and 0800 (Figure 2.1).

The most dramatic difference between violet-green and tree swallows was in the observed rate of pair copulation attempts. Tree swallows copulated much more frequently than violet-green swallows (Kolmogorov-Smirnov test:  $P<.001$ ). The rate of pair copulation attempts for tree swallows was significantly higher during the fertile period than the post-fertile period (Table 2.3) which is consistent with the hypothesis that frequent pair copulations serve a paternity protection function.

Tree swallows laid their eggs between 0630 and 0730 ( $N=3$ ), which is similar to the range of laying times (0620-0805) for tree swallows in Ontario



Figure 2.4. Mean frequency of pair copulations, including unsuccessful and successful copulation attempts at each hour of the morning during the egg laying period (from the first day of egg laying until and including the day when the penultimate egg was laid). Frequencies were calculated per 30 min of observation time. Bars indicate standard errors and the number of observed pairs are shown above each bar.



(Venier and Robertson 1991). Thus, the fertilization window for tree swallows would have occurred sometime between 0700 to 0900. There was a distinct peak in the frequency of pair copulations first thing in the morning (Figure 2.4) but this peak occurred prior to egg laying when there would have been an egg blocking the passage of sperm to the infundibulum where fertilization of the next egg would occur.

There was no increase in the number of intrusions, chases or extra-pair copulation attempts by male intruders during the fertile period compared to the other two periods (Figure 2.2) and no pattern with respect to time of day (Figure 2.3). The power of my tests was too low to determine whether there was an effect of the presence of male intruders on any of the measures of mate association or the frequency of pair copulations within the fertile period (Table 2.4).

Tree swallows left their nest sites unattended for  $35\pm 4\%$  (range: 6-66%) of the time that they were observed during the fertile period, substantially less than violet-green swallows left their nest sites unattended ( $59\pm 4\%$ ; range: 20-87%) (Kolmogorov-Smirnov test:  $P < .001$ ).

Table 2.5 summarizes my results for the predictions that test whether males of each species were using mate guarding or frequent pair copulations to defend their paternity.

## **Discussion**

First I examine whether my observations fit my predictions about how the frequency and duration of mate guarding and pair copulations would vary with respect to fertility and the risk of extra-pair fertilizations for each species.

Second, I examine the dichotomy between the two paternity defense strategies

Table 2.5. Summary of results for the predictions that test whether males of each species were using mate guarding or frequent pair copulations to defend their paternity. I report that the results were equivocal if the predicted trend was not significant and the power of the test was less than 80%. \* indicates that the behaviour was infrequent for that species relative to the other.

Prediction	Violet-green swallows	Tree swallows
<i>If males guarded mates to defend paternity then:</i>		
Males followed females rather than the reverse	Yes	No
Mate following was most frequent in fertile period	Yes	Equivocal*
Mate association was longest in fertile period	Yes	Yes*
Mate following was most frequent during the insemination window	Equivocal	Equivocal*
Mate following was most frequent when a male intruder was present	Equivocal	Equivocal*
Mate association was longest when a male intruder was present	Equivocal	Equivocal*
<i>If pairs copulated frequently to defend paternity then:</i>		
Pair copulations were most frequent in the fertile period	Equivocal*	Yes
Pair copulations were most frequent during the insemination window	Equivocal*	No
Pair copulations were most frequent when a male intruder was present	Yes*	Equivocal

and propose factors that may have caused violet-green swallows to behave differently from tree swallows.

### **Observations and predictions**

Given the definition of mate guarding as "the close following of a female by her mate during the fertile period" (Beecher and Beecher 1979; Birkhead 1979), there is no question that male violet-green swallows were mate guarding. Although alternative hypotheses have been proposed for the functional significance of males following females (see Birkhead and Møller 1992 for a review), three of my results indicate that male violet-green swallows were following their mates to protect their paternity: (1) males followed females rather than the reverse, (2) following behaviour and the duration of mate association peaked during the female's fertile period, and (3) following behaviour was most consistently high within what was likely the "insemination window" after egg laying. I was unable to test whether males increased mate following and mate association when extra-pair males intruded during the fertile period because of small sample sizes. In addition I may have missed events that would have heightened the males' perceived risk of extra-pair fertilizations during watches when no intrusions were recorded. For example, an extra-pair male could have intruded just minutes before an observation period began or on a foraging flight during the watch when the pair was out of view.

Although they were infrequent, the timing of pair copulations by violet-green swallows was related to the risk of extra-pair copulation. During 5 of the 9 watches when both a pair copulation and an intrusion occurred, the intruder arrived within 1 min prior to the copulation attempt. Males of other mate guarding species are known to copulate with their mates immediately following the intrusion of a male into the territory and these copulations were interpreted

as a response that would reduce the threat of extra-pair copulations (Westneat 1987; Birkhead et al. 1989; Simmons 1990).

The low frequency of pair copulations by violet-green swallows fits the pattern for a mate guarder (Birkhead et al. 1987; Møller and Birkhead 1991). But, to date, no one has explained why mate guarders do not use frequent pair copulations as well as mate guarding to defend their paternity. There are numerous costs that could be associated with copulating (Daly 1978) but no one has demonstrated their effect on the frequency of pair copulations. Several studies have shown that pair copulations attract extra-pair males who disrupt the pair and attempt extra-pair copulations (Trail 1985; Hatchwell 1988; Birkhead et al. 1985) and there is evidence to support the idea that birds could be selected to copulate inconspicuously and infrequently to avoid such costly interference, e.g., copulating pairs of common guillemots *Uria aalge*, living at high densities experienced higher rates of interference than those living at low densities and the frequency of pair copulations was lower at high densities (Hatchwell 1988). The data I collected on violet-green swallows, however, did not support this idea. First, violet-green swallows do not copulate inconspicuously within their nests unlike some other cavity nesting birds (e.g., bank swallows *Riparia riparia*, Beecher and Beecher 1979). I never saw male violet-green swallows enter nests with their mates. Second, although I originally suspected that the positive association between pair copulation attempts and extra-pair male intrusions was due to pair copulations attracting male intruders, that was rarely the case. During 7 of the 9 watches when both occurred, the extra-pair male intruded before the pair copulated rather than after. Thus, there was no evidence to support the idea that pair copulations provoked intrusions by extra-pair males. An explanation for the low number of

pair copulations by violet-green swallows will require further research into the costs of copulations for each sex.

The lack of mate guarding and the frequency of pair copulations by tree swallows in my study correspond to the results from studies of tree swallows in Ontario (Leffelaar and Robertson 1984; Venier and Robertson 1991). Mates did spend a greater proportion of time together during the fertile than the post-fertile period but, like Leffelaar and Robertson (1984), I do not think that this constituted "mate guarding" because males rarely followed their mates during this period. Instead, greater mate association during the fertile period was likely due to an increase in the time that mates spent copulating.

The frequency of pair copulations peaked during the fertile period as expected, but not at the time of day during egg laying when fertilization was most likely. Instead, the peak in copulation attempts occurred during the first hour of observation in the morning before eggs would have been laid. This finding differed from the results reported by Venier and Robertson (1991). They showed that the frequency of morning copulations was low during egg laying and attributed their finding to a decline in female availability for copulation at that time of the day. Females were not available because they were inside their nests laying eggs. I also found that the lowest rates of pair copulation occurred between 0600 and 0800 when females were laying eggs. But my study showed that females were available for copulations before 0600. In fact, pairs spent a greater proportion of their time present together between 0500 and 0600 ( $65\pm 14\%$ ) than at any other time of the day. The time that mates spent together after 0900 was only  $20\pm 7\%$ . Once females finished laying, they left their nests to forage. Thus, females made themselves less available for pair copulations after egg laying than before. I can think of three factors that could determine

why females would stay around nests before laying and not afterward. By staying near her nest before laying a female could (1) minimize the risk of being out of reach of a safe haven for her egg when it came time to lay; (2) minimize her physical exertion and thereby minimize the risk of injury to herself and the egg that she is carrying; and (3) avoid paying the costs of foraging with the extra weight of the fully developed egg inside her. Once the egg has been laid, there would be no risks of egg loss or injury and lower costs of foraging. Thus, a female in need of food for her own maintenance and to complete her clutch would gain more by foraging after her egg was laid than before.

Several studies have shown that the last male to copulate with the female before fertilization will have the greatest chance of fertilizing her egg (Compton et al. 1978; Birkhead et al. 1988) and a recent examination of the morphology of the sperm storage tubules in the oviducts of females indicated that last-male precedence for fertilization is possible for tree swallows (Briskie and Montgomerie 1993). Thus, if females were not available for frequent pair copulations during the "insemination window" then the best strategy for males would be to copulate with their mates just before laying.

### **Comparison of paternity defense strategies**

The different paternity defenses used by violet-green and tree swallows are consistent with the dichotomy found in surveys of monogamous species (Birkhead et al. 1987; Møller and Birkhead 1991). The main factor distinguishing species which used mate guarding from those which used frequent pair copulations was the male's ability to follow his mate and prevent extra-pair copulations. Those species that were restricted from mate following used frequent pair copulations to compete with any extra-pair copulations that females received while they were away. Violet-green swallows and tree

swallows both nest in secondary cavities and forage away from their nest sites. I assumed that violet-green swallows would compete for nest sites as did tree swallows (Holroyd 1975), thus, I predicted that the need to guard nest sites would restrict male violet-green swallows from following their mates. My results did not support this prediction. Violet-green swallows left their nests unattended a large proportion of the time to forage with their mates out of sight of their nests. There was no indication that nest guarding restricted mate following. In contrast, tree swallows spent less time away from their nests and when one member of the pair left to forage, the other stayed behind to guard the nest. Clearly, it is necessary to test my assumption that violet-green swallows compete for nest sites.

Although long periods of absence did not usually result in nest loss for violet-green swallows, some intra-sexual fights at nests were observed and nests were occasionally usurped by other species, (e.g., tree swallows, house wrens *Troglodytes aedon* ; pers. obs.). However, when nests were usurped, violet-green swallows were always able to reneest in an unoccupied site nearby. Violet-green swallows occupied 31 to 47% of the nest boxes available to them between 1988 and 1990. Other species, including tree swallows, nested in approximately 25% of the boxes designated for violet-green swallows leaving between 30 to 40% of the nests unoccupied in each year (pers. obs.). In contrast, competition for nest sites around the marsh was very high for tree swallows. Nest usurpations by conspecifics and nest site limitations have been documented for tree swallows in other locations (e.g., Holroyd 1975; Leffelaar and Robertson 1985; Lombardo 1986) and my study site was no exception. Males and females frequently chased conspecifics away from the vicinity of their nests and 90 to 95% of all available nest sites were occupied in 1989 and 1990



(pers. obs.). These results indicate that nest sites in west Creston were not as limited for violet-green swallows as for tree swallows, hence pressure for nest guarding was not as great and male violet-green swallows were less restricted from following their mates.

But pressure for nest guarding may not be the only factor that determines whether males should guard mates rather than nests. The optimal allocation of time to one or the other activity depends on the relative benefits of each. Other factors, including the availability of mates, energetic constraints, risk of predation, etc., could influence these benefits. Temporary removal experiments of males (Chapter 3) and females (Chapter 4) have been done to assess the relative availability of females and nest sites for each species. The results suggest that male violet-green swallows may benefit more by guarding mates than nests because females are more limited than nest sites. Further studies are required to test whether manipulations of nest and mate availability can be done to alter the paternity defense strategies of violet-green and tree swallows. If nest sites are limited for other populations of violet-green swallows (Brawn and Balda 1988) it would be useful to compare the time allocated to guarding nests versus mates at these sites to the time allocated by violet-green swallows in west Creston. In addition, future research should explore the effects of other factors, such as energetic constraints and risk of predation on the relative benefits of guarding mates versus nests.

## **References**

- Bailey, F.M. 1928. *Birds of New Mexico*. Washington: Judd and Detweiler, Inc.
- Beecher, M.D, and Beecher, I.M. 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.
- Birkhead, T.R. 1979. Mate guarding in the magpie *Pica pica*. *Anim. Behav.* 27: 866-874.
- Birkhead, T.R. 1982. Timing and duration of mate guarding in magpies, *Pica pica*. *Anim. Behav.* 30: 277-283.
- Birkhead, T.R., Atkin, L., and Møller, A.P. 1987. Copulation behaviour of birds. *Behaviour* 101: 101-138.
- Birkhead, T.R., Hunter, F.M. and Pellat, J.E. 1989. Sperm competition in the zebra finch, *Taeniopygia guttata*. *Anim. Behav.* 38: 935-950.
- Birkhead, T.R., Johnson, S.D., and Nettleship, D.N. 1985. Extra-pair matings and mate guarding in the common murre, *Uria aalge*. *Anim. Behav.* 33: 608-619.
- Birkhead, T.R. and Møller, A.P. 1992. *Sperm Competition in Birds*. London: Academic Press.
- Birkhead, T.R., Pellat, J.E. and Hunter, F.M. 1988. Extra pair copulation and sperm competition in the zebra finch. *Nature* 334: 60-62.
- Brawn, J.D. and Balda, R.P. 1988. Population biology of cavity nesters in northern Arizona: Do nest sites limit breeding densities? *Condor* 90: 61-71.
- Brown, C.R., Knott, A.M., and Damrose, E.J. 1992. Violet-green Swallow. In: *The Birds of North America* (Ed. by Poole, A., Stettenheim, P. and Gill, F.) No. 14. Philadelphia: The Academy of Natural Sciences; Washington, D.C: The American Ornithologists' Union.
- Briskie, J.V. and Montgomerie, R. 1993. Patterns of sperm storage in relation to sperm competition in passerine birds. *Condor* 95: 442-454.
- Burleigh, T.D. 1972. *Birds of Idaho*. Idaho: The Caxton Printers Ltd.

- Butler, R.W. 1988. Population dynamics and migration routes of Tree Swallows, *Tachycineta bicolor*, in North America. *J. Field. Ornithol.* 59: 395-402.
- Cheng, K.M., Burns, J.T., and McKinney, F. 1983. Forced copulation in captive Mallards (*Anas platyrhynchos*): III. Sperm competition. *Auk* 100: 302-310.
- Cohen, J. 1977. *Statistical power analysis for the behavioral sciences*. New York, Academic Press.
- Cohen, R.R. 1984. Criteria for distinguishing breeding male tree swallows from brightly colored females prior to capture. *N. Am. Bird Bander* 9: 2-3.
- Compton, M.M., Van Krey, H.P., and Siegel, P.B. 1978. The filling and emptying of the uterovaginal sperm-host glands in the domestic hen. *Poult. Sci.* 57: 1696-1700.
- Daly, M. 1978. The cost of mating. *Am. Nat.* 112: 771-774.
- Davies, N.B. 1985. Cooperation and conflict among dunnocks, *Prunella modularis*, in a variable mating system. *Anim. Behav.* 33: 628-648.
- Davies, N.B. 1991. Mating systems. In: *Behavioural ecology: an evolutionary approach* (Ed. by J.R. Krebs and N.B. Davies), pp. 263-294. Oxford: Blackwell Scientific Publications.
- Hatchwell, B.J., 1988. Intraspecific variation in extra-pair copulation and mate defence in common guillemots *Uria aalge*. *Behaviour* 107: 157-185.
- Hollander, M. and Wolfe, D.A. 1973. *Nonparametric Statistical Methods*. New York, John Wiley & Sons.
- Holroyd, G.L. 1975. Nest site availability as a factor limiting population size of swallows. *Can. Field-Nat.* 89: 60-64.
- Howarth, B. 1974. Sperm storage as a function of the female reproductive tract. In: *The oviduct and its functions*. (Ed. by Johnson, A.D. and Foley C.E.) pp. 237-270. New York: Academic Press.

- Hussell, D.J. 1983. Age and plumage color in female Tree Swallows. *J. Field Ornithol.* 54: 312-318.
- Lambrecht, J. 1989. Mate guarding in geese: awaiting female receptivity, protection of paternity or support of female feeding? In: *The Sociobiology of Sexual and Reproductive Strategies*. (Ed. by Rasa, A.E., Vogel, C., and Volland, E.), pp. 48-60. London: Chapman and Hall.
- Leffelaar, D. and Robertson, R.J. 1984. Do male tree swallows guard their mates? *Behav. Ecol. Sociobiol.* 16: 73-79.
- Leffelaar, D. and Robertson, R.J. 1985. Nest usurpation and female competition for breeding opportunities by Tree Swallows. *Wilson Bull.* 97: 221-224.
- Lombardo, M.P. 1986. A possible case of adult intraspecific killing in the Tree Swallow. *Condor* 88: 112.
- Lumpkin, S. 1983. Female manipulation of male avoidance of cuckoldry behaviour in the ring dove. In: *Social Behaviour of Female Vertebrates*. (Ed. by S.K. Wasser), pp. 91-112. New York: Academic Press, Inc.
- Møller, A. P. 1985. Mixed reproductive strategy and mate guarding in a semi-colonial passerine, the swallow *Hirundo rustica*. *Behav. Ecol. Sociobiol.* 17: 401-408.
- Møller, A.P. and Birkhead, T.R. 1991. Frequent copulations and mate guarding as alternative paternity guards in birds - a comparative study. *Behaviour* 118: 170-186.
- Nichols, W.F. 1938. Some notes from Negit Island, Mono Lake, California. *Condor* 40: 262.
- Parker, G.A. 1974. Courtship persistence and female guarding as male time investment strategies. *Behaviour* 48: 157-184.
- Rice, W.R. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223-225.

- Robertson, R.J. and Rendell, W.B. 1990. A comparison of the breeding ecology of a secondary cavity nesting bird, the Tree Swallow, (*Tachycineta bicolor*) breeding in nest-boxes and natural cavities. *Can. J. Zool.* 68:1046-1052.
- Robertson, R.J., Stutchbury, B.J. and Cohen, R.R. 1992. Tree Swallow. In: *The Birds of North America* (Ed. by Poole, A., Stettenheim, P. and Gill, F.) No. 11. Philadelphia: The Academy of Natural Sciences; Washington, D.C: The American Ornithologists' Union.
- Siegel, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. Tokyo: McGraw-Hill Kogakusha.
- Simmons, R.E. 1990. Copulation patterns of African marsh harriers: evaluating the paternity assurance hypothesis. *Anim. Behav.* 40: 1151-1157.
- Sturkie, P.D. 1976. *Avian Physiology*. 3rd edn. New York: Springer-Verlag.
- Stutchbury, B.J. and Robertson, R.J. 1985. Floating populations of female Tree Swallows. *Auk* 102: 651-654.
- Systat, Inc. 1986. *SYSTAT*. Illinois, U.S.A.
- Trail, P.W. 1985. Courtship disruption modifies mate choice in a lek-breeding bird. *Science* 227: 778-780.
- Venier, L.A. and Robertson, R.J. 1991. Copulation behaviour of the tree swallow, *Tachycineta bicolor* : paternity assurance in the presence of sperm competition. *Anim. Behav.* 42: 939-948.
- Westneat, D.F. 1987. Extra-pair copulations in a predominantly monogamous bird: observations of behaviour. *Anim. Behav.* 35: 865-876.
- Wilkinson, L. 1986. *SYSTAT: The System for Statistics*. Evanston, Illinois: SYSTAT, Inc.

### Chapter 3

#### **Mate guarding versus nest guarding: measuring the relative risks of paternity loss and nest loss in two species of swallows**

##### **Abstract**

Temporary male removal experiments were used to measure the relative risks of paternity loss and nest loss in a species that guards mates, the violet-green swallow *Tachycineta thalassina*, and a species that guards nest sites, the tree swallow *Tachycineta bicolor*. The risk of paternity loss for detained male violet-green swallows was considered high because numerous male intruders (mostly non-territorial floaters) tried to gain extra-pair copulations with unguarded females. Female violet-green swallows were able to escape unwanted male advances by flying away but some females willingly copulated with selected intruders. Released male violet-green swallows chased intruders from their female mates and resumed mate-guarding but used no alternative form of paternity defense to reduce the risk of paternity loss. In contrast, when male tree swallows were detained, relatively few male intruders (usually territorial neighbours) tried to gain extra-pair copulations with unguarded females. Female tree swallows aggressively defended their nests from male intruders but were unable to keep them away and some female tree swallows received forced extra-pair copulations inside their nest boxes. Released male tree swallows were able to lower the risk of paternity loss by copulating frequently with their mates at the nest box. The risk of nest loss for male violet-green swallows was considered low because intruders were clearly interested in unguarded females and not unguarded boxes. Male intruders spent very little time at nest boxes and were rarely seen in the vicinity of nests when females

were absent. In contrast, the risk of nest loss for male tree swallows was considered high because intruders spent a lot of time at nest boxes even when females were absent. Released male tree swallows always regained possession of nests but only after expending time and energy chasing and fighting intruders. These results were used to explain the allocation of time and energy to guarding mates versus nests by each species.

### **Introduction**

Mate guarding is a widespread behaviour used by males to ensure paternity but males of several bird species do not guard their mates (see Birkhead et al. 1987 for species lists). Defense of a nest site is one constraint on the time and energy that can be allocated to mate guarding (Butler 1982; Møller and Birkhead 1991). A male who stays behind to guard his nest is unable to follow his mate when she leaves to forage. Conversely, a male who follows his mate away from the nest site may be vulnerable to nest usurpation. Little attention has been focused on why individuals guard mates rather than nests, or vice versa. The question is particularly interesting in light of recent suggestions that males use frequent pair copulations to defend their paternity when they are constrained from mate guarding (Møller and Birkhead 1991; Birkhead and Møller 1992). Although it has been assumed that frequent pair copulations are not as effective as mate guarding (Birkhead and Møller 1992), they undoubtedly reduce the risk of paternity loss to some extent. Thus, the use of frequent pair copulations may be an important factor influencing whether individuals guard nests rather than mates.

Overall, the decision to guard mates versus nests depends on the relative benefits of each activity to individual reproductive success. In part, benefits result from the relative risks of paternity loss and nest loss. Risks are defined as

the probability or chance of a loss rather than the actual or realized loss. Thus, relative risks can be measured by temporarily detaining males and observing what happens to unguarded mates and nests. For example, if competitors tried to acquire extra-pair copulations with unguarded mates but did not try to usurp nest sites then, clearly, the benefits of mate guarding would outweigh the benefits of nest guarding. The tradeoff would be less clear if detained males experienced high risks of both paternity loss and nest loss but observations of released males would reveal (1) whether any alternative form of paternity defense, such as frequent pair copulations, reduced the risk of paternity loss and (2) whether males could regain nest sites that had been usurped and thereby reduce the risk of nest loss.

In previous studies, detained mate guarders suffered a high risk of paternity loss due to a high rate of attempted extra-pair copulations with unguarded females (Bjorklund and Westman 1983; Møller 1987a; Birkhead et al. 1989; Lambrecht 1989; Bjorklund et al. 1992) and female acceptance or inability to refuse extra-pair copulations (Bjorklund and Westman 1983; Møller 1987a; Birkhead et al. 1989). Only one of these studies reported the behaviour of released males; male zebra finches *Taeniopygia guttata* tended to copulate with their mates when they were reunited (Birkhead et al. 1989). None of these studies reported the risk of nest loss, thus, the relative risks of paternity and nest loss could not be compared for detained mate guarders. The same has been true for studies of nest guarding behaviour. Detained male nest guarders were shown to suffer high risks of nest loss due to the arrival of male intruders who attempted to usurp unguarded nests (Robertson and Stutchbury 1988) but the risks of paternity loss were not noted.



I set out to compare the relative risks of paternity loss and nest loss within each of two congeners, violet-green swallows *Tachycineta thalassina*, which guard mates (Beasley, unpubl. data), and tree swallows *Tachycineta bicolor*, which guard nests (Leffelaar and Robertson 1984). Because violet-green and tree Swallows are closely related, similar behaviour patterns may result from phylogenetic constraints but differences in time allocated to guarding mates versus nests suggest adaptive responses to environmental conditions.

As aerial insectivores, both species forage away from the nest site so males would have to leave nests undefended to guard mates. Several studies have demonstrated that tree swallows experience intense intra- and interspecific nest competition in numerous locations (Holroyd 1975; Harris 1979; Stutchbury and Robertson 1985). Recent studies have shown that, even without being detained, male tree swallows experienced high levels of paternity loss due to frequent promiscuous matings (Morrill and Robertson 1990; Lifjeld and Robertson 1992; Lifjeld et al. 1993; Dunn and Robertson 1993) but the use of frequent pair copulations by tree swallows has also been documented (Venier and Robertson 1991), thus, male tree swallows may be able to reduce the risk of paternity loss enough with frequent pair copulations to make nest guarding more beneficial than mate guarding. On the basis of this background information I predicted (1) that male tree swallow intruders would try both to copulate with unguarded mates and usurp unguarded nests while males were detained and (2) that released male tree swallows would try to reduce their risks of paternity loss using frequent pair copulations.

When I set out to document the paternity defense tactics of male violet-green swallows little was known about their breeding ecology except that, like tree swallows, they nested in cavities that are excavated by other species and they

were shown to experience nest competition at one study site (Brawn and Balda 1988). Thus, I predicted that nest guarding would restrict mate guarding and I expected them to use frequent pair copulations like tree swallows. Instead, I found that male violet-green swallows allocated their time to mate guarding rather than nest defense and copulated with their mates relatively infrequently. Thus, I predicted that detained male violet-green swallows would experience higher risks of paternity loss than nest loss because (1) male intruders would spend more time and effort trying to copulate with unguarded females than usurping unguarded nests, and (2) released males would not reduce their risks of paternity loss using other paternity defenses such as frequent pair copulations. Here I document the paternity defense strategies of each species and test my predictions about their relative risks of paternity and nest loss.

## **Methods**

### **Study Area and Subjects**

The study was conducted at the Creston Valley Wildlife Management Area in southeastern British Columbia (49°05' N, 116°35'W) between April and June 1988 to 1990. Tree swallows nested in boxes mounted on poles approximately 30 m apart along several dikes around marshland. Violet-green swallows nested in boxes mounted 15 to 30 m apart on the walls of cabins, barns and garages on hillsides adjacent to the marsh. Contents of nest boxes were checked every third day before laying and every day throughout the laying period so that experiments could be conducted at a consistent time in relation to the first and last days of laying.

I captured birds with mist nets in April and marked each with colored leg bands and streaks of acrylic paint on the wing, tail and breast feathers in specific color patterns for individual identification. Violet-green swallows could

be sexed easily by plumage, but the similar plumage of male and older female (after first year) tree swallows meant that the sex of birds had to be distinguished by observing their behaviour, particularly during copulation attempts (Cohen 1984).

### **Procedures**

Marked pairs were observed for 30 min periods every 3 to 5 days within 7 days prior to the removal of the male from each pair. Males were removed after each pair had been observed copulating and before their last day of laying. I captured males in mist nets near their nests and detained them for 1 to 4 h in a soft cotton bag in the dark to minimize stress. Males were removed from 8 violet-green swallow pairs and 8 tree swallow pairs. Following the removal period, I released males near their nests and observed them for 1 h after they returned to their nest sites. I observed other pairs of birds from which males were not removed for 30 min periods either before or after removal experiments were conducted (N=8 for violet-green swallows, N=19 for tree swallows).

During all observation periods I watched the nest site and surrounding area. I continuously observed the pair (or female only) and any male intruders that landed within 10 m of the nest box or female. I recorded the time of all arrivals and departures and the frequencies of several behavioural interactions between individuals. Specifically, I counted social interactions including vocalizations and displays, e.g., bill snaps, gapes and wipes; aggressive movements, such as swoops and hovers over a perched bird and supplantings of one bird by another; following behaviour which consisted of chases overhead and departures and arrivals from a perch within one minute of the female doing so; and successful and unsuccessful copulation attempts by extra-pair males (extra-pair copulations) and mates (pair copulations). As it was not always

possible to observe cloacal contact, I inferred that copulations were successful based on the positions of birds' tails. Each time cloacal contact was inferred was considered a single copulation.

I combined data collected in 1988 and 1989 for violet-green swallows and I combined data collected in 1989 and 1990 for tree swallows after finding no difference between years for any of the variables considered. Data collected during watches of marked pairs prior to the removal of the male were averaged to obtain behavioural values for pre-removal periods. These were compared to data collected when male mates were detained (removal periods) or to data collected after detained males were reunited with their mates (release periods). Because the average date of the season (day 1 = 1 April), day before egg laying, and clutch size were significantly lower during pre-removal periods than removal or release periods (Table 3.1) I also compared data collected during watches of marked pairs from which males were not removed (independent control values) to data collected during removals and releases. These data were collected at similar average dates, days of nesting and clutch sizes (Table 3.1). Due to a limited sampling period, I was unable to control for individual differences between pairs from which males were not removed and pairs from which they were but, as there was no reason to predict a directional difference due to individual variation, I considered consistent differences in the predicted direction to result from the experimental treatment.

All observations were conducted between 0500 and 1300 hours. Males were detained at approximately the same time of day as when pre-removal watches and independent control watches were conducted (Table 3.1). But released males were observed later in the morning than when birds in control periods were watched.

Table 3.1. Mean ( $\pm$  SE) for date (day 1 = April 1), day before egg laying, number of eggs in the nest and mean time of day when pre-removal, removal, release, and independent control observation periods were conducted.

Variable	Violet-green Swallows			Tree Swallows		
	pre-removals N=8	removals & releases N=8	independ. controls N=8	pre-removals N=8	removals & releases N=8	independ. controls N=19
Date	62.2 $\pm$ 4.2	* 66.8 $\pm$ 3.7	NS 63.4 $\pm$ 3.4	48.1 $\pm$ 2.2	* 51.0 $\pm$ 2.3	NS 50.9 $\pm$ 1.6
Day	-7.5 $\pm$ 1.1	* -2.6 $\pm$ 0.9	NS -3.8 $\pm$ 0.5	-5.4 $\pm$ 2.0	* -1.4 $\pm$ 1.4	NS -2.2 $\pm$ 0.7
Clutch	0.3 $\pm$ 0.2	* 2.8 $\pm$ 0.2	NS 2.3 $\pm$ 0.4	0.5 $\pm$ 0.3	* 1.5 $\pm$ 0.5	NS 0.7 $\pm$ 0.3
Time of Day	7:30 -8:00	NS 6:50 <sup>^</sup> -8:50	NS 8:15 -8:45	7:10 -7:40	NS 8:20 <sup>^</sup> -10:20	NS 7:40 -8:10
	7:30 -8:00	NS 8:50 <sup>+</sup> -9:50	NS 8:15 -8:45	7:10 -7:40	* 10:45 <sup>+</sup> -11:45	* 7:40 -8:10

\*  $P < 0.01$ , NS  $P > 0.10$ ; Wilcoxon paired-sample test were used to compare removal and release periods to pre-removal periods; Mann-Whitney  $U$  tests were used to compare removal and release periods to independent control periods.

<sup>^</sup> removal period; <sup>+</sup> release period - values for these two periods were the same for all variables except time of day.

To measure the risk of paternity loss for detained males, I compared the number of male intruders, the duration of intruder visits and the responses of male intruders to unguarded females that occurred during removal periods and pre-removal or independent control periods. As well, I compared female responses to male intruders during removal periods with female responses to male mates during pre-removal and independent control periods. To determine whether paternity risks were reduced by alternative paternity defense methods I compared the frequency of pair interactions (particularly the rate of pair copulations) that occurred during release periods and pre-removal or independent control periods.

Measuring the risk of nest loss was less direct. If the unattended female was present at the nest site, any male intruders at the nest may have been trying to steal copulations rather than the nest. Females rarely spent the entire removal period at the box so I was able to record the time that male intruders spent at the nest site alone. In addition, I examined female responses to male intruders at the box to determine whether females defended the nest and I measured the time that it took male mates to regain their nest sites from intruders.

### **Statistical Analyses**

Given that I tested the hypotheses that the removal of the male would increase the risks of paternity loss and nest loss, I used one-tailed statistical tests. When comparing the events that occurred during pre-removal periods to those that occurred while males were detained or after they were released I used matched Wilcoxon paired-sample tests. When comparing the events that happened during independent controls to those that happened during either removal or release periods I used Mann-Whitney  $U$  tests (Siegel 1956). Statistics were computed with the SYSTAT statistical package (SYSTAT, Inc.

1986) and manual (Wilkinson 1986). As each prediction was tested with two comparisons (e.g., events of removal periods compared to events of pre-removal and independent control periods) statistical significance for each comparison was accepted at  $p < 0.025$  to maintain an experiment-wise error at 0.05 (Bonferroni correction, Snedecor and Cochran 1980). Unless otherwise stated, non-significant results must be considered inconclusive because small samples would not produce sufficient power ( $1 - \beta < 0.8$ ) to detect differences (Cohen 1977). Numbers reported in the text are means  $\pm$  standard errors unless otherwise stated.

## Results

### Paternal loss vs. nest loss for violet-green swallows

More male intruders arrived while resident males were detained ( $2.50 \pm 0.42$ ) than during pre-removal ( $1.00 \pm 0.27$ ) (Wilcoxon paired-sample test,  $p = .009$ ) or independent control periods ( $1.00 \pm 0.27$ ) (Mann-Whitney,  $U = 10$ ,  $p = .010$ ). Male intruders stayed for a significantly longer proportion of the time during removal than independent control periods but not pre-removal periods ( $p = 0.1$ ,  $1 - \beta = 0.67$ ) (Figure 3.1). Male intruders spent very little time alone at the nest during any of the watches. On average male intruders spent only  $1.3 \pm 2.4\%$  ( $N = 8$ ) of the time alone at the nest box when resident males were detained. There was no detectable difference in the time that the female was present alone or with others during removal and pre-removal or independent control periods ( $p > 0.25$ ,  $1 - \beta = 0.1 - 0.2$ ) (Figure 3.1).

Only 3 of 20 intruders (15%) were neighbouring males known to have mates of their own. Some of the others may have had mates at distant nest sites but I suspect that most of them were unmated "floaters" because there were always extra males perched in the vicinity of the nest sites and five of the non-

Figure 3.1. Comparison of the proportion of time that male intruders were perched in the vicinity of the nest with and without the female resident when male mates were temporarily detained (removal) versus when they were not detained (pre-removal and independent control). The total proportion of time that the female resident was perched in the vicinity of the nest was compared between removal and control periods to give an idea of how accessible she was to intruders at the nest site. Means and standard errors are shown. \*  $P < .025$ , \*\*  $P < .005$  for all tests; <sup>a</sup> Wilcoxon paired-sample test to compare pre-removal ( $n=8$ ) and removal periods ( $n=8$ ); <sup>b</sup> Mann-Whitney  $U$  test to compare removal ( $n=8$ ) and independent control periods ( $n=8$  for violet-green swallows;  $n=19$  for tree swallows).





neighbour male intruders were banded males that had been captured and observed several times in the vicinity of the experimental nests within 1 month before the experiments.

Male intruders followed females at much higher rates during removal than during pre-removal or independent control periods (Figure 3.2). Several swoops and unsuccessful extra-pair copulation attempts were observed while male mates were detained but none were observed during pre-removal or independent control periods (Figure 3.2). Two of the 8 unguarded females accepted extra-pair copulations from 2 marked non-neighbours that had been seen in the vicinity of the nest several times during pre-removals. One of these males had been mated to the experimental female in the previous year. No extra-pair copulations were observed when male mates were present (Figure 3.2).

Although females responded with vocalizations, open bill threat displays, swoops and chases to male intruders and not to mates, these responses were very infrequent (Figure 3.3). Generally, females were not aggressive to male intruders, instead, they rejected intruders' advances by flying away.

Male intruders were chased from the immediate vicinity of the female within  $947.8 \pm 318.3$  s (approximately  $16 \pm 5$  min) ( $N=6$ ) after male mates were released, but male intruders continued to perch in sight although, they were usually more than 30 m from the pair or nest.

Male mates resumed mate guarding after they were released (Figure 3.4). I could not detect differences in the frequencies of following between release periods and either pre-removal or independent control periods ( $p > 0.25$ ,  $1 - \beta = 0.19 - 0.45$ ) with one exception. Males did not arrive within 1 min of females as often during release as during pre-removal or independent control periods

Figure 3.2. Mean frequency of responses of intruding males to females during each type of observation period. Bars indicate standard errors. See Methods for definitions of responses. \*  $P < .025$ , \*\*  $P < .005$  for all tests; <sup>a</sup> Wilcoxon paired-sample test to compare pre-removal ( $n=8$ ) and removal periods ( $n=8$ ); <sup>b</sup> Mann-Whitney  $U$  test to compare removal ( $n=8$ ) and independent control periods ( $n=8$  for violet-green swallows;  $n=19$  for tree swallows).

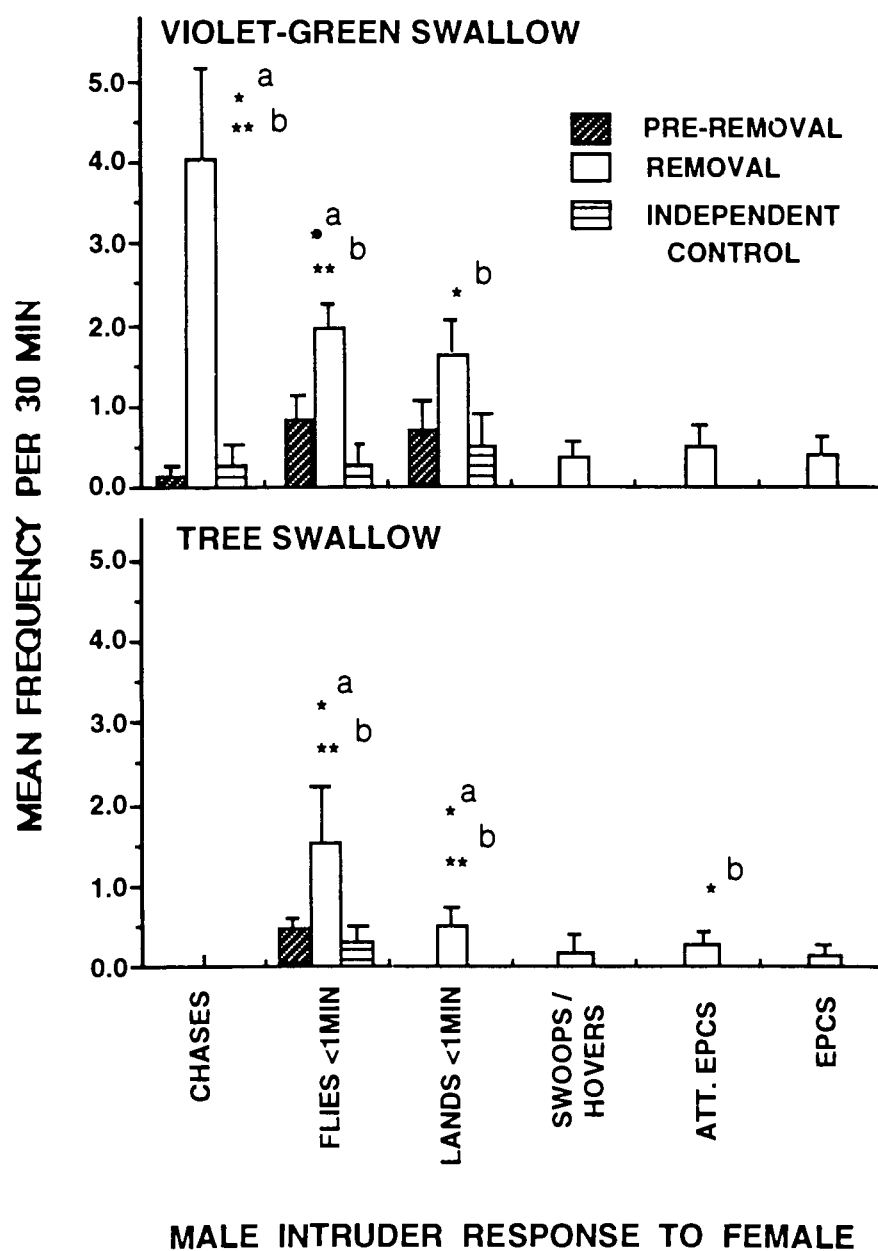
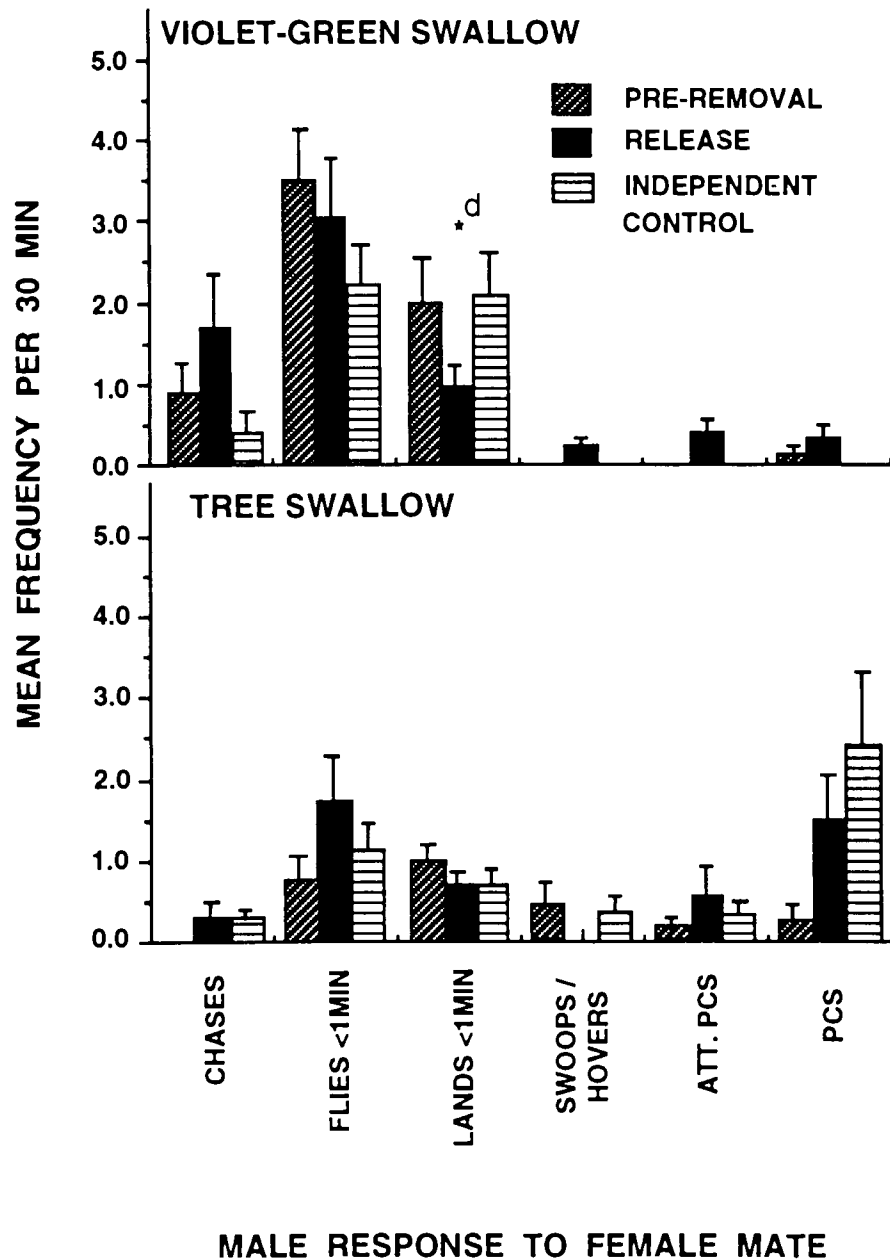


Figure 3.3. Mean frequency of responses of females to male intruders during removals versus to male mates during pre-removal and independent control periods. Bars indicate standard errors. See Methods for definitions of responses. \*  $P < .025$ , \*\*  $P < .005$  for all tests; <sup>a</sup> Wilcoxon paired-sample test to compare pre-removal ( $n=8$ ) and removal periods ( $n=8$ ); <sup>b</sup> Mann-Whitney  $U$  test to compare removal ( $n=8$ ) and independent control periods ( $n=8$  for violet-green swallows;  $n=19$  for tree swallows).



Figure 3.4. Mean frequency of responses of males to female mates during each type of observation period. Bars indicate standard errors. See Methods for definitions of responses. \*  $P < .025$  for all tests; <sup>d</sup> Wilcoxon paired-sample test to compare pre-removal (n=8) and release periods (n=8).



(Figure 3.4). Males attempted to copulate with their mates after they were released but no attempted copulations were observed during pre-removal or independent control periods (Figure 3.4). I could not detect a difference in the frequencies of successful pair copulations between release and either pre-removal or independent control periods ( $p > 0.3, 1-\beta = 0.12-0.23$ ) and the rates of pair copulations were very low during all watches (Figure 3.4).

### **Paternity loss vs. nest loss for tree swallows**

Male intruders were never observed in the vicinity of nests during pre-removal and independent control periods but  $1.38 \pm 0.26$  male intruders arrived while male tree swallows were detained. The differences between removal and pre-removal (Wilcoxon paired-sample test,  $p = .012$ ), or independent control periods (Mann-Whitney,  $U = 38, p = .025$ ) were significant. Male intruders stayed for a greater proportion of the time while mates were detained than during pre-removal or independent control periods (Figure 3.1). Unlike violet-green swallows, male tree swallow intruders were present alone as much as with the female (Figure 3.1) and they spent a large proportion of the time perched at the nest box ( $20.3 \pm 0.9\%$  of the removal period ( $N=8$ )). I could not detect any difference in the time that the female was present when her mate was detained versus during pre-removal or independent control periods ( $p > 0.1, 1-\beta = 0.21$ ) (Figure 3.1).

Male intruders were predominantly neighbouring males with mates (7 of 11 male intruders: 64%). Of the four non-neighbours, one had been banded in the vicinity of the site a month earlier and another later occupied a neighbouring nest that had been abandoned by the original nest owners after a failed nest attempt.

Male intruders never followed females flying overhead during any of the observation periods but they did follow females away from and returning to the nest more often during removal than pre-removal or independent control periods (Figure 3.2). Their general reluctance to follow females differed from the behaviour of male violet-green swallow intruders. Male intruders hovered over females and attempted extra pair-copulations only when males were detained (Figure 3.2). During two removal periods, I strongly suspect that male intruders successfully completed extra-pair copulations inside the nest box. Each time the male intruder entered the nest box following the female and I heard vocalizations and observed wing tips moving at the entrance hole indicating some sort of struggle. In one case the male intruder left the box after 12 sec; in the other, he left after 5 min. Each female then appeared at the entrance with her crown feathers dishevelled. On other occasions I have found paired birds clasped in a mounted position inside nest boxes and noted wet cloacal protruberances on both birds. Thus, it seems likely that male intruders were forcing extra-pair copulations with females inside boxes during the removal periods. One of these male intruders was identified as a neighbour whose mate was in the egg laying stage. The other was the male intruder that later occupied an abandoned neighbouring nest.

Unlike violet-green swallows, female tree swallows responded aggressively to male intruders that approached the nest box during removal periods. They swooped, supplanted, chased, hit and fought male intruders in contrast to non-aggressive interactions with their own mates during pre-removals and independent controls (Figure 3.3).

Released male tree swallows chased male intruders away from their nests within  $587.8 \pm 148.4$  s (approximately 10 min) (N=4) but in 3 cases, released

males spent more than 5 min fighting with intruders. Male intruders did not persist in the area after they had been chased. I watched those that were neighbours return to their own nest sites.

Pair copulations tended to be more frequent during release than pre-removal periods but the difference was non-significant (Wilcoxon paired-sample test,  $p=.06$ ,  $1-\beta=.77$ ) (Figure 3.4). I could not detect any difference in the frequencies of pair copulations between release and independent control periods (Mann-Whitney,  $U=85$ ,  $p>>.05$ ,  $1-\beta=.15$ ) (Figure 3.4), and of attempted pair copulations between releases and pre-removals or independent controls but the trend indicated that there were more during release periods (Figure 3.4). Again, these results were calculated with low power ( $1-\beta=.28$  and  $.41$ , respectively), and thus they are inconclusive.

Males tended to follow mates away from nests more during release than pre-removal periods but, overall, the low rates at which males followed their mates and the high rates of pair copulations were opposite to the behavioural interactions of released male violet-green swallows and their mates (Figure 3.4).

Table 3.2 summarizes my results for predictions that test whether the risks of nest loss and/or the risks of paternity loss were increased when males of each species were temporarily detained.

## **Discussion**

The observed risks of paternity loss and nest loss followed my expectations; detained male violet-green swallows experienced a higher risk of paternity loss than nest loss whereas detained male tree swallows experienced high risks of both paternity and nest loss. It is difficult to assess the relative benefits of guarding mates versus nests for tree swallows because released males were

Table 3.2. Summary of the key results for predictions that test whether the risks of nest loss and/or paternity loss were increased when males of each species were temporarily detained. EPC = extra pair copulation, PC = pair copulation.

Hypothesis	Prediction	Violet-green Swallows	Tree Swallows
Removal increased risk of paternity loss	Male intruders followed females most in removal	True	True
	No. of EPC attempts highest during removal	True	True
	Females accepted or forced to accept EPCs	True	True
	Frequent PCs not used after release	True	False
Removal increased risk of nest loss	Male intruder alone at nest during removal	Rarely	Often
	Released males chased intruders from nests rather than females	False	True



able to reduce the risk of paternity loss with frequent pair copulations and reduce the risk of nest loss by regaining possession of their nests. Contrary to my expectation, the risk of nest loss for detained male violet-green swallows appeared to be very low. Factors that contributed to the risks of each species will be compared in an effort to identify conditions that favour guarding mates rather than nests and vice versa.

The main factor contributing to the high risk of paternity loss for detained male violet-green swallows was the large number of male intruders that arrived and persisted in trying to copulate with unguarded females. The low risk of nest loss was apparent from the fact that intruders ignored nest boxes. They seemed to be preoccupied with gaining access to females. In contrast, male tree swallow intruders tried to usurp undefended nests and copulate with unguarded females at the nest site. Thus, although there was rarely more than one male tree swallow intruder that arrived during each removal period, he was sufficient to threaten both the nest ownership and paternity of the detained male tree swallow.

The behaviour of male violet-green swallow intruders clearly indicated that they were trying to gain direct access to females. Male tree swallow intruders, on the other hand, tried to gain indirect access to females by usurping the nest site. The reason behind these different strategies was revealed by a comparison of the availability of nest sites for each species.

Despite previous evidence of nest competition in violet-green swallows (Brawn and Balda 1988), there was a high proportion of unoccupied artificial nest boxes (>30%, N=150) and a variety of suitable alternative nesting sites in my study area. Thus, the reproductive success of female violet-green swallows was not limited by available nest sites. In fact, each year I observed a few males

occupying nest boxes for several days and then leaving because they could not attract a mate. Thus, there appeared to be numerous unmated male "floaters" in the population. In addition, unlike the intruders that arrived while males were temporarily removed in other mate guarding species (Bjorklund and Westman 1983; Møller 1987a; Birkhead et al. 1989; Bjorklund et al. 1992), most of the male violet-green swallow intruders were unmated "floaters" that had been present during pre-removal periods and continued to lurk near pairs even after males were released. These results suggest that the operational sex ratio was male-biased, hence, females were a limited resource for male violet-green swallows. Further research is needed to confirm this suggestion but, if true, it would explain why male intruders tried to gain direct access to mated females rather than indirect access via nest defense and why mated males have been selected to guard mates rather than nests.

In contrast, tree swallows in West Creston, like other populations of tree swallows (Holroyd 1975; Harris 1979; Stutchbury and Robertson 1985), were limited by nest sites. More than 95% of the artificial boxes (N=42) added to those already inhabited (N=125) were occupied the same spring and many males and females were unable to acquire nest sites. The scarcity of nest sites and the abundance of female "floaters" meant that a male tree swallow that acquired a nest site usually also acquired a mate. In other populations males have been able to defend two nest sites and attract two mates (Dunn and Hannon 1991; Dunn and Robertson, 1993). Unlike violet-green swallows, most of the male tree swallow intruders were territorial neighbours with mates of their own. These males defended their own nests as well as unguarded neighbouring nests from intrusions by "floater" males. I suspect that unmated male "floaters" flew over nests and, in two removal periods, they persisted in

trying to usurp unguarded nests. But in the other cases, territorial neighbours arrived first and became well established before "floaters" appeared. Thus, even if a neighbouring male were unable to mate with the original female at the unguarded nest he would probably be successful in attracting a female "floater" to the nest as a second mate. Thus, the high level of competition for nest sites among female tree swallows explains why males compete for females indirectly by competing for nest sites and why mated male tree swallows have been selected to defend nests rather than guard mates.

The risk of paternity loss for detained males depended not only on male intrusions but also on how females responded to those intrusions. Unguarded female violet-green swallows accepted some extra-pair copulations whereas unguarded female tree swallows did not willingly accept but were forced to succumb to some extra-pair copulations. Female violet-green swallows did not use aggression to fend off male intruders, instead, they seemed able to reject unwanted intruders' advances by flying away or retreating alone inside their nest boxes. The same has been found for females of a few other species (Wagner 1991; Bjorklund et al. 1992). The extra-pair copulations that were accepted came from male "floaters" that had been in the vicinity of the nest site during the entire season, one of whom had been mated to the experimental female in the previous year. Unguarded female tree swallows aggressively defended nests from male intruders but they were vulnerable to forced copulations inside their nest boxes. In fact, female nest defense seemed to lead to an increase in the risk of paternity loss for their detained mates.

The fact that female tree swallows are known to receive extra-pair copulations at territorial neighbours' nest boxes even when their mates were not detained (Morrill and Robertson 1990; Venier et al. 1993) suggests that male

tree swallows normally experience high risks of paternity loss. However, recent evidence indicates that 50% of the breeding population does not experience extra-pair paternity (Lifjeld and Robertson 1992; Lifjeld et al. 1993). Thus, the observed increase in forced extra-pair copulations that occurred while mates were detained suggests that male presence may lower the risk of paternity loss in those cases when female mates are not promiscuous.

The third factor contributing to the high risk of paternity loss for detained male violet-green swallows was that they did not use frequent pair copulations or any other alternative paternity defense after they were released. This differs from the pair interactions observed after periods of separation in some other species of mate-guarders (Birkhead et al. 1989) but not all (Frederick 1987). It is possible that females did not accept frequent pair copulations, as was the case for female white ibises *Eudocimus albus* (Frederick 1987), and as indicated by females' refusals of some attempted pair copulations by released mates. But why would females not provide additional assurance of paternity to their mates? Explanations require an analysis of the costs and benefits of frequent pair copulations from the females' perspective. Alternatively, female refusal may not matter if the behavioural repertoire of violet-green swallows does not include frequent pair copulations as a paternity defense mechanism. This idea is supported by the low rate of attempted and successful pair copulations observed during all watches of violet-green swallows but it requires further study.

In contrast to male violet-green swallows, released male tree swallows attempted and succeeded in copulating frequently with their mates. I was unable to compare the rate of pair copulations after males were released with those of unmanipulated pairs at exactly the same time of day but my results did

indicate that pair copulations were as frequent after males were released late in the morning as they had been during control periods early in the morning. Thus, male tree swallows may have been copulating at maximum rates to assure their paternity even when they had not been detained. This idea is akin to previous conclusions that frequent pair copulations served as an alternative paternity defense for tree swallows (Venier and Robertson 1991) and other species constrained from mate guarding by nest guarding duties (Birkhead et al. 1987; Birkhead 1988; Møller and Birkhead 1991). Female tree swallows' acceptance of frequent pair copulations is interesting in light of my suggestion that female violet-green swallows may limit the number of pair copulations they receive. For nest-defending tree swallows, frequent pair copulations may be the only means available for females to assure their mates of paternity and thereby ensure paternal care for their offspring. If so, one would expect that parental care by male tree swallows would vary with rates of pair copulations but recent studies have found no such relationship (Lifjeld et al. 1993). Other possible benefits of frequent pair copulations have been proposed for females and require testing (see Petrie 1992).

As stated in the introduction, the decision to guard mates versus nests depends on the relative benefits of the two activities. I measured the relative risks of paternity and nest loss to assess which activity would be most vital to ensuring a male's reproductive success. I did not measure other potential costs and benefits of the two activities that could influence the allocation of time between them but, from my observations, I can suggest several that merit further research.

One important cost of mate-guarding is the energy required to perform the activity. The constant vigilance and frequent chases performed by mate-

guarding male violet-green swallows would have required extensive energy expenditure (Møller 1987b). Guarding a nest would be less energetically demanding. Thus, the decision to guard his mate rather than his nest would depend on the male's ability to meet greater energy requirements.

An important benefit of sustained nest defense by tree swallows was that it reduced the fighting and hence the risk of injury involved in maintaining occupation of a nest site. This was evident when released male tree swallows had to fight intruders to regain possession of their nests. Thus, it is possible that the cost of regaining a usurped nest was greater than the cost of regaining paternity for male tree swallows.

Mate-guarding served as more than an effective paternity defense for male violet-green swallows. The presence of the male mate deterred intruders from harrassing and chasing their females. By reducing harrassment, I suspect that mate-guarding allowed females to expend energy on foraging rather than escaping from unwanted intruders' advances (Ashcroft 1976; Lumpkin 1981, 1983; Lambrecht 1989). Thus, mate-guarding would have enhanced female reproductive condition and thereby increased the reproductive success of both male and female mates.

These suggestions constitute a small sample of the possible costs and benefits that could influence the decision to guard mates versus nests. Further research is required to quantify their effects before the reproductive value of guarding mates and nests can be assessed in a common currency.

In conclusion, mate-guarding by male violet-green swallows was correlated with the high risk of paternity loss suffered by detained males. Conditions that contributed to the high risk of paternity loss were (1) the large number of male intruders (mainly unmated male "floaters") that tried to gain direct access to

unguarded females, (2) female acceptance of some copulation attempts and (3) no use of any alternative paternity defense after detained mates were released. The low risk of nest loss for violet-green swallows was attributed to a greater scarcity of females than nest sites but further research is needed to confirm this suggestion. In contrast, limited nest site availability created a high risk of nest loss for detained male tree swallows and caused male intruders to seek mating opportunities indirectly by first obtaining nests and then attracting females. Although detained males suffered a high risk of paternity loss due to a few forced extra-pair copulations (mostly by mated neighbours), released male tree swallows were able to lower their risk of paternity loss with frequent pair copulations. Future manipulations of nest site availability could be used to vary competition for nests in ways that would cause males to switch from guarding mates to guarding nests and vice versa.

## References

- Ashcroft, R. 1976. A function of the pair bond in the common eider. *Wildfowl* 27: 101-105.
- Birkhead, T.R. 1988. Behavioural aspects of sperm competition in birds. *Adv. Stud. Behav.* 18: 35-72.
- Birkhead, T.R., Atkin, L., and Møller, A.P. 1987. Copulation behaviour of birds. *Behaviour* 101: 101-138.
- Birkhead, T.R., Hunter, F.M. and Pellat, J.E. 1989. Sperm competition in the zebra finch, *Taeniopygia guttata*. *Anim. Behav.* 38: 935-950.
- Birkhead, T.R. and Møller, A.P. 1992. *Sperm Competition in Birds*. London: Academic Press.
- Bjorklund, M. and Westman, B. 1983. Extra-pair copulations in the Pied Flycatcher (*Ficedula hypoleuca*). *Behav. Ecol. Sociobiol.* 13: 271-275.

- Bjorklund, M., Møller, A.P., Sundberg, J., and Westman, B. 1992. Female great tits, *Parus major*, avoid extra-pair copulation attempts. *Anim. Behav.* 43: 691-693.
- Brawn, J.D. and Balda, R.P. 1988. Population biology of cavity nesters in northern Arizona: Do nest sites limit breeding densities? *Condor* 90: 61-71.
- Butler, R.W. 1982. Wing fluttering by mud-gathering Cliff Swallows: avoidance of "rape" attempts? *Auk* 99: 758-761.
- Cohen, J. 1977. *Statistical Power Analysis for the Behavioral Sciences*. New York: Academic Press.
- Cohen, R.R. 1984. Criteria for distinguishing breeding male tree swallows from brightly colored females prior to capture. *N. Am. Bird Bander* 9: 2-3.
- Dunn, P.O. and Hannon, S.J. 1991. Intraspecific competition and the maintenance of monogamy in tree swallows. *Behav. Ecol.* 2: 258-266.
- Dunn, P.O. and Robertson, R.J. 1993. Extra-pair paternity in polygynous tree swallows. *Anim. Behav.* 45: 231-239.
- Frederick, P. 1987. Responses of male white ibises to their mate's extra-pair copulations. *Behav. Ecol. Sociobiol.* 21: 223-228.
- Harris, R.W. 1979. Aggression, superterritories and reproductive success in tree swallows. *Can. J. Zool.* 57: 2072-2078.
- Holroyd, G.L. 1975. Nest site availability as a factor limiting population size of swallows. *Can. Field-Nat.* 89: 60-64.
- Lambrecht, J. 1989. Mate guarding in geese: awaiting female receptivity, protection of paternity or support of female feeding? In: *The Sociobiology of Sexual and Reproductive Strategies*. (Ed. by Rasa, A.E., Vogel, C., and Voland, E.), pp. 48-60. London: Chapman and Hall.



- Leffelaar, D. and Robertson, R.J. 1984. Do male tree swallows guard their mates? *Behav. Ecol. Sociobiol.* 16: 73-79.
- Lifjeld, J.T. and Robertson, R.J. 1992. Female control of extra-pair fertilization in tree swallows. *Behav. Ecol. Sociobiol.* 31: 89-96.
- Lifjeld, J.T., Dunn, P.O., Robertson, R.J. and Boag, P.T. 1993. Extra-pair paternity in monogamous tree swallows. *Anim. Behav.* 45: 213-229.
- Lumpkin, S. 1981. Avoidance of cuckoldry in birds: the role of the female. *Anim. Behav.* 29: 303-304.
- Lumpkin, S. 1983. Female manipulation of male avoidance of cuckoldry behaviour in the ring dove. In: *Social Behaviour of Female Vertebrates*. (Ed. by S.K. Wasser), pp. 91-112. New York: Academic Press, Inc.
- Møller, A.P. 1987a. Mate guarding in the swallow *Hirundo rustica*: an experimental study. *Behav. Ecol. Sociobiol.* 21: 119-123.
- Møller, A.P. 1987b. Extent and duration of mate guarding in swallows *Hirundo rustica*. *Ornis. Scand.* 18: 95-100.
- Møller, A.P. and Birkhead, T.R. 1991. Frequent copulations and mate guarding as alternative paternity guards in birds - a comparative study. *Behaviour* 118: 170-186.
- Morrill, S.B. and Robertson, R.J. 1990. Occurrence of extra-pair copulation in the tree swallow (*Tachycineta bicolor*). *Behav. Ecol. Sociobiol.* 26: 291-296.
- Petrie, M. 1992. Copulation frequency in birds: why do females copulate more than once with the same male? *Anim. Behav.* 44:790-792.
- Robertson, R.J. and Stutchbury, B.J. 1988. Experimental evidence for sexually selected infanticide in tree swallows. *Anim. Behav.* 36: 749-753.
- Siegel, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. Tokyo: McGraw-Hill Kogakusha.

- Snedecor, G.W. and Cochran, W.G. 1980. *Statistical Methods*. 7th edn. Iowa: The Iowa State University Press.
- Stutchbury, B.J. and Robertson, R.J. 1985. Floating populations of female Tree Swallows. *Auk* 102: 651-654.
- Systat, Inc., 1986. *SYSTAT*. Illinois, U.S.A.
- Venier, L.A. and Robertson, R.J. 1991. Copulation behaviour of the tree swallow, *Tachycineta bicolor* : paternity assurance in the presence of sperm competition. *Anim. Behav.* 42: 939-948.
- Venier, L.A., Dunn, P.O., Lifjeld, J.T., and Robertson, R.J. 1993. Behavioural patterns of extra-pair copulation in tree swallows. *Anim. Behav.* 45: 412-415.
- Wagner, R.H. 1991. Evidence that female razorbills control extra-pair copulations. *Behaviour* 118: 157-169.
- Wilkinson, Leland. 1986. *SYSTAT: The System for Statistics*. Evanston, Illinois: SYSTAT, Inc.

## Chapter 4

### **Female floaters: a factor in the decision to guard mates versus nests in two species of swallows**

#### **Abstract**

Temporary female removal experiments were used to determine whether unmated female floaters would replace detained female violet-green swallows *Tachycineta thalassina*, a mate-guarding species, in the same way that they replaced detained female tree swallows *Tachycineta bicolor*, a nest guarding species. Very few female intruders visited nest sites while female violet-green swallows were detained and none tried to usurp nest boxes. In contrast, numerous female intruders attempted to usurp the nest boxes of detained female tree swallows. Released female violet-green swallows never encountered female intruders when they first returned to their nests whereas released female tree swallows usually chased and fought female intruders to regain possession of their nests. The temporary removal of female mates also allowed me to determine the effect of female absence on male promiscuity. Overall, extra-pair copulations were no more frequent when female mates were detained than at other times but one male of each species did obtain extra-pair matings while their original mates were absent. All males of both species readily accepted their original mates when they were released after 2 h in captivity. Male violet-green swallows spent more time guarding mates after they were released than during control watches but they did not use frequent pair copulations or any other alternative means of paternity defense. Male tree swallows copulated frequently with their mates during all observation periods but attempted a higher rate of pair copulations after their mates were released.

These results were discussed in relation to the decision to guard mates versus nests for each species.

## **Introduction**

Theory predicts that monogamous males experience selection to avoid paternity loss by mate guarding (Birkhead et al. 1987). But time and energy for mate-guarding may be constrained by other activities, such as nest guarding (Butler 1982; Møller and Birkhead 1991). Tree swallows *Tachycineta bicolor* experience such intense competition for nest cavities that males guard nests rather than mates (Leffelaar and Robertson 1984). I expected to find the same nest guarding priority in another obligate cavity nester, the violet-green swallow *Tachycineta thalassina*. Instead, I found that male violet-green swallows guard their mates at all times and often leave nest sites undefended (Chapter 2).

To determine why male violet-green swallows guard mates rather than nests I tested whether an experimentally detained male was more likely to be cuckolded than lose his nest (Chapter 3). I did this by temporarily removing males during their mates' fertile periods. A large number of unmated males tried to gain access to unguarded females but they did not try to usurp nest sites when male mates were removed. In addition, I observed males occupying nest boxes early in the season and then abandoning these boxes because they could not attract mates. From these results, I hypothesized that the operational sex ratio of the violet-green swallows in my study area was extremely male-biased and that there were fewer females than nest sites. In this paper I report my findings from a test of this hypothesis.

I temporarily removed females from mated pairs of violet-green swallows and observed whether female intruders replaced them. I conducted the same experiment on pairs of tree swallows so that I could compare the number of

unmated female floaters in a population of violet-green swallows to that of a closely related species, known to have intense female nest competition (Leffelaar and Robertson 1985; Stutchbury and Robertson 1985, 1987). I predicted that female violet-green swallows would not be replaced by female floaters whereas female tree swallows would (Stutchbury and Robertson 1987).

The temporary removal of females also allowed me to examine male behaviour while female mates were detained and after they returned. Several studies have shown that monogamous males attempted to acquire extra-pair copulations whenever the opportunity arose, including times when they were free from performing other duties, such as mate guarding (Brodsky 1988) and when they themselves were not being guarded by their female mates (Wagner 1992). Thus, I predicted that males of both species would attempt more extra-pair copulations while their mates were absent because male violet-green swallows would be free from guarding mates and male tree swallows would be accessible to extra-pair females at nest sites unguarded by their original mates.

To date no studies have reported how males respond to their female mates after the latter have been absent for extended periods. I was particularly interested in whether males would demonstrate a preference for their returning mates over replacement females and whether males would try to reduce the possibility of being cuckolded by using frequent pair copulations or other forms of paternity defense. Although it has been suggested that the existence of floater females would enable males to replace unfaithful mates (Zenone et al. 1979; Gowaty 1981), the cost of a later date of nest initiation in terms of reproductive output (e.g., DeSteven 1978) may make it more beneficial for males to accept their original mates (Smith 1989), especially, if they can use frequent pair copulations to try to outcompete potential competitors' sperm. The

latter has been shown in tree swallows (Venier and Robertson 1991, Chapter 2) but not in violet-green swallows (Chapters 2, 3). In my male removal study of violet-green swallows, released males were unable to copulate frequently with their mates despite several attempts because females refused frequent pair copulations. The period of female absence during this study provided me with another opportunity to look for alternative paternity defenses in violet-green swallows.

## **Methods**

### **Study Area and Subjects**

The study was conducted at the Creston Valley Wildlife Management Area in southeastern British Columbia (49°05' N, 116°35'W) between April and June 1990. Tree swallows nested in boxes mounted on poles approximately 30 m apart along several dikes around marshland. Violet-green swallows nested in boxes mounted 15 to 30 m apart on the walls of cabins, barns and garages on hillsides adjacent to the marsh. Contents of nest boxes were checked every third day before laying and every day throughout the laying period so that experiments could be conducted at a consistent time in relation to the first day of laying.

I captured birds with mist nets in April and marked each with coloured leg bands and streaks of acrylic paint on the wing, tail and breast feathers in specific colour patterns for individual identification. Violet-green swallows could be sexed easily by plumage, but the sex of male and older female (after first year) tree swallows was difficult to determine (Hussell 1983) so subsequent behaviour, especially during copulation attempts, was used to confirm the sex of marked individuals (Cohen 1984).

## Procedures

Marked pairs were observed for 30 min periods every 3 to 5 days within 7 days prior to the removal of the female from each pair. I captured the females of 7 violet-green and 8 tree swallow pairs inside their nest boxes and detained them for 2 h in the dark in a soft cotton bag to minimize stress. Following the detention period, I released females and observed them for 1 to 2 h after they returned to their nest sites. Finally, I observed the same pairs during at least one 30 min period within 2 to 3 days after removal experiments were conducted. All observations were conducted between 0500 and 1300 hours on days after pairs had been observed copulating and before they began laying.

During all observation periods I watched the nest site and surrounding area. I continuously observed the pair (or male only) and any female intruders that landed within 10 m of the nest box or male. I recorded the time of all arrivals and departures and the frequencies of several behavioral interactions between individuals. I assessed the frequency of social contact between males and females by counting vocalizations and bill displays such as snaps and gapes. I determined the frequency of following behaviour by counting chases and departures and arrivals from a perch less than one minute after a female did so. I counted male approaches toward perched females ("swoops/hovers") as preliminary moves toward copulation attempts in addition to unsuccessful attempted copulation mounts and successful copulations judged by the appearance of cloacal contact between males and females. As it was not always possible to observe cloacal contact, I used the positions of the birds' tails as an indication of whether contact was established. Each cloacal contact was considered a single copulation.

## Statistical Analyses

Data collected during watches of marked pairs prior to the removal of the females were averaged to obtain pre-removal values. Data collected on days after the removals were averaged to obtain post-removal values. Pre- and post-removal values were compared to data collected when female mates were detained (removal periods) and data collected when detained females were reunited with their mates (release periods). Dates, days with respect to egg laying, time of day and the duration of each type of observation period are summarized in Table 4.1.

I used Friedman tests followed by multiple comparisons of the behaviour of birds during the treatment period (either the removal or release period) to their behaviour during each control period (pre- and post-removal periods) for each analysis of multiple groups (Siegel 1956; Hollander and Wolfe 1973). I used Wilcoxon paired-sample tests to compare male responses to female intruders versus original mates during release periods (Siegel 1956). One-tailed tests were used to determine whether the number and duration of female intrusions and number of extra-pair mating attempts increased during removal versus pre- and post-removal periods and whether the intensity of mate guarding or the frequency of pair copulations increased during release versus pre- and post-removal periods. Two-tailed tests were used to compare male responses to female intruders versus original mates. Statistics were computed with the SYSTAT statistical package (SYSTAT, Inc. 1986) and manual (Wilkinson, 1986). Statistical significance was accepted at  $p < 0.05$ . Unless otherwise stated, non-significant results must be considered inconclusive because small samples would not produce sufficient power (i.e.,  $1 - \beta < 0.80$ ) to detect



Table 4.1. Mean ( $\pm$  SE) date (day 1 = April 1) and day before egg laying (day 0 = day when first egg was laid), mean time of day when pairs were observed and the total duration (h) of pre-removal, removal, release and post-removal observation periods.

Variable	Violet-green Swallows			Tree Swallows		
	pre-removals N=7	removals & releases N=7	post-removals N=7	pre-removals N=8	removals & releases N=8	post-removals N=8
Date	58.1 $\pm 2.3$	60.4 $\pm 2.1$	63.8 $\pm 3.3$	41.5 $\pm 1.9$	43.6 $\pm 2.0$	44.8 $\pm 2.0$
Day	-21.7 $\pm 2.4$	-19.3 $\pm 2.3$	-16.0 $\pm 3.2$	-11.3 $\pm 2.4$	-9.1 $\pm 2.0$	-8.1 $\pm 2.0$
Time of Day	6:36 -7:14	6:00 <sup>^</sup> -8:12 8:12 <sup>†</sup> -9:29	7:11 -8:04	7:25 -8:00	5:30 <sup>^</sup> -7:40 7:40 <sup>†</sup> -9:36	7:23 -7:54
Total Duration	10.3	15.4 <sup>^</sup> 8.9 <sup>†</sup>	13.4	10.9	17.3 <sup>^</sup> 16.0 <sup>†</sup>	8.8

<sup>^</sup> removal period; <sup>†</sup> release period - values for these two periods were the same for date and day.

differences (Cohen, 1977). Numbers reported in the text are means  $\pm$  standard errors unless otherwise stated.

## Results

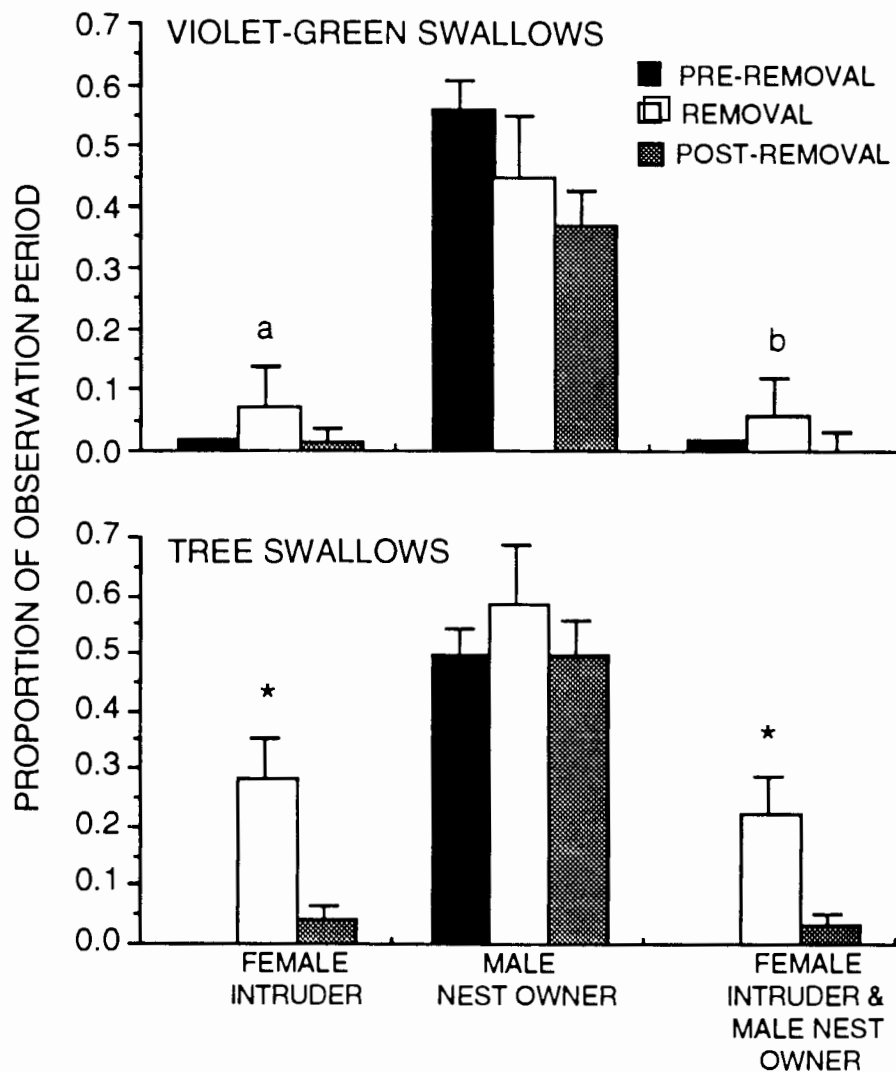
### Violet-green swallows

There was no detectable difference in the number of female violet-green swallows intruding during removal ( $0.43 \pm 0.20$  during 2 h), pre-removal ( $0.14 \pm 0.14$  during 1 h) and post-removal periods ( $0.00 \pm 0.00$  during 1 h) ( $X_r^2 = 1.50$ ,  $P=0.47$ ,  $N=7$ ,  $1-\beta \sim 0.58$ ), nor in the proportion of the time spent by female intruders near nests or males during the three periods (Figure 4.1). (I did not correct for the duration of removal versus pre- and post-removal periods because I found no difference between the number of intruders that arrived during 30 min, 1 h and 2 h periods when I observed non-experimental nests as part of another study (Chapter 2).)

Female violet-green swallow intruders did not try to usurp nest sites from detained females. On average, they were present for only 6 min of release periods and they were never present when the original females first returned to their nests. Resident females did not chase female intruders more often during release periods ( $0.21 \pm 0.14$  per 30 min) than during pre-removal ( $0.02 \pm 0.02$  per 30 min) and post-removal periods ( $0.00 \pm 0.00$  per 30 min) ( $X_r^2 = 0.64$ ,  $P=0.725$ ,  $N=7$ ,  $1-\beta \sim 0.33$ ). No fights between original female violet-green swallows and female intruders were observed.

Two female violet-green swallow intruders appeared during 3 of the 7 removal periods and both were marked. The female intruder at one nest had been captured earlier at a neighbour's nest but was rarely seen in the study area. The female, who intruded during the other two removal periods, had

Figure 4.1. Mean proportion of the observation period when the female intruder was present, the male nest owner was present, and the female intruder and male nest owner were present at the same time (N=7 for violet-green swallows; N=8 for tree swallows). Bars indicate standard errors. <sup>a</sup> $\chi^2=2.64$ ,  $P=0.267$ ,  $1-\beta=0.43$ ; <sup>b</sup> $\chi^2=4.79$ ,  $P=0.091$ ,  $1-\beta=0.28$ ; \*  $\chi^2=9.44$ ,  $P=0.01$  in both cases, comparisons of removals to pre-removals ( $X=11.5$ ,  $P=0.01$ ) and post-removals ( $X=9.5$ ,  $P=0.03$ ).

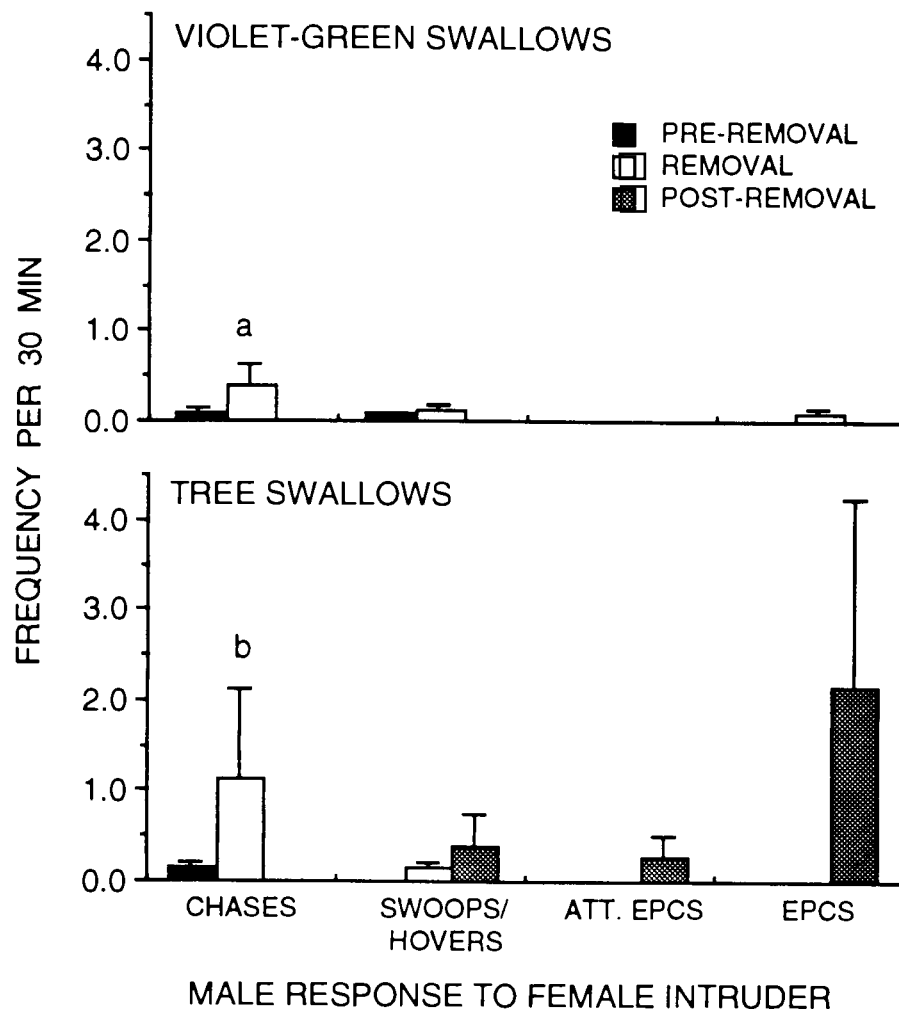


initiated a nest in the study area but was apparently exploring several alternative sites.

No differences were detected in the time that male violet-green swallows were present during removal, pre-removal and post-removal periods ( $X^2=1.14$ ,  $P=0.57$ ,  $N=7$ ,  $1-\beta\sim 0.28$ ) and although they appeared to be accompanied by female intruders during more of the time while mates were detained, they were not accompanied significantly more than during the control periods (Figure 4.1). If male violet-green swallows had been actively seeking extra-pair matings I expected them to behave like unmated male floaters sneaking around and chasing females in receptive condition (Chapter 3). Instead, I could detect no difference in the frequencies of behaviours used by violet-green swallow males to gain extra-pair matings during removal, pre- or post-removal periods (Figure 4.2) ( $1-\beta\sim 0.19-0.35$ ). Most of the time, males behaved as though they were waiting for their mates at the nest box but I suspect that one male obtained a successful extra-pair copulation with his female neighbour while his mate was detained. The male flew over and tried to mount his female neighbour at her nest box while her mate was absent (approximately 8 min). She fought with him briefly and flew. He chased her to a tree where they landed behind the foliage. Then I heard the male give the same "flutey call" (Cohen 1987) that was commonly given prior to successful pair copulations. A few seconds later, the male returned to his nest box. The entire interaction lasted only 40 s. The female neighbour remained in the tree for 2 more minutes and then returned to her nest box and was rejoined by her mate.

When I compared the responses of male violet-green swallows to female intruders during removal periods versus to mates during pre- and post-removal periods (after correcting for the time that males and females were present

Figure 4.2. Comparison of the frequencies of responses of males to intruding females during pre-removal, removal and post-removal periods (N=7 for violet-green swallows; N=8 for tree swallows). Chases occurred when males followed females from a perch or in the air, swoops/hovers consisted of any approach toward a perched female, and attempted copulation mounts (att. epcs) were distinguished from successful extra-pair copulations (epcs) by the position of birds' tails. Bars indicate standard errors. <sup>a</sup>  $\chi^2=0.07$ ,  $P=0.965$ ,  $1-\beta\sim 0.35$ ; <sup>b</sup>  $\chi^2=2.44$ ,  $P=0.296$ ,  $1-\beta\sim 0.23$ .



together respectively), there tended to be more vocalizations to female intruders than mates, however, no significant differences in the frequency of these or other interactions were detected (Figure 4.3) ( $1-\beta \sim 0.11-0.37$ ).

I was unable to compare the frequencies of male violet-green swallow responses to female intruders versus mates during release periods because intruder females were present during only 2 releases and in both cases, the female intruders were accompanied by other males (likely their mates).

Female violet-green swallows were unguarded less of the time during release than pre-removal periods but not during post-removal periods (Figure 4.4). Males chased and departed following their mates more often during release than pre-removal periods (Figure 4.5) but otherwise they did not respond differently to their original mates after their long periods of absence ( $1-\beta \sim 0.12-0.48$ ). In particular, male violet-green swallows did not attempt or achieve frequent pair copulations during release periods.

### **Tree swallows**

In contrast to violet-green swallows, there were significantly more female tree swallows intruding during the removal period ( $1.13 \pm 0.23$  during 2 h) than during the pre-removal period ( $0.13 \pm 0.13$  during 1 h) ( $X=10$ ,  $P=0.01$ ) but not during the post-removal period ( $0.63 \pm 0.32$  during 1 h) ( $X=4$ ,  $P=0.30$ ,  $1-\beta \sim 0.80$ ) ( $X_r^2 = 5.69$ ,  $P=0.05$ ,  $N=8$ ). Comparisons of removals to each control period showed that female tree swallows stayed significantly longer during removal than pre-removal and post-removal periods (Figure 4.1).

Unlike violet-green swallows, female tree swallow intruders tried to usurp nests from detained females and persisted at nests after original female mates returned for an average of 20 min. Interactions between returning female tree

Figure 4.3. Mean frequency of male responses to female intruders during removals and female mates during pre- and post-removal periods (N=3 for violet-green swallows; N=7 for tree swallows). Frequencies were calculated per min of time that the male spent with female intruders during removals and mates during pre- and post-removals. Bars indicate standard errors. See Methods for definitions of responses. <sup>a</sup> $X_r^2=4.67$ ,  $P=0.097$ ,  $1-\beta\sim 0.37$ ; <sup>b</sup> $X_r^2=2.00$ ,  $P=0.368$ ,  $1-\beta\sim 0.26$ ; <sup>c</sup> $X_r^2=3.07$ ,  $P=0.215$ ,  $1-\beta\sim 0.48$ ; <sup>d</sup> $X_r^2=2.57$ ,  $P=0.276$ ,  $1-\beta\sim 0.41$ .

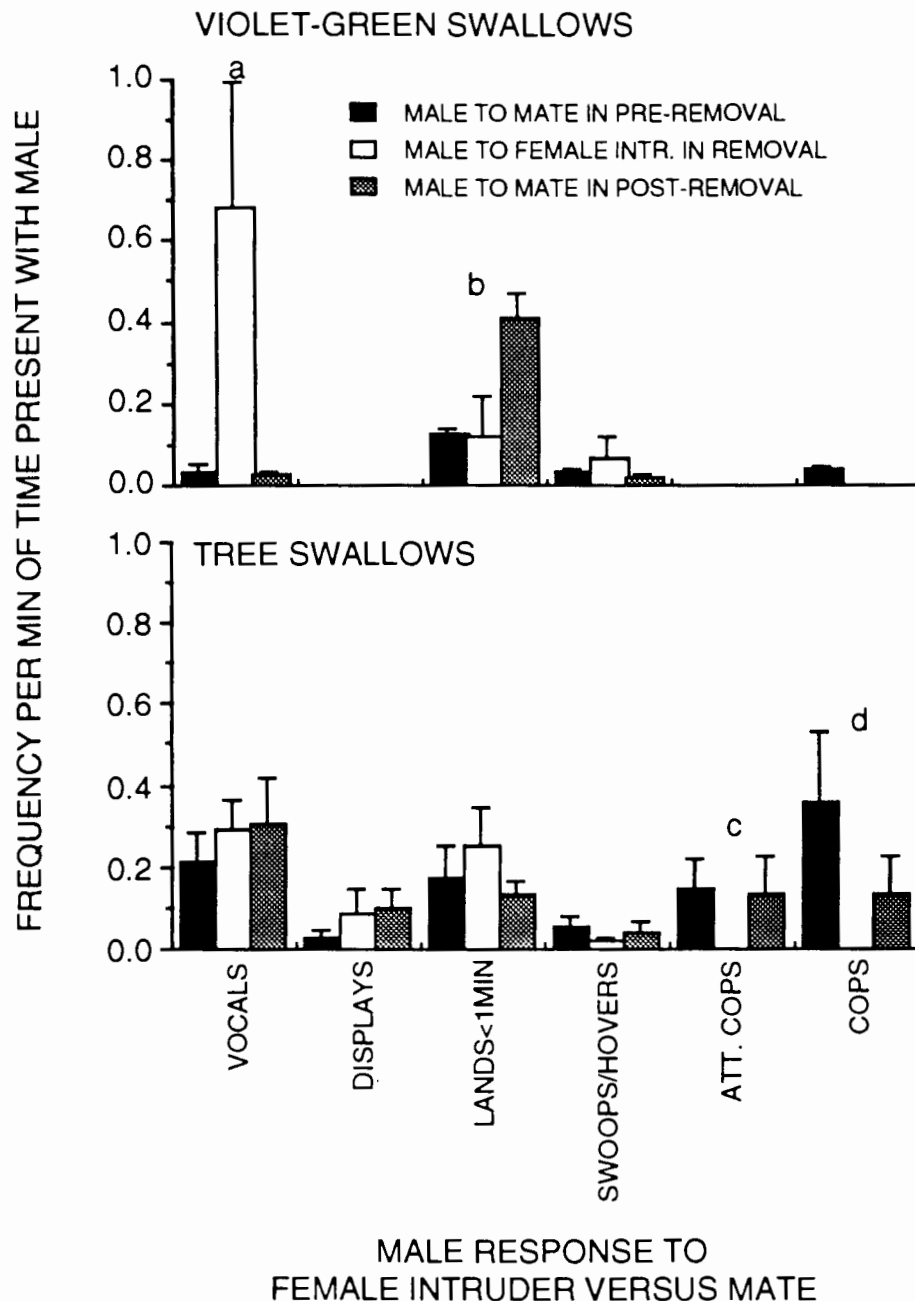


Figure 4.4. Mean proportion of the observation period when the female and male nest owners were present at the same time, the female was present alone, the male was present alone and the sum of the latter two variables which equals the proportion of time when the female was unguarded by the male (N=7 for violet-green swallows; N=8 for tree swallows). Bars indicate standard errors. <sup>a</sup> $\chi^2=4.79$ ,  $P=0.091$ ,  $1-\beta\sim 0.41$ ; \*  $\chi^2=6.00$ ,  $P=0.05$ , comparisons of removals to pre-removals ( $X=9$ ,  $P=0.02$ ) and post-removals ( $X=6$ ,  $P=0.12$ ).

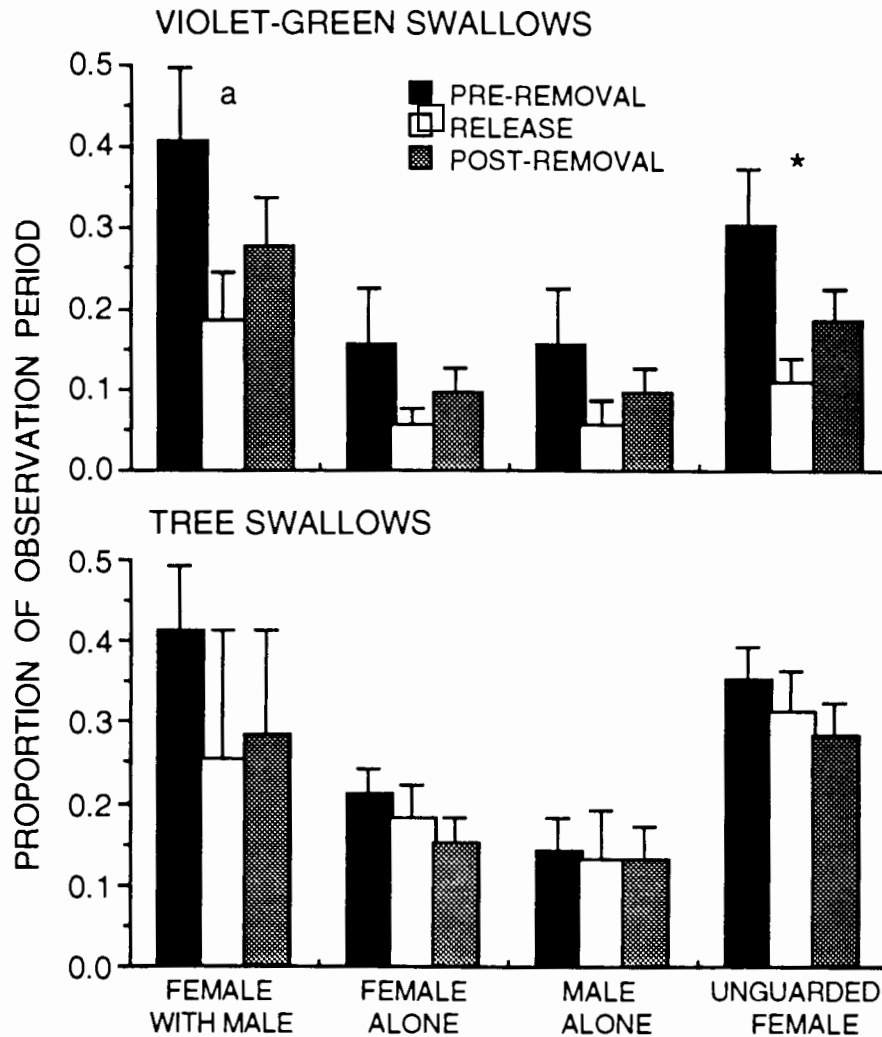
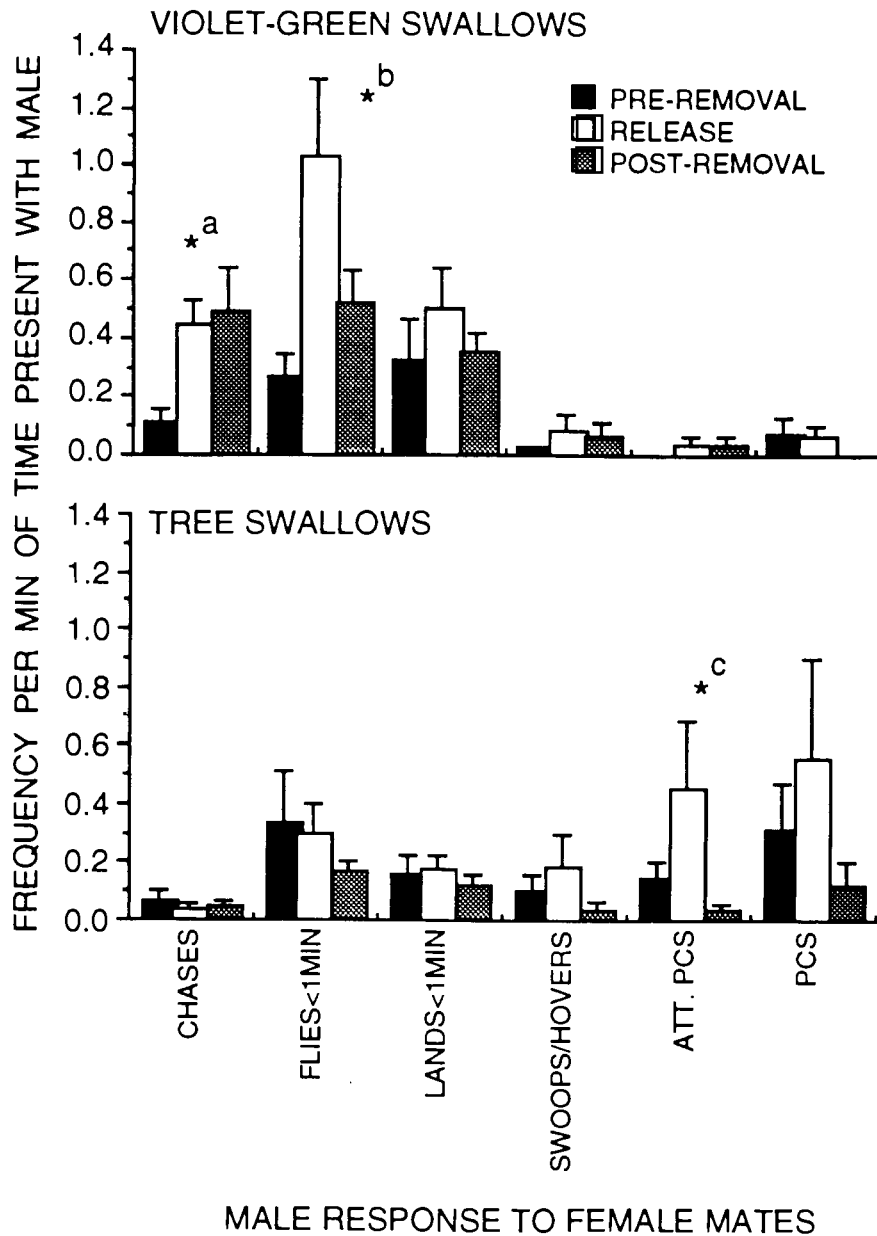




Figure 4.5. Mean frequency of responses of males to original female mates during pre-removal, release and post-removal periods (N=6 for violet-green swallows; N=8 for tree swallows). Bars indicate standard errors. See Methods for definitions of responses. \*  $aX_r^2 = 9.00$ ,  $P=0.01$ , comparisons of releases to pre-removals ( $X = 9$ ,  $P=0.01$ ) and post-removals ( $X = 0$ ,  $P=1.00$ ); \*  $bX_r^2 = 7.00$ ,  $P=0.03$ , comparisons of releases to pre-removals ( $X = 9$ ,  $P=0.01$ ) and post-removals ( $X = 3$ ,  $P=0.387$ ); \*  $cX_r^2 = 6.25$ ,  $P=0.04$ , comparisons of releases to pre-removals ( $X = 5$ ,  $P=0.22$ ) and post-removals ( $X = 10$ ,  $P=0.01$ ).



swallows and female intruders involved numerous chases ( $1.06 \pm 0.37$  per 30 min) and fights ( $0.69 \pm 0.23$  per 30 min). Chases were significantly more frequent during release periods than during pre-removal ( $0.00 \pm 0.00$  chases per 30 min) ( $X = 10.5$ ,  $P = 0.01$ ) but not post-removal periods ( $0.47 \pm 0.26$  chases per 30 min) ( $X = 7.5$ ,  $P = .07$ ) ( $X_r^2 = 7.31$ ,  $P = 0.026$ ,  $N = 8$ ). Fights occurred only during release periods but no statistical difference in the frequency of fighting was detected among the three periods ( $X_r^2 = 4.69$ ,  $P = .096$ ,  $N = 8$ ,  $1 - \beta \sim 0.63$ ).

Female tree swallow intruders appeared during 7 of the 8 removal periods. Most of the intruders were brown, second-year (SY) females but there were also two different blue, after-second-year (ASY) females (recognized by a brownish tinge of colour over their bills (Hussell 1983)). Four female intruders were marked and had been observed within the study site earlier in the season. None of the intruders were nesting neighbours (all neighbours were marked). Although it was difficult to count the total number of different intruders (because unmarked birds may have intruded several times), at least 8 different intruders were distinguished for all removals combined.

No differences were detected in the time that male tree swallows were present during removal, pre-removal and post-removal periods ( $X_r^2 = 1.75$ ,  $P = 0.42$ ,  $N = 8$ ,  $1 - \beta \sim 0.11$ ) but unlike violet-green swallows, male tree swallows spent more time accompanied by female intruders during removal periods than the other two periods (Figure 4.1).

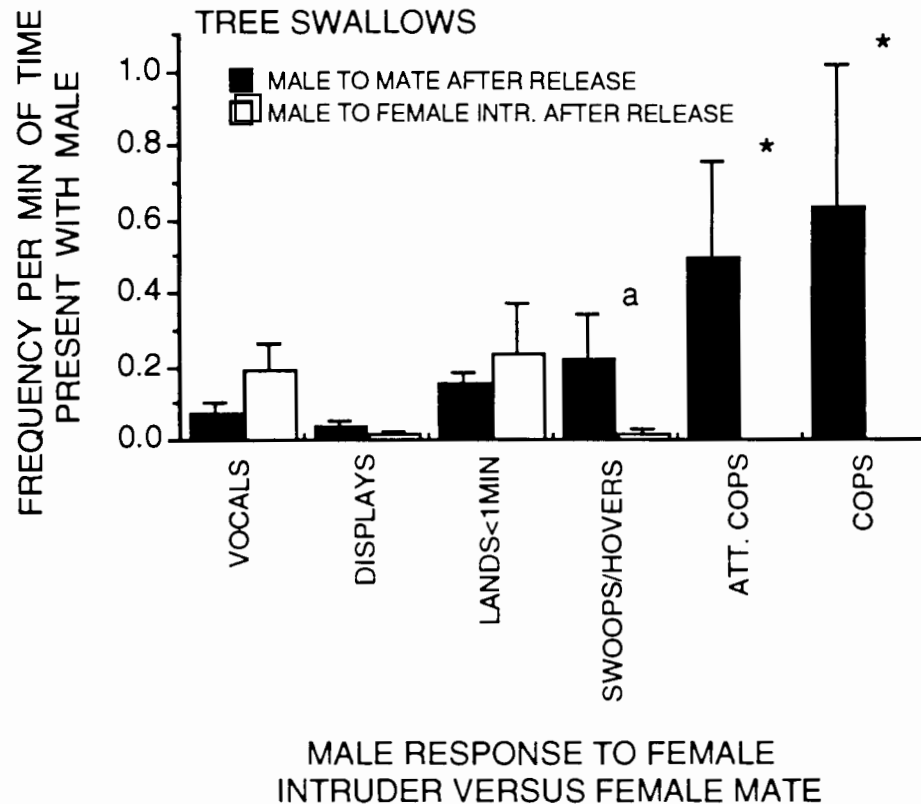
There were no statistical differences in the frequencies of behaviors used by male tree swallows to gain extra-pair matings among the three periods (Figure 4.2)

( $1 - \beta \sim 0.17 - 0.23$ ). I did not observe any extra-pair copulations during removals but I suspect that one forced extra-pair copulation occurred between a male and

a female intruder inside his nest box before his original mate returned after being released. I watched the male follow a female intruder inside his nest box and then I heard vocalizations and saw wing tips moving at the entrance hole indicating some sort of struggle. They remained inside the box together for 11.5 min and when the female intruder emerged, she appeared to be unharmed and perched on the box with the male. On other occasions I have found paired birds clasped in a mounted position inside nest boxes and noted wet cloacal protruberances on each bird of the pair. Thus, it seems likely that an extra-pair copulation occurred inside the box. In addition, I saw the same male copulate with a visiting female neighbour on top of his nest box during a post-removal period. The male's mate was absent for at least 12.5 min while a female neighbour (from a nest 20 m away) landed on top of his nest box and received a total of 36 successful copulation mounts and 8 other attempted mounts. The female neighbour solicited these copulations by edging closer to the male after landing beside him. She was at the box with the male for approximately 11 min and left immediately when the resident female returned.

The responses of male tree swallows to female intruders during removal periods did not differ from their responses to mates during pre- and post-removal periods (Figure 4.3) ( $1-\beta \sim 0.10-0.48$ ) but males were unable to mount female intruders whereas they frequently mounted and successfully copulated with mates. Likewise, during release periods, male tree swallows attempted and succeeded at copulating significantly more often with mates than female intruders (Figure 4.6). Other male responses to female intruders versus mates during release periods did not differ ( $1-\beta \sim 0.21-0.41$ ).

Figure 4.6. Mean frequency of male responses to female intruders and female mates during release periods (N=7 for tree swallows). Frequencies were calculated per min of time that the male spent with female intruders and mates respectively. Bars indicate standard errors. See Methods for definitions of responses. <sup>a</sup>Wilcoxon paired-sample test,  $P=0.07$ ,  $1-\beta\sim 0.41$ ; \* Wilcoxon paired-sample test,  $0.01 < P < 0.05$ .



Unlike violet-green swallows, the proportion of time that female tree swallows were unguarded did not increase significantly after females were released (Figure 4.4) ( $1-\beta=0.05-0.14$ ) and male tree swallows attempted significantly more pair copulations during release than pre- or post-removal periods (Figure 4.5). Other pair interactions were not detectably different during the three periods ( $1-\beta=0.07-0.20$ ).

Table 4.2 summarizes the results for the predictions derived from hypotheses about female competition for nest sites, constraints on male promiscuity, male preferences for replacement versus original mates and the use of alternate paternity defenses after female mates were temporarily detained.

## **Discussion**

Although female violet-green swallows intruded at 3 of the 7 nests belonging to detained females, intruders did not try to usurp nest sites. Thus, female nest owners left nests undefended for 2 h without risk of nest loss. This result indicated that there were few if any female violet-green swallows restricted from breeding due to nest limitation in the Creston population. The incidental responses of three females that had been experimental subjects provided additional support for the idea that nest sites were not limited for violet-green swallows. These females abandoned their original nests and re-nested in nearby unused nest boxes 1 to 2 weeks after they had been temporarily removed. Nest switching by these females had no effect on the results of the study but did demonstrate the excess of nest sites relative to females.

I found an abundance of unmated male violet-green swallows when I temporarily removed males in earlier experiments (Chapter 3). The large difference in the replacement rates of temporarily removed males (20 intruders, 17 of which were suspected of being unmated in 8 trials) versus females

Table 4.2. Summary of results for the predictions derived from hypotheses about female competition for nest sites, constraints on male promiscuity, male preferences for replacement versus original mates and the use of alternate paternity defenses after female mates were temporarily detained. I report that the results were equivocal if the predicted trend was not significant and the power of the test was less than 80%. \* indicates that the behaviour was infrequent or much shorter in duration for that species relative to the other. Epcs and pcs refer to extra-pair copulations and pair copulations respectively.

Parameter	Prediction	Violet-green Swallows	Tree Swallows
No. of female intrusions	Highest during removal	Equivocal*	True
Duration of intrusions	Longest during removal	Equivocal*	True
Intruder's response	Usurp nest site	False	True
Response of released female	Fight to regain nest	False	True
Male's response to female intruders	Attempt more epcs during removal	Equivocal*	Equivocal
Male's response to mate	Chase away after release	False	False
	Follow more often after release	True	Equivocal*
	Spend longer time associated after release	True	Equivocal*
	Attempt frequent pcs more often after release	Equivocal*	True

(2 intruders, only 1 of which was suspected of being unmated in 7 trials) indicated that the floating population of violet-green swallows in Creston was male-biased. Male-biased floating populations have been documented for many other species (Stewart and Aldrich 1951; Hensley and Cope 1951; Bellrose 1976) and the main factor producing such a bias is generally thought to be greater mortality of females due to higher costs of reproduction (McKinney 1986). At present there is no information on sex-specific mortality rates or causes of mortality for violet-green swallows and further research on their population dynamics is required. Regardless of how they were caused, male-biased operational sex ratios tended to result in high male-male competition for females and have been associated with increased intensity and duration of mate guarding in many species of birds (Mumme et al. 1983; Møller 1987), mammals (Barash 1981) and invertebrates (Manning 1980). The combination of intense male competition for mates and unlimited nest site availability for females appears to have selected for mate guarding rather than nest guarding by male violet-green swallows.

The situation was very different for tree swallows. The replacement of detained females by female intruders indicated that, unlike violet-green swallows, there were more females than nest sites. Temporary male removals showed that males were also restricted from breeding by nest site availability (Chapter 3). Thus, limited nest sites created a demand for nest guarding by both sexes of nest owners and constrained the ability of male tree swallows to guard their mates away from their nest sites.

The presence of female floaters may have provided certain benefits for male tree swallow nest owners. For example, female floaters have been known to become second mates of bigamous male nest owners (Quinney 1983; Dunn

and Hannon 1991; Dunn and Robertson 1992) and/or replacements when original mates abandoned nests (Stutchbury and Robertson 1987). In addition, the fact that female nest owners guarded nests from female floaters resulted in regular nest attendance by female nest owners, i.e., females returned to nests often and sometimes foraged nearby (pers. obs.). Regular nest attendance by female mates allowed males to maintain regular contact with their mates without having to follow them away from the nest site. Thus, the presence of female floaters seemed to facilitate the simultaneous guarding of nests and mates by male tree swallows.

The scarcity of females in the population of violet-green swallows meant that there was no obvious increase in the number of opportunities for extra-pair matings when female violet-green swallow mates were detained. Tree swallows, on the other hand, had many more opportunities but, despite numerous approaches over extra-pair females, male tree swallows were no more successful than male violet-green swallows at obtaining extra-pair copulations while their mates were detained. Female intruders may not have been in fertile condition if they had not yet progressed through the events such as pair bonding, nest building, etc., that invoke oestrus. The circumstances under which extra-pair copulations were observed for each species indicated that mated males acquired extra-pair copulations opportunistically. It seemed that opportunities for extra-pair matings arose when female mates were absent and when extra-pair females were not being closely guarded. Thus, I would expect that opportunities for extra-pair matings would be more common for tree swallows than violet-green swallows because there would be a greater proportion of the time when female mates were absent and extra-pair mates were unguarded for the former. Recent studies using non-observational



techniques showed that male tree swallows engaged in many extra-pair copulations with neighbour females (Morrill and Robertson 1990; Lifjeld and Robertson 1992; Lifjeld et al. 1993; Dunn and Robertson 1993) and rare observations have indicated that extra-pair matings involved males visiting female neighbours at their boxes and vice versa (Venier et al. 1993, pers. obs.). None of these sorts of extra-pair copulations were detected during removal periods probably because males were engaged with female intruders at their nest sites but one was observed incidentally during a post-removal period.

Male violet-green swallows were not able to show a preference between their original mates and female replacements because the latter were rarely available. When female intruders did visit, male violet-green swallows virtually ignored them. Their fervor when being reunited with their original mates, on the other hand, was unmistakable (see discussion below).

In contrast to violet-green swallows, male tree swallows were as receptive to female intruders as to their original mates. Males may have been trying to acquire a replacement female in case their original mates abandoned them but, because males continued to behave receptively to female intruders even after their original mates had returned, it is likely that males were anxious to acquire a second mate at their nest box. The fact that female intruders were not receptive to copulations supports the idea that it would be costly for a male to replace his original mate (Smith 1989). More time would be required for a male to initiate egg laying with a replacement than with his original mate.

Male violet-green swallows resumed mate guarding at a greater level of intensity after females returned than during control periods. The long period of female absence did not cause males to reject their mates, nor did it provoke any alternative form of paternity guard, such as frequent pair copulations. Unlike the

responses of males who had been detained (Chapter 3), males whose mates had been detained did not even attempt frequent pair copulations when they were reunited with their mates during release periods. One possible explanation is that phylogenetic constraints restrict the occurrence of behaviour such as frequent pair copulations.

Male tree swallows accepted returning mates and, unlike violet-green swallows, they ardently tried to ensure their paternity with frequent pair copulations. The high frequency of attempted and successful pair copulations during all periods reinforced the idea that male tree swallows use frequent pair copulations regularly as an alternative paternity defense to mate guarding (Venier and Robertson 1991; Chapters 2, 3). The same has been found for males of several other species that guard nests rather than mates (Birkhead et al. 1987; Birkhead 1988; Møller and Birkhead 1991).

My results also support a recent explanation for why females allow mates to copulate with them frequently. Females may be trying to ensure an exclusive hold on mates (Petrie 1992). A female may be able to reduce her mate's abilities and opportunities to mate with other females by monopolizing his time, sperm and sexual energy via frequent pair copulations. If so, one would expect females to solicit frequent pair copulations at times when they have the greatest risk of sharing or losing their mates, i.e., when other females are present. In my study, female tree swallows experienced the highest risks of sharing their mates during release periods when female intruders were still present. My results indicate that pair copulations were more frequent during release than control periods but the difference was not significant. A larger sample would determine whether a correlation exists and experimental manipulations could be done to test whether the presence of female intruders influences the frequency at which

females solicit pair copulations. The fact that frequent pair copulations by violet-green swallows were not observed fits this theory as well. Female violet-green swallows appeared to have a low, if any risk of sharing their mates with other females.

In conclusion, the absence versus presence of female floaters was correlated to mate guarding versus nest guarding in populations of violet-green and tree swallows. The absence of female floaters was indicative of an unlimited resource of nest sites for violet-green swallows. Unlimited nest sites combined with a surplus of male floaters (Chapter 3) appears to have selected for mate guarding by male violet-green swallows. In contrast, the apparent surplus of female tree swallows prevented from breeding due to limited nest sites has led to selection for nest guarding by tree swallows.

Although the presence of female floaters provided male tree swallows with additional mating opportunities, extra-pair matings were not observed more frequently for tree swallows than violet-green swallows. It would be interesting to compare the actual frequencies of extra-pair fertilizations between the two species using non-observational techniques. The use of frequent pair copulations as an alternative paternity defense by male tree swallows but not violet-green swallows provokes interesting questions about phylogenetic constraints and female mating strategies that require further investigation.

## **References**

- Barash, D.P. 1981. Mate guarding and gallivanting by male hoary marmots (*Marmota caligata*). *Behav. Ecol. Sociobiol.* 9: 187-193.
- Bellrose, F.C. 1976. *Ducks, Geese, and Swans of North America*. Stackpole, Harrisburg, Pa.

- Birkhead, T.R. 1988. Behavioural aspects of sperm competition in birds. *Adv. Stud. Behav.* 18: 35-72.
- Birkhead, T.R., Atkin, L., and Møller, A.P. 1987. Copulation behaviour of birds. *Behaviour* 101: 101-138.
- Brodsky, L.M. 1988. Mating tactics of male rock ptarmigan *Lagopus mutus* : a conditional strategy. *Anim. Behav.* 36: 335-342.
- Butler, R.W. 1982. Wing fluttering by mud-gathering Cliff Swallows. Avoidance of "rape" attempts? *Auk* 99: 758-761.
- Cohen, J. 1977. *Statistical Power Analysis for the Behavioral Sciences*. New York, Academic Press.
- Cohen, R.R. 1984. Criteria for distinguishing breeding male Tree Swallows from brightly colored females prior to capture. *N. Am. Bird Bander* 9: 2-3.
- Cohen, R.R. 1987. Violet-green Swallows (*Tachycineta thalassina* ) have at least ten distinct vocalizations. *J. Colo.-Wyo. Acad. Sci.* 19: 18.
- DeSteven, D. 1978. The influence of age on the breeding biology of the Tree Swallow (*Iridoprocne bicolor* ). *Ibis* 120: 516-523.
- Dunn, P.O. and Hannon, S.J. 1991. Intraspecific competition and the maintenance of monogamy in tree swallows. *Behav. Ecol.* 2: 258-266.
- Dunn, P.O. and Robertson, R.J. 1992. Geographic variation and the importance of male parental care and mating systems in tree swallows. *Behav. Ecol.* 3: 291-299.
- Dunn, P.O. and Robertson, R.J. 1993. Extra-pair paternity in polygynous tree swallows. *Anim. Behav.* 45: 231-239.
- Gowaty, P.A. 1981. Aggression of breeding eastern bluebirds (*Sialia sialis*) toward their mates and models of intra- and interspecific intruders. *Anim. Behav.* 29: 1013-1027.

- Hensley, M.M. and Cope, J.B. 1951. Further data on removal and repopulation of the breeding birds in a spruce-fir community. *Auk* 68: 483-493.
- Hollander, M. and Wolfe, D.A. 1973. *Nonparametric Statistical Methods*. New York, John Wiley & Sons.
- Hussell, D.J. 1983. Age and plumage color in female Tree Swallows. *J. Field Ornithol.* 54: 312-318.
- Leffelaar, D. and Robertson, R.J. 1984. Do male tree swallows guard their mates? *Behav. Ecol. Sociobiol.* 16: 73-79.
- Leffelaar, D. and Robertson, R.J. 1985. Nest usurpation and female competition for breeding opportunities by Tree Swallows. *Wilson Bull.* 97: 221-224.
- Lifjeld, J.T. and Robertson, R.J. 1992. Female control of extra-pair fertilization in tree swallows. *Behav. Ecol. Sociobiol.* 31: 89-96.
- Lifjeld, J.T., Dunn, P.O., Robertson, R.J. and Boag, P.T. 1993. Extra-pair paternity in monogamous tree swallows. *Anim. Behav.* 45: 213-229.
- Manning, J.T. 1980. Male time investment strategies in *Asellus*. *Behaviour* 74: 254-271.
- McKinney, F. 1986. Ecological factors influencing the social systems of migratory dabbling ducks. In: *Ecological Aspects of Social Evolution* (Ed. by D.I. Rubenstein and R.W. Wrangham), pp. 153-171. Princeton: Princeton University Press.
- Møller, A.P. 1987. Duration and intensity of mate guarding in the swallow *Hirundo rustica*. *Ornis. Scand.* 18: 95-100.
- Møller, A.P. and Birkhead, T.R. 1991. Frequent copulations and mate guarding as alternative paternity guards in birds - a comparative study. *Behaviour* 118: 170-186.

- Morrill, S.B. and Robertson, R.J. 1990. Occurrence of extra-pair copulation in the tree swallow (*Tachycineta bicolor*). *Behav. Ecol. Sociobiol.* 26: 291-296.
- Mumme, R.L., Koenig, W.D., and Pitelka, F.A. 1983. Mate guarding in the acorn woodpecker: within-group reproductive competition in a cooperative breeder. *Anim. Behav.* 31:1094-1106.
- Petrie, M. 1992. Copulation frequency in birds: why do females copulate more than once with the same male? *Anim. Behav.* 44: 790-792.
- Quinney, T.E. 1983. Tree Swallows cross a polygyny threshold. *Auk* 100: 245-250.
- Siegel, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. Tokyo: McGraw-Hill Kogakusha.
- Smith, S.M. 1989. Extra-pair copulations in black-capped chickadees: the role of the female. *Behaviour* 107: 15-23.
- Stewart, R.E. and Aldrich, J.W. 1951. Removal and repopulation of breeding birds in a spruce-fir community. *Auk* 68: 471-482.
- Stutchbury, B.J. and Robertson, R.J. 1985. Floating populations of female Tree Swallows. *Auk* 102: 651-654.
- Stutchbury, B.J. and Robertson, R.J. 1987. Behavioral tactics of subadult female floaters in the tree swallow. *Behav. Ecol. Sociobiol.* 20: 413-419.
- Systat, Inc., 1986. SYSTAT. Illinois, U.S.A.
- Venier, L.A. and Robertson, R.J. 1991. Copulation behaviour of the tree swallow, *Tachycineta bicolor*: paternity assurance in the presence of sperm competition. *Anim. Behav.* 42: 939-948.
- Venier, L.A., Dunn, P.O., Lifjeld, J.T., and Robertson, R.J. 1993. Behavioural patterns of extra-pair copulation in tree swallows. *Anim. Behav.* 45: 412-415.

Wagner, R.H. 1992. Mate guarding by monogamous female razorbills. *Anim. Behav.* 44: 533-538.

Wilkinson, Leland. 1986. SYSTAT: The System for Statistics. Evanston, Illinois: SYSTAT, Inc.

Zenone, P.G., Sims, M.E., and Erickson, C.J. 1979. Male ring doves behaviour and the defense of genetic paternity. *Am.Nat.* 114: 615-626.

## Chapter 5

### Nest guarding versus mate guarding by male violet-green swallows: the effect of nest site intruders

#### Abstract

I presented models of conspecific males and females at the nest sites of violet-green swallows *Tachycineta thalassina* during the female's fertile period to determine (1) whether resident males would increase the time spent guarding nest sites from a male model and consequently reduce the time spent guarding mates, (2) whether resident females would increase the time spent guarding nest sites from a female model and (3) whether resident males would try to court and/or copulate with a female model at their nests. Resident males spent significantly more time guarding their nest sites and did not follow their mates as closely when a male model was present. Mate guarding was not reduced substantially, however, because resident females rarely flew out of sight when their mates remained at the nest with the model. These results indicate that allocation of time to nest guarding can be increased when the risk of nest loss is enhanced. But the tradeoff between nest guarding and mate guarding was not clear cut because females flew circling within 15 m of nests while their mates were responding to the model. Female residents responded aggressively to female models and increased the time they spent guarding nests. Resident males showed little response to female models and did not attempt extra-pair copulations. There was no increase in pair copulation rates when male or female models were present. Thus, violet-green swallows did not switch between the paternity defense strategies.



## Introduction

One of the most common methods of paternity defense found in birds is known as mate guarding. Mate guarding involves the close following of females by their mates during the female's fertile period (Birkhead 1979). Mate guarding places a high demand on males in terms of time and energy (Møller 1987) and it restricts the male's ability to perform other activities, such as guarding nest sites (Birkhead et al. 1987; Birkhead and Møller 1992). Comparative studies have shown that nest guarders use alternative methods, such as frequent pair copulations to defend their paternity (Birkhead and Møller 1992). But little has been done to test experimentally whether the amount of time spent guarding mates can be modified by altering the need to guard nests within a single species. I set out to test whether an increased demand to guard nests from conspecific male intruders would reduce the time that males of a single species spent mate guarding and, if so, whether males would substitute frequent pair copulations to defend their paternity.

Violet-green swallows *Tachycineta thalassina* guard their mates prior to and during egg laying (Chapter 2). Observations revealed that males spent a high proportion of their time with their mates and frequently followed their mates to and from the nest (Chapter 2). Temporary male removal experiments showed that absent males experienced a high risk of mate loss but a relatively low risk of nest loss (Chapter 3). Temporary female removal experiments showed that female mates were not replaced and thereby demonstrated a shortage of female mates as the reason for high male-male competition for mates (Chapter 4). If mate guarding evolved due to the relatively low cost of leaving nest sites unguarded compared to the high cost of leaving mates unguarded, then males should alter their guarding priorities in response to nest availability versus mate availability. Males that experience heightened risks of nest loss are expected to

decrease their mate guarding and increase nest guarding. I experimentally increased the risks of nest loss by placing a model of a male intruder at the nest of a male whose mate was in fertile condition. I predicted that the male would spend more time guarding his nest and less time guarding his mate. I expected that the time males spent associated with their mates and the frequency of following would be reduced by the presence of a male nest intruder. If these predictions held true, I expected that males would attempt more pair copulations with their mates after periods of time that they spent apart. If males did not increase their nest guarding then I would assume either (1) the cost of losing the nest to the male intruder was not higher than the cost of losing fertilizations or (2) the mate guarding behavioural response of male violet-green swallows was fixed and inflexible.

In addition to testing the male's response to a male conspecific nest intruder I was interested in examining both the resident male's and female's responses to a female conspecific nest intruder. I expected males would respond by attempting to attract the model as an additional mate. Females of many species respond aggressively to models of conspecific female intruders (Weatherhead and Robertson 1980; Yasukawa and Searcy 1982; Gowaty and Wagner 1988; Hobson and Sealy 1990). Thus, I expected females to respond by increasing the time they spent nest guarding.

## **Methods**

### **Study Area and Subjects**

The study was conducted at the Creston Valley Wildlife Management Area in southeastern British Columbia (49°05'N, 116°35'W) between April and June of 1989 and 1990. Violet-green swallows nested in boxes mounted 15 to 30 m apart on the walls of cabins, barns and garages on hillsides adjacent to the marsh. I captured birds with mist nets in April and marked each with colored leg

bands and streaks of acrylic paint on the wing, tail and breast feathers in specific color patterns for individual identification. Violet-green swallows could be sexed easily by plumage.

Contents of nest boxes were checked every third day before laying and every day throughout the laying period to enable precise calculation of each female's fertile period.

### **Presentation of Model Intruders at Nest Sites**

A conspecific taxidermic male model was presented at the nests of 25 pairs and a conspecific taxidermic female model was presented at the nests of 13 pairs of swallows. Models were presented between 5 days before egg laying and the day before the last egg was laid, i.e. while the female of each pair was in her fertile period. The presence of eggs in the nest did not influence the type or intensity of the responses of males or females to the models. The sequence of events for each model presentation was as follows. A pole was erected within 1 m of a nestbox and the behaviour of the pair at the nest was observed for 30 min. Then a taxidermic model was perched on top of the pole at nest height and the behaviour of the pair was observed for another 30 min. Then the model was removed and the behaviour of the pair was observed for a final 30 min. Model presentations occurred throughout the morning (0500 - 1200).

### **Observations of Pair Behaviour**

My main goals were to measure the responses of the resident males and females to the models and determine whether the presence of an intruder altered the time that resident males spent defending their nests rather than defending their mates. I recorded all interactions between the pair and between each member of the pair and the model and the time when each member of the pair arrived and departed. For most analyses I used only those trials for which I had evidence that the model was recognized as a threat to at

least one member of the pair. Such evidence included any aggressive action toward the model (e.g., swoops, hits, pecking) by either the male or female resident.

I combined data collected in 1989 and 1990 after determining that there were no detectable differences between years.

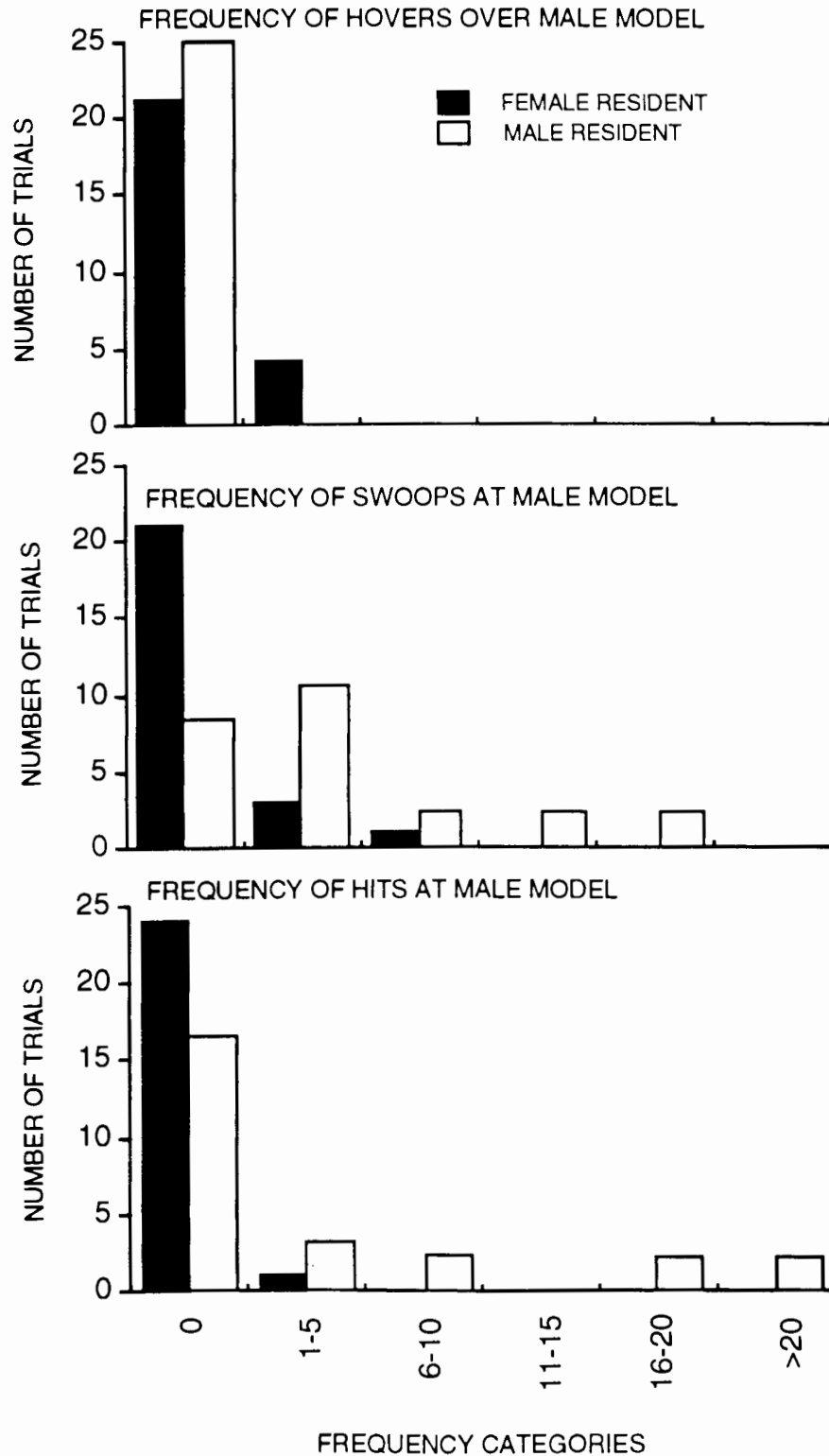
### **Statistical Analyses**

I used a G-test with Williams correction to test whether the probability of each type of response to the model was independent of the sex of the resident (Sokal and Rohlf 1981). I used one-tailed Friedman tests followed by multiple comparisons of the behaviour of birds during the treatment period to their behaviour during each control period (pre- and post-model periods) (Siegel 1956; Hollander and Wolfe 1973). I used one-tailed tests because I expected that the presence of the model would alter the behaviour of the male and female residents in a specific direction for each prediction (i.e., males would increase the time spent guarding their nests and decrease the time they spent guarding their mates). Statistics were computed with the SYSTAT statistical package (SYSTAT, Inc. 1986) and manual (Wilkinson, 1986). Statistical significance for each test was accepted at  $p < 0.05$ . Unless otherwise stated, non-significant results must be considered inconclusive because small samples would not produce sufficient power ( $1 - \beta < 0.8$ ) to detect differences (Cohen 1977). Numbers reported in the text are means  $\pm$  standard errors unless otherwise stated.

### **Results**

In 18 of 25 model presentations, males responded aggressively to the male model by swooping over and hitting it (Figure 5.1). Females responded aggressively in 7 of the 25 trials but not as aggressively as their mates (G test: hovers  $G=5.20$ ,  $P=.025$ ; swoops  $G=14.28$ ,  $P=.005$ ; hits  $G=8.53$ ,  $P=.005$ ) (Figure

Figure 5.1. Frequency distribution of the aggressive responses by male and female residents to a male model displayed 1m from the nest site over 30 min.



5.1). Live male intruders arrived in the vicinity of the nest while the model was present in 15 of the 25 trials, and males chased these male intruders away in 13 of these instances. In 2 trials male intruders attempted to copulate with the male model.

Using only the 18 trials when males responded to the models, I found that males spent a higher proportion of the observation period perched in the vicinity of their nests when male models were present than during the pre- and post-model control periods and they spent more time perched alone (without their mates) during the model period than the pre-model control period (Table 5.1).

Female mates were not out of sight when males were perched alone. Instead, females repeatedly circled overhead within sight of their mates (Figure 5.2). Males did not reduce the rate at which they followed females away from the nest but they tended not to return following their mates as often while male models were present (Table 5.2). Instead, males often returned to perch near the nest ahead of their mates when male models were present (Figure 5.2).

Very few successful or attempted pair copulations were observed during observation periods and there was no evidence that pair copulations were more frequent after models had been presented ( $0.11 \pm 0.08$  per 30 min) compared to before ( $0.11 \pm 0.08$  per 30 min) or during model presentations ( $0.11 \pm 0.08$  per 30 min).

In 10 of 13 trials females responded aggressively to female models positioned at their nests (Figure 5.3). Compared to their mates, resident males were less aggressive to female models (G test: hovers  $G=1.06, P>.25$ ; swoops  $G=1.71, P>.1$ ; hits  $G=81.76, P=.005$ ). Resident males did not attempt extra pair copulations with female models however male intruders did attempt to copulate with the female model in 4 trials.

Table 5.1. The proportion of the observation period that male and female residents spent perched in the vicinity of their nest sites before, during and after the presentation of the male model 1 m from the nest. Mean values,  $\pm$ SE, and sample sizes are shown.

Treatment	Total time <sup>a</sup> male perched	Total time <sup>b</sup> female perched	Time male <sup>c</sup> perched without female
Pre-Model N=18	0.17 $\pm$ 0.05	0.23 $\pm$ 0.06	0.03 $\pm$ 0.02
Male Model N=18	0.30 $\pm$ 0.04	0.25 $\pm$ 0.04	0.09 $\pm$ 0.03
Post-Model N=18	0.17 $\pm$ 0.03	0.19 $\pm$ 0.04	0.05 $\pm$ 0.01

<sup>a</sup>F=7.86, P=0.02, model vs pre-model P=.008, model vs post-model P=.049;

<sup>b</sup>F=1.86, P=0.39, 1- $\beta$ ~0.21;

<sup>c</sup>F=8.44, P=0.02, model vs pre-model P=.008, model vs post-model P=.566.

Figure 5.2 Cartoon demonstrating the proximity of mates during the pre-model, male model and post-model time periods.

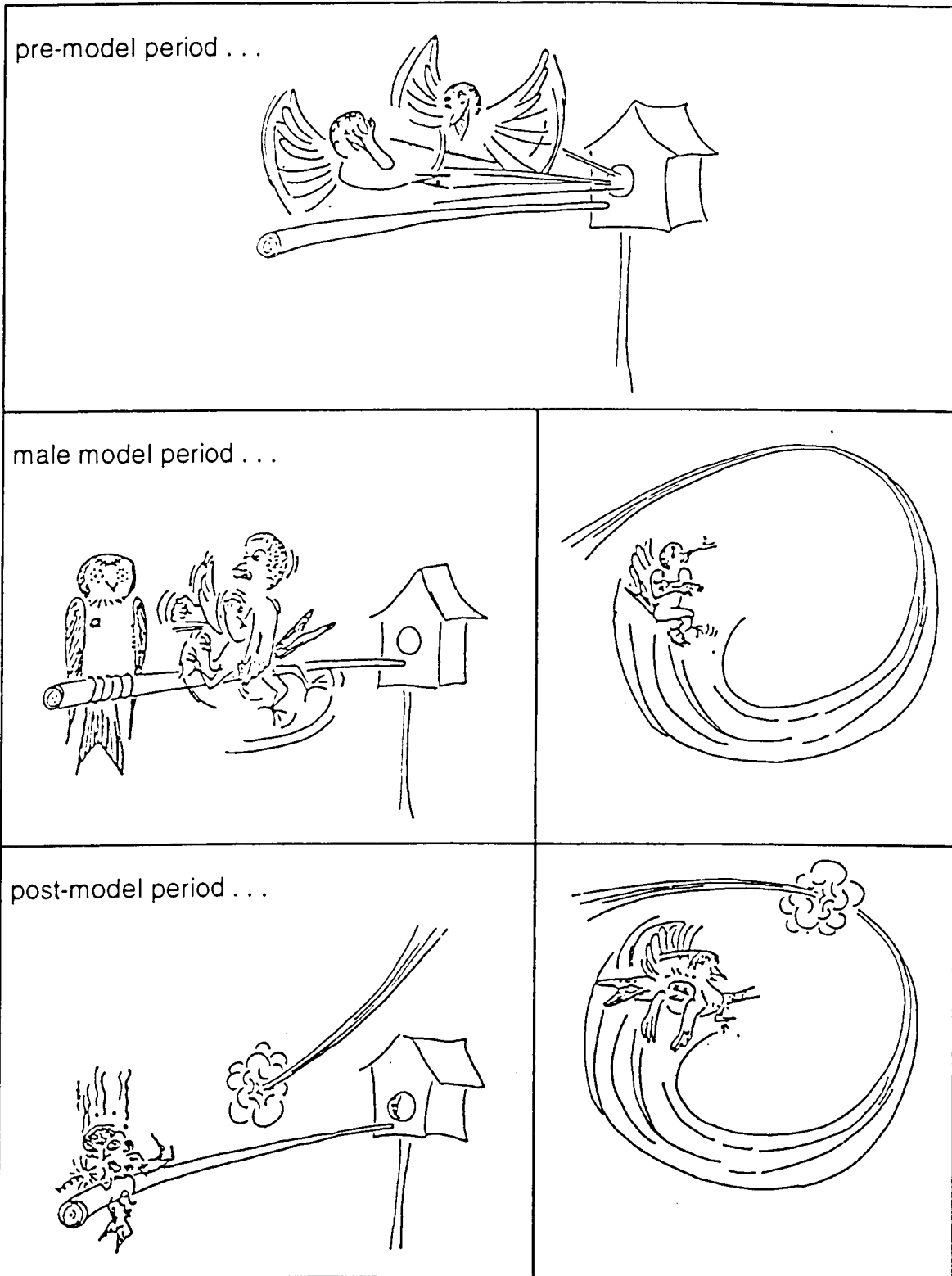




Table 5.2. The proportion of female flights followed by her mate away from and returning to the vicinity of the nest before, during and after the presentation of the male model 1 m from the nest. Mean values,  $\pm$ SE, and sample sizes are shown.

Treatment	Female flights <sup>a</sup> followed away from perch	Female flights <sup>b</sup> followed returning to perch
Pre-Model	0.56 $\pm$ 0.07 N=18	0.51 $\pm$ 0.11 N=14
Male Model	0.52 $\pm$ 0.05 N=18	0.37 $\pm$ 0.06 N=14
Post-Model	0.53 $\pm$ 0.07 N=18	0.51 $\pm$ 0.11 N=14

<sup>a</sup>F=0.25, P=0.88, 1- $\beta$ ~0.31;

<sup>b</sup>F=3.79, P=0.15, 1- $\beta$ ~0.13

Figure 5.3. Frequency distribution of the aggressive responses by male and female residents to a female model displayed 1m from the nest site over 30 min.



Using only the 10 trials in which female residents responded to the model I found that females spent significantly more time perched alone at nests when a female model was present than during the control periods (Table 5.3). Although females perched alone, males remained in sight, circling close overhead in the same way that females circled during male model presentations. Females were followed away from the nest less often during model presentations than during the pre-model period. There was not enough power to detect a difference in following on flights returning to the nest between the model and control periods (Table 5.4).

### **Discussion**

The presence of a conspecific male model was perceived as a threat by some male violet-green swallows but not all. There may be several reasons why some males did not respond to the male model. In one case the male and female were out of sight during the entire model period. In 5 of the trials there was a live male intruder that may have preoccupied the male's defenses. In 2 cases, live male intruders attempted to copulate with the model suggesting that the model may have appeared to be female rather than male (but if so, it is strange that the female did not attack the model).

When males did respond to male models as threats, they spent less time perched with their females and they followed their females away from perches less often than during controls. Thus, males appeared to be protecting their nests rather than their mates and the increase in time spent nest guarding reduced the time available to spend in close proximity to their mates. Males were able to keep their mates in sight, however, because females circled overhead whenever their mates remained at the nest. Thus, the tradeoff between mate guarding and nest guarding was less clear cut than I had

Table 5.3. The proportion of the observation period that male and female residents spent perched in the vicinity of their nest sites before, during and after the presentation of the female model 1 m from the nest. Mean values,  $\pm$ SE, and sample sizes are shown.

Treatment	Total time <sup>a</sup> female perched	Total time <sup>b</sup> male perched	Time female <sup>c</sup> perched without male
Pre-Model N=10	0.30 $\pm$ 0.09	0.25 $\pm$ 0.09	0.06 $\pm$ 0.03
Female Model N=10	0.46 $\pm$ 0.09	0.19 $\pm$ 0.05	0.31 $\pm$ 0.08
Post-Model N=10	0.28 $\pm$ 0.06	0.17 $\pm$ 0.05	0.16 $\pm$ 0.07

<sup>a</sup>F=2.45, P=0.29, 1- $\beta$ ~0.24;

<sup>b</sup>F=0.35, P=0.83, 1- $\beta$ ~0.11;

<sup>c</sup>F=8.15, P=0.02, model vs pre-model P=.008, model vs post-model P=.06

Table 5.4. The proportion of female flights followed by her mate away from and returning to the vicinity of the nest before, during and after the presentation of the female model 1 m from the nest. Mean values,  $\pm$ SE, and sample sizes are shown.

Treatment	Female flights <sup>a</sup> followed away from perch	Female flights <sup>b</sup> followed returning to perch
Pre-Model	0.64 $\pm$ 0.07 N=9	0.46 $\pm$ 0.12 N=8
Female Model	0.36 $\pm$ 0.06 N=9	0.32 $\pm$ 0.07 N=8
Post-Model	0.50 $\pm$ 0.07 N=9	0.50 $\pm$ 0.10 N=8

<sup>a</sup>F=8.72, P=0.01, model vs pre-model P=.005, model vs post-model P=0.20

<sup>b</sup>F=3.94, P=0.14, 1- $\beta$ ~0.14

expected. The female's behaviour enabled males to increase nest defense to some extent without a substantial reduction in mate guarding.

Females were not only reluctant to leave the nest site without their mates, they also followed them back to the vicinity of the nest when males returned ahead of them. These observations imply that female violet-green swallows were involved in maintaining a close association with their mates. A similar result was found in an experimental study that examined the tradeoff between mate association and foraging in great tits *Parus major* (Mace 1989). Female great tits actively chose to keep close to their caged mates early in the day when females were most fertile, and therefore when extra-pair males were most likely to be seeking extra-pair copulations (Mace 1989). Several studies have shown that the presence of the male mate deters intruders from harrassing and chasing females and thereby enables females to concentrate on foraging rather than escaping the advances of unwanted intruders (Ashcroft 1976; Lumpkin 1981, 1983; Lambrecht 1989). Female violet-green swallows would likely experience these benefits from mate guarding given the high rate at which unguarded females were chased by extra-pair males when their mates were temporarily detained (Chapter 3). Other benefits are possible. Mace (1989) suggested that females who stayed close to their mates would ensure that they received a full dose of sperm. This would be important if copulations with extra-pair females reduced sperm density to an extent that could influence a female mate's chances of being fertilized. Observations of extra-pair copulations by violet-green swallows were very rare so this seems unlikely. A third suggestion is that a female should assist her mate's efforts to mate guard and thereby avoid losing her mate's confidence of paternity. Males of some species have responded to female "infidelity" by deserting nests, forcing renests or reducing male parental care (Zenone et al. 1979; Davies 1985; Gowaty 1981; Møller 1988), however, I

found no evidence of reduced parental care by males with lowered confidence of paternity (Chapter 6).

It is possible that resident males responded to male models as a threat to their paternity rather than as a threat to their nests. If so, I would have expected males to guard mates more closely than nests. They did not. I considered using a model of an interspecific nest competitor instead of a male conspecific but when I observed interspecific interactions at nests I found that both members of the pair attacked the interspecific intruder and consequently, the pair spent little time apart during the model presentation. The different responses of male and female residents to conspecific models of each sex showed that the sex of each model was recognizable. The sex specific responses of residents to models allowed me to determine that males would stay to guard against male intruders at the nest site while their female mates left to forage, but only for brief periods of time.

Whenever female violet-green swallows flew out of sight of the nest for more than one minute, their male mates followed them. Thus, the cost of losing sight of a mate for more than a minute seemed greater than the cost of leaving the nest unguarded from an intruding conspecific male. In previous experiments, I showed that conspecific males never tried to usurp nests. Instead, they chased females to acquire extra-pair matings (Chapter 3). Thus, the male's decision to switch between guarding his nest and mate in this study may be based on the conditions that he had experienced on average. It would be better to measure the response of males to threats of nest loss of longer duration or more frequent occurrence.

Meek and Robertson (1994) found that male eastern bluebirds *Sialia sialis* in Ontario spent less time associated with their mates and more time guarding territories at sites that contained two nest boxes. These sites experienced

higher rates of intrusions by interspecific nest competitors (tree swallows *Tachycineta bicolor*). Gowaty et al. (1989) found that male eastern bluebirds in South Carolina spent more time guarding their mates on territories that contained two nest boxes. In their study, two-box sites experienced higher rates of intrusions by conspecific males competing for mates. These contrasting results suggest that male mating strategies may be flexible depending on the type of competition experienced by eastern bluebirds. When competition is greater for mates than nests (as seemed to be true for bluebirds in South Carolina) males spent more time mate guarding. Under conditions of greater competition for nests than mates (as in Ontario), males spent more time nest guarding. My results indicate that the same would be true for male violet-green swallows living under different conditions of competition.

The aggressive response of females to female conspecific models may have served three purposes: (1) to avoid conspecific nest usurpation as shown for female tree swallows (Leffelaar and Robertson 1985), (2) to prevent conspecific brood parasitism as found in eastern bluebirds (Gowaty and Wagner 1988) and /or (3) to prevent resident males from pairing polygynously as shown for red-winged blackbirds *Agelaius phoeniceus* (Yasukawa and Searcy 1982). The fact that female violet-green swallows were rarely observed defending their nests during control observations suggests that these problems were uncommon in my study population. Although I observed female violet-green swallows fighting each other at nest boxes early in the nesting season, later, there were enough extra nest sites available to allow some females to switch sites (Chapter 4). Parentage analysis is needed to test for cases of brood parasitism in nests of violet-green swallows but I saw no evidence of a second female entering the nest of another during the egg laying period and no days when two new eggs were found in a nest in the 120 nests that I followed through



laying. I did observe one case of bigamy in which a male attracted a second mate (a re-nesting female) after he and his first mate had started feeding the first brood. The scarcity of females in the population (Chapter 4), however, makes it unlikely that females would need to worry about defending against polygamy.

Males of species that guard nests rather than mates tend to tradeoff the nest guarding responsibility with their mates and consequently reduce the time spent guarding their mates at the nest as well as away from it (Leffelaar and Robertson 1984). This happened to some extent when models of each sex were presented at the nests of violet-green swallows. When the male model was present, females circled over as if they were anxious to forage. The sex roles were reversed during the female model presentation. Thus, the increased threat of nest loss in my study resulted in the first step toward ecological conditions that favour the use of alternative paternity defenses. The question remains whether a greater threat of nest loss could lead to the use of an alternative paternity defense such as frequent pair copulations by violet-green swallows.

## References

- Ashcroft, R. 1976. A function of the pair bond in the common eider. *Wildfowl* 27: 101-105.
- Birkhead, T.R. 1979. Mate guarding in the magpie *Pica pica*. *Anim. Behav.* 27: 866-874.
- Birkhead, T.R., Atkin L., and Møller, A.P. 1987. Copulation behaviour of birds. *Behaviour* 101: 101-138.
- Birkhead, T.R. and Møller, A.P. 1992. *Sperm Competition in Birds*. London: Academic Press.
- Cohen, J. 1977. *Statistical Power Analysis for the Behavioral Sciences*. New York: Academic Press.

- Davies, N.B. 1985. Co-operation and conflict among dunnocks *Prunella modularis*, in a variable mating system. *Anim. Behav.* 33: 628-648.
- Gowaty, P.A. 1981. Aggression of breeding eastern bluebirds (*Sialia sialis*) toward their mates and models of intra- and interspecific intruders. *Anim. Behav.* 29: 1013-1027.
- Gowaty, P.A. and Wagner, S.J. 1988. Breeding season aggression of female and male eastern bluebirds (*Sialia sialis*) to models of potential conspecific and interspecific egg dumpers. *Ethology* 78: 238-250.
- Gowaty, P.A., Plissner, J.H. and Williams, T.G. 1989. Behavioral correlates of uncertain parentage: mate guarding and nest guarding by eastern bluebirds, *Sialia sialis*. *Anim. Behav.* 38: 272-284.
- Hobson, K.A. and Sealy, S.G. 1990. Breeding-season aggression of female yellow warblers to models of male and female conspecific intruders. *Anim. Behav.* 39: 809-811.
- Hollander, M. and Wolfe, D.A. 1973. *Nonparametric Statistical Methods*. New York, John Wiley & Sons.
- Lambrecht, J. 1989. Mate guarding in geese: awaiting female receptivity, protection of paternity or support of female feeding? In: *The Sociobiology of Sexual and Reproductive Strategies*. (Ed. by Rasa, A.E., Vogel, C., and Volland, E.), pp. 48-60. London: Chapman and Hall.
- Leffelaar, D. and Robertson, R.J. 1984. Do male tree swallows guard their mates? *Behav. Ecol. Sociobiol.* 16: 73-79.
- Leffelaar, D. and Robertson, R.J. 1985. Nest usurpation and female competition for breeding opportunities by Tree Swallows. *Wilson Bull.* 97: 221-224.
- Lumpkin, S. 1981. Avoidance of cuckoldry in birds: the role of the female. *Anim. Behav.* 29: 303-304.

- Lumpkin, S. 1983. Female manipulation of male avoidance of cuckoldry behaviour in the ring dove. In: *Social Behaviour of Female Vertebrates*. (Ed. by S.K. Wasser), pp. 91-112. New York: Academic Press, Inc.
- Mace, R. 1989. Great tits choose between food and proximity to a mate. The effect of time of day. *Behav. Ecol. Sociobiol.* 24:285-290.
- Meek, S.B. and Robertson, R.J. 1994. Interspecific competition for nest boxes affects mate guarding in eastern bluebirds, *Sialia sialis* *Anim. Behav.* 47: 295-302.
- Møller, A.P. 1987. Extent and duration of mate guarding in swallows *Hirundo rustica*. *Ornis Scand.* 18: 95-100.
- Møller, A.P. 1988. Paternity and paternal care in the swallow, *Hirundo rustica*. *Anim. Behav.* 36: 996-1005.
- Siegel, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. Tokyo: McGraw-Hill Kogakusha.
- Sokal, R.R. and Rohlf, F.J. 1981. *Biometry*. 2nd ed. W.H. Freeman and Company.
- Systat, Inc., 1986. *SYSTAT*. Illinois, U.S.A.
- Weatherhead, P.J. and Robertson, R.J. 1980. Sexual recognition and anticuckoldry behaviour in savannah sparrows. *Can. J. Zool.* 58: 991-996.
- Wilkinson, L. 1986. *SYSTAT: The System for Statistics*. Evanston, Illinois: SYSTAT, Inc.
- Yasukawa K., and Searcy W.A. 1982. Aggression in female red-winged blackbirds: a strategy to ensure male parental investment. *Behav. Ecol. Sociobiol.* 11: 13-17.
- Zenone, P.G., Sims, M.E., and Erickson, C.J. 1979. Male ring doves behaviour and the defense of genetic paternity. *Am. Nat.* 114: 615-626.

## Chapter 6

### Parental care by male violet-green swallows and tree swallows with experimentally lowered paternity assurance

#### Abstract

Temporary removals of males during their mates' fertile periods were conducted to lower the confidence of paternity of male violet-green swallows *Tachycineta thalassina* and male tree swallows *Tachycineta bicolor*. Subsequently, the level of parental care provided by males with experimentally lowered confidence of paternity was compared to the level provided by control males. I expected that the removal period would have a greater effect on reducing the confidence of paternity, and hence, the parental care of male violet-green swallows than male tree swallows because the former defend their paternity by mate guarding whereas the latter defend their paternity by using frequent pair copulations. No differences in male attendance at the nest or in the proportion of feeding visits by removed versus control males were found for either species. The benefit of male parental care in terms of reproductive output was difficult to assess because nestling growth rates, maximum mass and fledging success did not differ between removal and control groups. Missed opportunities for promiscuous matings could have been a potential cost of providing parental care for some males because nesting asynchrony was such that fertile females were available for promiscuous matings with 4 of 20 (20%) male violet-green swallows and 18 of 20 (90%) male tree swallows while they helped rear young at their nests. Further research is recommended to determine whether the cost-benefit tradeoffs of providing male parental care vary among species that use different forms of paternity defense.

## Introduction

Males of several species of birds provide parental care to broods that partly consist of young sired by extra-pair males. Males of some species provide care at levels that reflect their paternity (i.e., their relatedness to the brood measured as a percentage of the number of young fertilized by them or as an index based on the number of extra-pair copulations received by the female) (Craig and Jamieson 1985; Møller 1988; Burke et al. 1989; Davies et al. 1992). But in other species, there is no correlation between male parental care and paternity (Gavin and Bollinger 1985; Frederick 1987; Westneat 1988; Davies et al. 1992; Wagner 1992; Whittingham et al. 1993).

There is evidence that males use time invested in paternity defense as an indicator of their paternity and hence as a way to gauge their paternal care (Burke et al. 1989), but the use of this gauge appears to depend on whether males are involved in polyandrous or monogamous relationships (Davies et al. 1992). Male parental care and confidence of paternity (i.e., a male's perception of his paternity) are both positively correlated to time invested in paternity defense in polyandrous situations but not monogamous ones (see review in Whittingham et al. 1993). The most likely explanation for this is that females alone cannot compensate sufficiently for reduced male care (Whittingham et al. 1992; Davies et al. 1992). If males cannot discriminate between related and unrelated young within a brood (Beecher 1988; Burke et al. 1989) then they will be unable to preferentially feed related young. If there is a high threshold level of parental care below which the entire brood will not survive, then monogamous males should not reduce their care except when their confidence of paternity reaches very low levels (Whittingham et al. 1992). Males that breed

in situations where other males or helpers can contribute in their stead could reduce their parental care at higher levels of confidence of paternity.

Another possible (additional but not exclusive) explanation for the difference in the tendency to reduce parental care in relation to confidence of paternity among species is that interspecific variation may exist in the ability of males to assess their paternity. It is possible that the form of paternity defense influences its reliability as an indicator of paternity. For example, mate guarding may provide a more reliable gauge of paternity than other forms of paternity defense because it involves a close association between a male and his mate at all times during her fertile period. The use of frequent pair copulations may be a less reliable means of assessing paternity because males spend less time monitoring the activity of their mates. To date no one has explored the possible connection between the form of paternity defense and its use as a gauge of paternity for males to determine how much male parental care to provide.

This study examines whether there is any correlation between the form of paternity defense and the tendency to reduce parental care in response to lowered paternity assurance. I experimentally lowered paternity assurance by temporarily removing male violet-green swallows *Tachycineta thalassina*, and male tree swallows *Tachycineta bicolor* during their mates' fertile periods. Previous work had identified interspecific variation in the paternity defense strategies used by these closely related congeners. Male violet-green swallows mate guard (Chapter 2) whereas male tree swallows use frequent pair copulations (Venier and Robertson 1991). In an earlier study (Whittingham et al. 1993), removal treatments did not lower the parental care provided by male tree swallows. A possible explanation for this result is that although the removal period reduced paternity assurance, males were able to regain their assurance

by using frequent pair copulations when they returned to their mates. Thus, the use of frequent pair copulations may have compensated for the period of absence. I suspected that the paternity assurance of a mate guarding male, on the other hand, would be more sensitive to a temporary removal because released males would be unable to reassure their paternity by using frequent pair copulations (Chapters 3,4,5). Thus, I predicted that the parental care provided by male violet-green swallows would be lowered by the removal treatment whereas the parental care of male tree swallows would be unaltered by the removal treatment.

It should be noted that both tree swallows and violet-green swallows mate monogamously so a male who reduced his parental care in response to lowered paternity assurance would risk losing reproductive success if his mate did not compensate for his reduction in feeds. Although this study did not examine this factor specifically, I did measure the nestling growth rates, maximum mass attained by nestlings and the fledging success of broods belonging to removal versus control males. If removals caused a reduction in male parental care, then I expected to see lower values of these three measures in broods of removal males unless their mates were able to compensate.

## **Methods**

### **Study Area and Subjects**

The study was conducted at the Creston Valley Wildlife Management Area in southeastern British Columbia (49°05'N, 116°35'W) between April and June 1988 to 1990. Tree swallows nested in boxes mounted on poles approximately 30 m apart along several dikes through marshland. Violet-green swallows nested in boxes mounted 15 to 30 m apart on the walls of cabins, barns and garages on hillsides adjacent to the marsh. I captured birds with mist nets in

April and marked each with colored leg bands and streaks of acrylic paint on the wing, tail and breast feathers in specific color patterns for individual identification. Violet-green swallows could be sexed easily by plumage, but the similar plumage of male and older female (after second year) tree swallows meant that the sex of birds had to be distinguished by observing their behaviour, particularly during copulation attempts (Cohen 1984).

Contents of nest boxes were checked every third day before laying and every day throughout the laying period to enable precise calculation of each female's fertile period. The availability of fertilizable females was determined by counting the number of females who were within 6 days of laying their first eggs until the day when their penultimate eggs were laid at nests within 100 m of the nests at which males were feeding young.

Individual nestlings in each brood were weighed every third or fourth day after hatching. The average growth rate of the nestlings in each nest was calculated by taking the average difference in the mass of nestlings between day 3 and day 9 and dividing by 6 days. These days straddle the inflection point of growth in each species (Beasley unpub. data). Fledging success was determined by the number of young in the nest at 16 days of age for tree swallows and 18 days of age for violet-green swallows (the last days on which the nests of each species could be visited without causing premature fledging) minus the number found dead in the box after fledging had occurred.

### **Manipulation of Paternity Assurance**

The paternity assurance of males in 9 marked pairs of violet-green swallows and 10 marked pairs of tree swallows was reduced by temporarily holding them in captivity for 2 to 4 h during their mate's fertile period. Control males (N=9 for violet-green swallows; N=10 for tree swallows) were captured, and immediately



released during their mate's fertile period. Details of the male removal experiments can be found in Chapter 3. Following the removal period, I released males and observed them for 1 h after they returned to their nest sites. During that release period I watched for signs of paternity defense in the form of pair copulations that could dilute or displace any sperm that the female may have received during her mate's absence.

### **Observations of Male Parental Care**

After eggs had hatched, I observed parents at nests to determine whether the male's nest attendance and/or share of feeding visits to nestlings and nest attendance were lowered as a result of them having been temporarily removed during their mates' fertile periods. I compared male's behaviour at nests that had been used for removals to nests that had not been used and for which the brood sizes and hatching dates were similar. I conducted 30 min observation sessions at each nest every 2 to 3 days from day 1 to day 21 post-hatching for violet-green swallows and day 1 to day 17 post-hatching for tree swallows. Observation sessions were spread throughout the day (0700 - 1800) to control for the effect of time of day on feeding visits and nest attendance. For each nest, I pooled data from all the observation sessions to calculate the mean proportion of time that the male was present in the vicinity of the nest and the mean proportion of feeding visits by both sexes that were made by the male.

I combined data collected over two years for each species after determining that there were no detectable differences between years.

### **Statistical Analyses**

Given that I tested the hypotheses that the removal of the male would lower paternity assurance and thereby lower male parental care I used one-tailed Mann-Whitney *U* tests (Siegel 1956) to compare (1) the level of care provided

by males that had been removed to those that had not, (2) the difference in care provided by removal and control males between those whose mates had received extra pair copulations during their removal and those whose mates had not, and (3) the differences in care provided by removal and control males between those who successfully achieved pair copulations after their release and those who did not. I also tested for a difference in the nestling growth rate, maximum nestling mass and fledging success between removal and control groups. Statistics were computed with the SYSTAT statistical package (SYSTAT, Inc. 1986) and manual (Wilkinson, 1986). Statistical significance for each test was accepted at 0.05. Unless otherwise stated, non-significant results must be considered inconclusive because small samples do not produce sufficient power ( $1-\beta < 0.8$ ) to detect differences (Cohen 1977). Numbers reported in the text are means  $\pm$  standard errors unless otherwise stated.

## **Results**

I am convinced that the removal served to reduce the paternity assurance of males for several reasons. First, the removal of males increased the rate of extra-pair copulation attempts on female mates in both species. Two of the 9 unguarded female violet-green swallows accepted extra-pair copulations and I strongly suspected that male intruders successfully completed extra-pair copulations inside the nest box with 2 of the 10 unguarded female tree swallows. No extra-pair copulations were observed during control watches. Second, released males chased male intruders away from their nests and/or mates in 8 of the 9 trials on violet-green swallows and in 3 of the 10 trials on tree swallows. Thus, males were aware of the increased rate of male intrusions during their absence. Third, there was a tendency for males of both species to

attempt copulations with their mates at higher rates after they were released than during control periods.

The parental care provided by males who had been removed was not significantly lower than the parental care provided by control males for either species (Table 6.1). Likewise, the difference in the level of parental care provided by removal and control males whose mates had received extra-pair copulations was no greater than the difference between removal and control males whose mates had not received extra-pair copulations in either species (Figure 6.1).

The difference in the proportion of feeding visits made by removal and control males was positive for male violet-green swallows that had copulated with their mates after they were released and negative for those who had not (Figure 6.2). This trend could indicate that pair copulations increased paternity assurance and consequently increased male parental care. Or, it could merely indicate that both the incidence of copulations and higher feeding rates were correlated to male vigor. In either case, a larger sample size is needed to verify the trend. There was no similar trend for tree swallows.

It was not possible to detect any effect of male removal on the growth rates, the maximum mass attained or the fledging success of nestlings (Table 6.2).

## **Discussion**

My results were consistent with those from most other studies of monogamous species that showed no effect of paternity assurance on male parental care (Gavin and Bollinger 1985; Frederick 1987; Westneat 1988; Wittingham et al. 1993; but see Møller 1988). Counter to my prediction, even the males of the mate-guarding species were not sensitive to the loss of time spent with their mates during the fertile period. Thus, there was no evidence to

Table 6.1. The number of feeding visits made by male violet-green swallows and tree swallows as a percentage of the total number of feeds made by both sexes, the amount of time that each male was present in the vicinity of his nest as a percentage of the total observation time (h), and the rate of feeds (per h) made by both parents together. Males that had been removed during their mates' fertile periods are compared to control males that were watched at their nests between hatching and fledging. Mean values,  $\pm$  SE, and sample sizes are shown.

	Variable	Removed Males	Control Males	P	Power
Violet-green swallows	proportion of feeds by males	0.29 $\pm 0.05$ N=9	0.29 $\pm 0.04$ N=9	.483	.00
	proportion of time male at nest	0.15 $\pm 0.03$ N=9	0.19 $\pm 0.04$ N=9	.254	.59
	total observation time	7.18 $\pm 0.67$ N=9	6.72 $\pm 1.27$ N=9	.314	.14
	total # feeds by both parents per h	13.50 $\pm 1.28$ N=9	15.60 $\pm 2.00$ N=9	.395	.74
Tree swallows	proportion of feeds by males	0.37 $\pm 0.04$ N=10	0.37 $\pm 0.03$ N=10	.330	.00
	proportion of time male at nest	0.13 $\pm 0.03$ N=10	0.13 $\pm 0.03$ N=10	.440	.00
	total observation time	5.72 $\pm 0.51$ N=10	6.41 $\pm 0.48$ N=10	.130	.71
	total # feeds by both parents per h	17.70 $\pm 1.10$ N=10	14.64 $\pm 0.82$ N=10	.071	.00

Figure 6.1. Mean difference in the level of male parental care (the proportion of total feeds made by the male and proportion of time that the male was present at the nest) by control and removal males whose mates had received extra-pair copulations (epc) during removals (N=3 for violet-green swallows; N=4 for tree swallows) and those whose mates had not (no epc) (N=6 for violet-green swallows; N=5 for tree swallows). Bars indicate standard errors. <sup>a</sup>P=.303; <sup>b</sup>P=.398; <sup>c</sup>P=.403; <sup>d</sup>P=.231

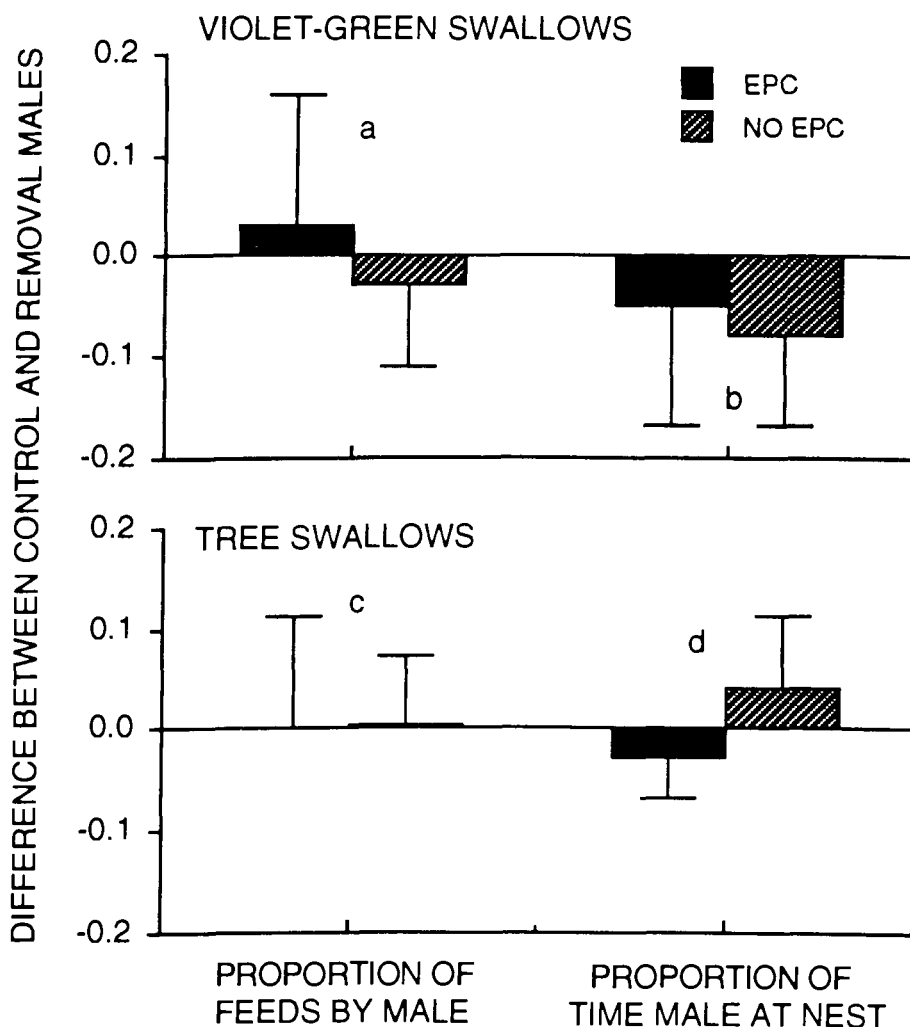


Figure 6.2. Mean difference in the level of male parental care (the proportion of total feeds made by the male and proportion of time that the male was present at the nest) by control males and removal males who copulated with their mates after they were released (pair copulation) (N=4 for violet-green swallows; N=4 for tree swallows) and those who did not (no pair copulation) (N=5 for violet-green swallows; N=5 for tree swallows). Bars indicate standard errors. <sup>a</sup>P=.071; <sup>b</sup>P=.312; <sup>c</sup>P=.312; <sup>d</sup>P=.451.

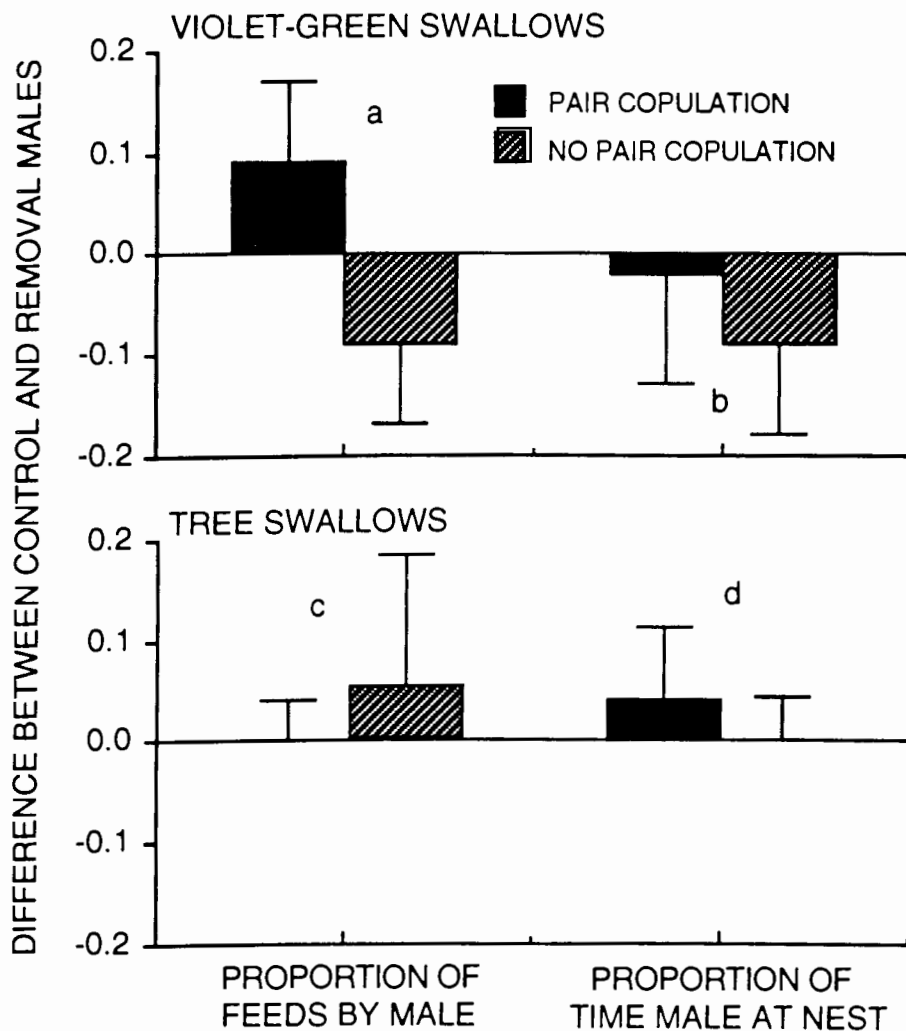


Table 6.2. Growth rates (g per nestling per day from day 3 to 9 inclusive post-hatch), maximum mass of nestlings (g per nestling per brood), and proportion of the brood that fledged. Broods of males that had been removed were compared to broods of control males. Mean values,  $\pm$ SE, and sample sizes are shown.

	Variable	Removed Males	Control Males	P	Power
Violet-green swallows	growth per day	2.00 $\pm$ 0.10 N=9	1.85 $\pm$ 0.08 N=9	.117	.00
	maximum mass	20.00 $\pm$ 0.61 N=9	20.54 $\pm$ 0.36 N=9	.213	.00
	proportion fledged	0.90 $\pm$ 0.07 N=9	0.90 $\pm$ 0.05 N=9	.390	.00
	brood size	4.22 $\pm$ 0.22 N=9	3.78 $\pm$ 0.32 N=9	.158	.00
Tree swallows	growth per day	2.54 $\pm$ 0.15 N=10	2.73 $\pm$ 0.10 N=10	.096	.77
	maximum mass	24.53 $\pm$ 0.45 N=10	24.34 $\pm$ 0.41 N=10	.435	.00
	proportion fledged	1.00 $\pm$ 0.00 N=10	1.00 $\pm$ 0.00 N=10	1.00	.00
	brood size	4.10 $\pm$ 0.48 N=10	4.50 $\pm$ 0.27 N=10	0.29	.55

support the idea that the form of paternity defense could alter the effect of paternity assurance on male parental care.

The lack of influence of paternity and paternity assurance on male parental care has been explained by assessing the costs and benefits of providing care. Males should care for offspring when the benefits of doing so outweigh the costs (Xia 1992; Whittingham et al. 1992; Westneat and Sherman 1993). If the main benefit is the enhanced survival and recruitment of related offspring then the benefits will not only increase with the degree of relatedness between the male and the brood; they will also increase as the ability of females to raise offspring with reduced levels of assistance from the male declines (Whittingham et al. 1992). As there was no difference in the parental care provided by removal and control males, it was reasonable to find no difference in offspring growth rates, maximum mass or fledging success between the two groups. It was not necessary for females to compensate for reduced male care, thus, it is not possible to comment on their ability to do so. Further studies that manipulate the relative parental contributions made by males and females (via the handicapping methods used by Wright and Cuthill 1989, for example) will be necessary to determine how well females compensate for any reduction in care provided by their mates and, therefore, to determine the benefit of maintaining male parental care.

If the main costs of providing care include (1) a restriction on the time and energy available to seek out opportunities for extra-pair matings, and (2) a reduced probability of survival and reproduction in the next season, then factors, such as the availability of fertile females during the nestling period and the risk of predation for care-giving males would help determine the costs of male parental care. Second matings were potentially available to 4 of the 18 violet-



green swallow males and 18 of the 20 tree swallow males after their first broods had hatched. Thus, potential costs in the form of missed additional matings did exist for both species, although less often for violet-green swallows. It was not possible to obtain information on the risk of predation for care-giving males.

I observed second matings by males who were providing care to their first broods in each species. A bigamous male violet-green swallow reduced his feeding rate at his original nest while he spent time guarding his second mate at a neighbouring nest. Once the second clutch was laid, he returned to help feed the young at his original nest. In contrast, a male tree swallow was able to continue feeding young at his first nest while he occasionally copulated with his second mate at a neighbouring nest. Neither male helped feed young from the second nest. These observations demonstrate an important factor that needs to be considered when analyzing the costs of male parental care. The pursuit of additional matings does not necessarily require a large reduction in male parental care. The reduction depends on the type of behaviour required to ensure paternity of the second brood. If mate guarding is required then the pursuit of additional matings could result in a substantial reduction in the time and energy available for parental care. If, on the other hand, visits long enough to complete extra-pair copulations are sufficient, then additional matings would cause little or no reduction in the level of male parental care. Thus, although there is no evidence that the form of paternity defense alters the effect of paternity assurance on male parental care, further research should consider whether the costs of providing male parental care vary among species that use different forms of paternity defense.

## References

- Beecher, M.D. 1988. Kin recognition in birds. *Behav. Genet.* 18: 465-482.
- Burke, T., Davies, N.B., Bruford, M.W. and Hatchwell, B.J. 1989. Parental care and mating behaviour of polyandrous dunnocks *Prunella modularis* related to paternity by DNA fingerprinting. *Nature* 338: 249-251.
- Craig, J.L. and Jamieson, I.G. 1985. The relationship between presumed gamete contribution and parental investment in a communally breeding bird. *Behav. Ecol. Sociobiol.* 17: 207-211.
- Cohen, J. 1977. *Statistical Power Analysis for the Behavioral Sciences*. New York: Academic Press.
- Cohen, R.R. 1984. Criteria for distinguishing breeding male Tree Swallows from brightly colored females prior to capture. *N. Am. Bird Bander* 9: 2-3.
- Davies, N.B., Hatchwell, B.J., Robson, T. and Burke, T. 1992. Paternity and parental effort in dunnocks *Prunella modularis*: how good are male chick-feeding rules? *Anim. Behav.* 43: 729-745.
- Frederick, P. 1987. Responses of male white ibises to their mate's extra-pair copulations. *Behav. Ecol. Sociobiol.* 21: 223-228.
- Gavin, T.A. and Bollinger, E.K. 1985. Multiple paternity in a territorial passerine: the Bobolink. *Auk* 102: 550-555.
- Møller, A.P. 1988. Paternity and paternal care in the swallow, *Hirundo rustica*. *Anim. Behav.* 36: 996-1005.
- Siegel, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. Tokyo: McGraw-Hill Kogakusha.
- Systat, Inc., 1986. *SYSTAT*. Illinois, U.S.A.

- Venier, L.A. and Robertson, R.J. 1991. Copulation behaviour of the tree swallow, *Tachycineta bicolor*: paternity assurance in the presence of sperm competition. *Anim. Behav.* 42: 939-948.
- Wagner, R.H. 1992. Confidence of paternity and parental effort in Razorbills. *Auk* 109: 556-562.
- Westneat, D.F. 1988. Male parental care and extra-pair copulations in the Indigo Bunting. *Auk* 105: 149-160.
- Westneat, D.F. and Sherman, P.W. 1993. Parentage and the evolution of parental behavior. *Behavioral Ecology* 4: 66-77.
- Wilkinson, Leland. 1986. *SYSTAT: The System for Statistics*. Evanston, Illinois: SYSTAT, Inc.
- Whittingham, L.A., Dunn, P.O., and Robertson, R.J. 1993. Confidence of paternity and male parental care: an experimental study in tree swallows. *Anim. Behav.* 46: 139-147.
- Whittingham, L.A., Taylor, P.D., and Robertson, R.J. 1992. Confidence of paternity and male parental care. *Am Nat.* 139: 1115-1125.
- Wright, J. and Cuthill, I. 1989. Manipulation of sex differences in parental care. *Behav. Ecol. Sociobiol.* 25: 171-181.
- Xia, X. 1992. Uncertainty of paternity can select against paternal care. *Am. Nat.* 139: 1126-1129.

## Chapter 7

### General Discussion

I have shown that male violet-green swallows ensure their paternity by guarding their mates unlike their close relative, the tree swallow, which uses frequent pair copulations (Chapter 2). The difference in paternity defense is correlated to different levels of nest guarding by violet-green and tree swallows. This result fits the findings of a broader comparison of species that either guard mates or use frequent pair copulations (Birkhead et al. 1989; Møller and Birkhead 1991). Species in the latter category appear to be prevented from guarding mates by other demands on their time, e.g., in some species, one member of the pair must remain at the nest site to prevent the nest being taken over by other birds. Males of these species attempt to minimize the risks of extra-pair copulations by using frequent pair copulations as an alternative paternity guard. By finding differences in the paternity defense strategies of closely related congeners I was able to rule out phylogenetic constraints and consider the time allocated to guarding mates versus nests as adaptive responses to environmental conditions. By identifying these conditions, my thesis attempts to contribute to our understanding of how alternative paternity defense strategies evolved.

To identify the environmental conditions that influence the decision to guard mates versus nests I performed the same manipulations on each species. The advantage of this approach was that it enabled me to measure responses consistently so that I could make comparisons between the two species. I caution that my results are valid only for the populations of violet-green and tree swallows that I studied in west Creston. My conclusions should be tested by conducting controlled comparisons between populations in different locations.

By temporarily removing males (Chapter 3) I was able to show that male violet-green swallows experienced a relatively low risk of nest loss (due to a low level of nest competition) compared to a high risk of paternity loss (due to a male-biased sex ratio and female acceptance of some extra-pair copulations). Clearly, the advantages of guarding mates exceeded the advantages of guarding nests for male violet-green swallows. In contrast, detained male tree swallows experienced both a high risk of nest loss (due to a high level of nest competition) and a high risk of paternity loss (due to neighbouring male intruders) and released male tree swallows were able to regain usurped nests and potentially reduce the risk of paternity loss by using frequent pair copulations. The equivalent risks of nest loss and paternity loss made it difficult to assess why male tree swallows guarded nests rather than mates. If I had measured actual losses rather than inferred losses, i.e., if a detained male had actually lost a measureable amount of reproductive success due to extra-pair fertilizations and/or nest loss, then it would have been possible to determine the relative value of these resources. Further research is needed to acquire this type of information and to assess additional costs, such as energetic constraints and the risk of predation which are associated with guarding nests versus mates.

Temporary female removals verified that (1) males outnumbered females in the population of violet-green swallows but not tree swallows (2) the supply of nest sites exceeded demand for violet-green swallows, but not tree swallows, and (3) frequent pair copulations were not used as an alternative paternity defense even after extended periods of mate separation by violet-green swallows whereas the opposite was true for tree swallows. Finding correlations between these environmental conditions and the tendency to guard mates or nests does not imply cause and effect. However, the identification of potential

causes is the first step toward determining which factors played a role in the evolution of different paternity defense strategies.

The correlation between mate guarding and a male-biased operational sex ratio in violet-green swallows corroborates the results of numerous studies on the allocation of time between guarding mates and seeking extra-pair matings (e.g., Møller 1987). But very few studies have examined the relative importance of competition for nest sites in determining the optimal allocation of time to mate guarding versus nest guarding. Meek and Robertson (1994) found a lower level of mate guarding at nests that experienced a higher average rate of intrusions by interspecific nest competitors. My study is the first to experimentally increase the risk of nest loss to test whether males would switch from guarding mates to guarding nests (Chapter 5). By increasing the relative risk of nest loss for violet-green swallows I was able to show a substantial increase in nest guarding and a slight decrease in mate guarding. The next step would be to manipulate the risk of paternity loss in addition to the risk of nest loss to determine their relative importance. This will require finding a method for altering the operational sex ratio in a wild population of violet-green swallows or the use of an alternative study system. Another approach would be to reduce the risk of nest loss or increase the risk of paternity loss for tree swallows and determine whether males increase the time that they spend guarding mates. By demonstrating flexibility in the tradeoff between guarding nests versus mates, my study paves the way for testing the influence of various factors on the use of different paternity defense options.

Most studies of mate guarding have demonstrated that the close association between mates during the fertile period is maintained by the male rather than the female (Chapter 2) (Birkhead and Møller 1992). But female violet-green swallows maintained contact with their mates while the latter were preoccupied

with nest guarding in response to the model intruder (Chapter 5). Further research is required to determine what female violet-green swallows gain from being guarded (see Ashcroft 1976; Lumpkin 1981, 1983; Lambrecht 1989) and to assess how these gains influence the tradeoff between guarding mates versus nests. For tree swallows, I found variation in the female's willingness to receive frequent pair copulations at different times of the day (Chapter 2). Time of day is important in determining the success of fertilization (Birkhead et al. 1989). In addition, the female's willingness to receive extra-pair copulations determines her mate's risk of paternity loss. These results point out that there is much to learn about the costs and benefits of different paternity defense options from the female's perspective as well as the male's. Work that has been initiated in this area dispels the myth that females play a "passive" role in mating strategies (Lifjeld and Robertson 1992; Petrie et al. 1992) but throughout my thesis I have raised further questions that need to be explored.

Some studies have found that males use time invested in paternity defense as an indicator of their paternity and hence as a way to gauge the amount of parental care that they should invest in offspring (Burke et al. 1989). My study provided a test of the idea that the form of paternity defense alters the male's tendency to reduce male parental care in response to lowered confidence of paternity. I found no evidence that it does so. Male violet-green swallows that were prevented from guarding mates during removals were as active in caring for young as control males. The same was true for tree swallows. These results support the idea that the parental contribution made by males may be essential for the successful rearing of offspring (Whittingham et al. 1992). The benefit of enhanced survival of offspring that receive care from their fathers exceeds the cost of missed mating opportunities (Whittingham et al. 1993). Incidental observations of bigamous relationships revealed that the type of paternity

defense strategy used for a male's second brood may or may not detract from the time and energy he can devote to help raise his first brood. If not, then there may be no tradeoff between seeking extra-pair copulations and providing male parental care.

The distinction between guarding mates and the use of frequent pair copulations suggests that they are alternative paternity guards but it is not obvious why the presence of one is associated with the absence of the other. I found it curious that male violet-green swallows did not resort to frequent pair copulations after periods when mate guarding had been suspended by temporary removals. Perhaps it is too costly to have both options in a behavioural repertoire but I have no idea why. Males of species that use frequent pair copulations have larger testes than males of species that do not (Birkhead and Moller 1992). Perhaps it would be too costly for a mate guarding male to carry testes large enough to deliver frequent inseminations. The suggestion that frequent pair copulations compensate for lack of mate guarding raises the question of its relative effectiveness. Birkhead and Møller (1992) showed that extra-pair copulations were more common in species that adopted the frequent pair copulation strategy, thus, it would be interesting to see whether the variance in the incidence of extra-pair paternity is greater for birds using frequent pair copulations compared to birds that guard mates.

By emphasizing the importance of costs and benefits in determining an organism's behaviour, this thesis has identified several factors that may explain the evolution of different paternity defense strategies in congeneric swallows. Flexibility in the time allocated to guarding mates versus nests was found in response to an elevated risk of nest loss. I conclude by encouraging further manipulations to determine the effects of the operational sex ratio and costs and benefits from the female's perspective on the tradeoff between guarding mates



and nests, not only in swallows, but in a variety of species that use alternative paternity defense strategies.

## References

- Ashcroft, R. 1976. A function of the pair bond in the common eider. *Wildfowl* 27: 101-105.
- Birkhead, T.R., Hunter, F.M. and Pellat, J.E. 1989. Sperm competition in the zebra finch, *Taeniopygia guttata*. *Anim. Behav.* 38: 935-950.
- Birkhead, T.R. and Møller, A.P. 1992. *Sperm Competition in Birds*. London: Academic Press.
- Burke, T., Davies, N.B., Bruford, M.W. and Hatchwell, B.J. 1989. Parental care and mating behaviour of polyandrous dunnocks *Prunella modularis* related to paternity by DNA fingerprinting. *Nature* 338: 249-251.
- Lambrecht, J. 1989. Mate guarding in geese: awaiting female receptivity, protection of paternity or support of female feeding? In: *The Sociobiology of Sexual and Reproductive Strategies*. (Ed. by Rasa, A.E., Vogel, C., and Volland, E.), pp. 48-60. London: Chapman and Hall.
- Lifjeld, J.T. and Robertson, R.J. 1992. Female control of extra-pair fertilization in tree swallows. *Behav. Ecol. Sociobiol.* 31: 89-96.
- Lumpkin, S. 1981. Avoidance of cuckoldry in birds: the role of the female. *Anim. Behav.* 29: 303-304.
- Lumpkin, S. 1983. Female manipulation of male avoidance of cuckoldry behaviour in the ring dove. In: *Social Behaviour of Female Vertebrates*. (Ed. by S.K. Wasser), pp. 91-112. New York: Academic Press, Inc.
- Meek, S.B. and Robertson, R.J. 1994. Interspecific competition for nest boxes affects mate guarding in eastern bluebirds, *Sialia sialis*. *Anim. Behav.* 47: 295-302.
- Møller, A.P. 1987. Extent and duration of mate guarding in swallows *Hirundo rustica*. *Ornis. Scand.* 18: 95-100.

- Møller, A.P. and Birkhead, T.R. 1991. Frequent copulations and mate guarding as alternative paternity guards in birds - a comparative study. *Behaviour* 118: 170-186.
- Petrie, M., Hall, M., Halliday, T.R., Budgey, H.V. and Pierpoint, C. 1992. Multiple mating in a lekking bird: why do peahens mate with more than one male and the same male more than once? *Behav. Ecol. and Sociobiol.* 31: 349-358.
- Whittingham, L.A., Dunn, P.O., and Robertson, R.J. 1993. Confidence of paternity and male parental care: an experimental study in tree swallows. *Anim. Behav.* 46: 139-147.
- Whittingham, L.A., Taylor, P.D., and Robertson, R.J. 1992. Confidence of paternity and male parental care. *Am Nat.* 139: 1115-1125.

**Appendix**  
**Time table for experiments conducted on pairs of violet-green swallows and tree swallows**

The following tables show the number of different pairs of each species observed in each year of the study. Observations of non-experimental pairs were compared to observations of experimental pairs. A subset of the pairs included in the analyses of male removal experiments were used in the analyses of male parental care for both species. Data were combined from observations taken over two years after determining that there were no differences between years.

**Violet-green swallows**

Focus of Study	Year	No. of Experimental Pairs	No. of Non-Experimental Pairs
Documenting paternity defense tactics	1988		15
Male removals	1988 1989	4 4	7 1
Male parental care	1988 1989	3 6	3 6
Female removals	1990	7	
Male model experiments	1989 1990	18 7	
Female model experiments	1989 1990	1 12	

**Tree swallows**

Focus of Study	Year	No. of Experimental Pairs	No. of Non-Experimental Pairs
Documenting paternity defense tactics	1990		14
Male removals	1989 1990	5 3	13 6
Male parental care	1989 1990	8 2	8 2
Female removals	1990	8	