INFLUENCE OF OLD NEST MATERIAL ON THE NUMBERS OF ECTOPARASITES IN NESTBOXES AND THE BREEDING ECOLOGY OF TREE SWALLOWS

by

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B.Sc. Biology (Honours), Queen's University, 1988

Thesis submitted in partial fulfilment of the requirements
for the degree of Master of Science
in the department
of
Biological Sciences

SIMON FRASER UNIVERSITY

December 1992

APPROVAL

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Degree: **Master of Science**

Title of Thesis:

INFLUENCE OF OLD NEST MATERIAL ON THE NUMBERS OF ECTOPARASITES IN NESTBOXES AND THE BREEDING ECOLOGY OF TREE SWALLOWS

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Date Approved 6 December 1992

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SWALLOWS

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ABSTRACT

Critics have hypothesized that by removing old nests from nestboxes, researchers may be eliminating a significant and natural factor that affects the ecology of hole-nesting birds, which is the haematophagous ectoparasites that live and survive in the old nest material. The hypothesis is that the ectoparasites are more numerous in nestboxes containing old material, than in those which have been cleaned. Thus, nest re-use may reduce reproductive success for hole-nesting birds. I tested the hypothesis by examining how the presence or absence of old material affects the number of ectoparasites in a nestbox, and how this affects nestbox selection, nest building, and reproductive success in Tree Swallows (*Tachycineta bicolor*).

Fleas (Ceratophyllidae) were significantly more numerous in nestboxes with old material, and there was a positive correlation between the volume of old material and the numbers of fleas, but blow flies (*Protocalliphora sialia*) were equally numerous in all nestboxes. Fowl mites (Dermanyssidae) were numerous in nestboxes with old material in 1991, but were rare in 1992. These results show that the numbers of ectoparasites are not necessarily greater in old nest material, but that other factors are important in determining their numbers.

When a choice of nestboxes was available, Tree Swallows preferred them empty and clean, or those where the old material had been microwaved. However, clean nestboxes and those with microwaved material also had more space inside, so these observations support two hypotheses: Tree Swallows avoid potentially high ectoparasite numbers in nests with old material, or they prefer large cavities.

Empty nestboxes affected nest building. The mass and volume of nests built in clean nestboxes were greater than for nests built on old material.

Reproductive success was expected to be lower for pairs using nestboxes with old material, than for those using clean nestboxes; but nesting phenology, reproductive success, nestling size, and adult feeding effort did not differ between pairs using either type. This study shows that a researcher's usual habit of removing old nests from nestboxes can indeed affect the numbers of some types of ectoparasites in nestboxes, but re-use of nests by hole-nesting birds does not necessarily lower their reproductive success.

for

Alanna and Geoffrey Vacca

for their generous hospitality and assistance

ACKNOWLEDGEMENTS

A special thanks goes to my senior supervisor, Dr. Nicolaas Verbeek, for his guidance and assistance with all aspects of this project. My other committee members, Dr. Ron Ydenberg and Dr. Peter Belton, had many helpful ideas and criticisms for the thesis. Thanks also go to the external examiner, Dr. H.R. MacCarthy, for taking the time to thoroughly review and comment on the thesis.

At the Creston Valley Wildlife Management Area, Brian Stushnoff, Steve Wilson, and Don Grayson allowed me to use the marsh and dykes for my study site, and they provided considerable logistic support. The Department of Agriculture in Creston provided the weather data. Pete Hurd, Yolanda Morbey, and Steve Wilson helped in the field, Barb Beasley, Karen Price, and Joanne Siderius allowed me to use some of their equipment, and Barb Beasley and Dr. David Wiggins took the time to send me some data and maps to help me get started at Creston. At S.F.U., the Borden Lab allowed me to use their microwave, the Dill Lab allowed me to use their computer, and Dr. Darren Gillis and Don Hugie provided computer and statistical assistance.

Many thanks go to Dr. Curtis Sabrosky who identified the blow flies. Dr. L. Scott Johnson, Dr. Daniel Roby, and Dr. David Winkler kindly sent unpublished manuscripts to me.

This research was funded by a Natural Sciences and Engineering Research Council (N.S.E.R.C.) of Canada operating grant to Dr. Nicolaas Verbeek, and an N.S.E.R.C. Graduate Scholarship, two S.F.U. Graduate Research Fellowships, an S.F.U. Special Graduate Research Fellowship, S.F.U. Special Graduate Entrance Scholarship, and a John K. Cooper Award to me.

It has been my good fortune to cross paths with many fine friends, both old and new, at Creston and S.F.U. In particular, Yolanda, Steve, Pete, Darren,

Stefanie Zaklan, Barb, Don, Pat Abbot, Sandra Alfoldy, Dr. Brent Charland, Allen and Cindy Gray, Dave Green, Hélène Harvey, Rob Houtman, Dr. Guy Martel, Wendy Proudfoot, Ann Rahme, Cathy and Rod Rogers, Sari Saunders, and Dr. Linda Verbeek were primarily responsible for so many enjoyable memories. I can't thank you all enough, and I'll not forget you.

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CHAPTER 1

GENERAL INTRODUCTION

Secondary cavity-nesting birds, or hole-nesters, are incapable of excavating their own tree cavity, and so they readily accept nestboxes as nesting sites. When breeding in nestboxes, these species are useful study subjects in ecology. Nestboxes are accessible and manipulable, and these bird species are conspicuous, easy to capture, manipulable, and they tolerate the activities of researchers. As a result, many important and often long-term studies have been conducted using populations of hole-nesting species breeding in nestboxes to address a wide range of topics (e.g., lifetime reproductive success, van Balen *et al.* 1987; costs of reproduction, Nur 1984a, b, 1988; survival, van Balen *et al.* 1987, Clobert *et al.* 1988; population dynamics, Tinbergen *et al.* 1987; dispersal, van Balen 1979; heritable characteristics, van Noordwijk *et al.* 1988, Wiggins 1990; mate choice, Lifjeld and Slagsvold 1988; mating strategies, Alatalo and Lundberg 1984, Leffelaar and Robertson 1986).

Some researchers, however, have recommended that the results from nestbox studies be interpreted with caution (van Balen *et al.* 1982, Korpimäki 1984, Nilsson 1984, Møller 1989, 1992, Robertson and Rendell 1990), because, although they are useful for research purposes, several characteristics of nestbox populations are unnatural. Nestboxes are typically built to uniform specifications, producing cavities that may be larger than the average tree cavity (e.g., Robertson and Rendell 1990), and resulting in larger clutches (e.g., Karlsson and Nilsson 1977, Rendell and Robertson 1993) and possibly higher reproductive success for birds breeding in nestboxes. The uniform dimensions of nestboxes can also affect the intensity of interspecific competition for nest-sites by preventing some competitors from gaining access to cavities because the dimensions of the cavity entrance are too small (e.g., van Balen *et al.* 1982, Robertson and Rendell 1990). Interspecific competition can affect reproductive success by reducing the number of cavities available to other hole-nesters (e.g., Rendell and Robertson 1989, Robertson and Rendell 1990) and because some species usurp cavities from others (e.g., Rendell and Robertson 1991). The threat of predation by mammals is typically eliminated during nestbox studies (Møller 1989, 1992, Rendell and Robertson 1990), resulting in higher reproductive success for birds using nestboxes than for those using tree cavities. The densities of breeding birds in nestbox populations may be unnaturally high, which can affect behaviour (e.g., number of extra-pair copulations, Gowaty and Bridges 1991, Venier and Robertson 1991) and reproductive success (e.g., frequency of predation, Dunn 1977; paternity, Gowaty and Bridges 1991). The favourable characteristics of nestboxes and nestbox habitats have been cited as the reason for biases in cavity use. In their comparison of the ecology of Tree Swallows (*Tachycineta bicolor*) breeding in nestboxes and tree cavities, Robertson and Rendell (1990) found that the age distribution of females nesting in nestboxes was different from that for birds nesting in tree cavities; significantly more females three years old or older, in contrast to those two years of age, nested in nestboxes than would be expected based on a model of annual adult survival that was used to estimate the proportions of these two age-classes available for breeding in the local population.

Recently, Møller (1989, 1992; see also Lindén and Møller 1989) pointed out another difference between nestboxes and tree cavities. Researchers typically remove old nest material from nestboxes after each breeding season, whereas old material accumulates in tree cavities. Møller hypothesized that this introduces an experimental artefact to nestbox studies that calls the validity of results from such studies into question. He claimed that by removing old material from nestboxes, researchers reduce the numbers of haematophagous ectoparasites there, and he noted that ectoparasites may have a significant effect on nestbox selection, reproductive success, and nestling growth. He concluded that investigations into the effects of ectoparasites on the ecology of hole-nesting birds were necessary to clarify the results of previous research.

The criticisms issued by Møller (1989, 1992) prompted a rebuttal in defense of nestbox studies which was based on philosophical and practical arguments (Koenig *et al.* 1992). However, to the best of my knowledge, only one empirical study (i.e., Thompson and Neill 1991) has addressed any hypotheses and predictions that arise from the observation that researchers regularly remove of old nests from nestboxes. In this thesis, I attempt to fill this gap in our knowledge of the ecology of hole-nesting birds and their ectoparasites by examining the effects of old material in nestboxes on the numbers of haematophagous ectoparasites found there, and the breeding ecology Tree Swallows.

In Chapter 2, I address the hypothesis that the numbers of ectoparasites are different between nestboxes with old material compared to those where old nests have been cleaned out. Møller (1989, 1992) claimed that hole-nesting birds encounter large ectoparasite populations in cavities with old material, but he had no empirical evidence for this. Many factors contribute to nest infection by ectoparasites and to their numbers in cavities, including the characteristics of the life-cycles for each species of ectoparasite and the conditions of the cavity microclimate, so the presence of old material in a nestbox may or may not influence the numbers of ectoparasites found there.

In Chapter 3, I examine whether or not old nest material affects nestbox selection and nest building behaviour by Tree Swallows, by allowing birds to choose to nest in nestboxes with and without old nest material. Several hypotheses are described that could explain how old material affects nestbox choice. Assuming that ectoparasites are more numerous in cavities with old material, that they lower reproductive success, and that hole-nesting birds can discriminate between nestboxes with and without high numbers of ectoparasites, birds should avoid cavities with old material whenever possible. Alternatively, they may choose cavities with old nest material, but incorporate materials in nests that prevent parasitism, such as green plant material (e.g., Wimberger 1984). Møller (1989, 1992) did not have evidence that old material affects cavity selection by hole-nesting birds, and the only study to date on the subject found that House Wrens (*Troglodytes aedon*) chose nestboxes randomly with respect to the presence or absence of old nests in nestboxes (Thompson and Neill 1991).

In Chapter 4, I contrast the reproductive success, nestling size, and feeding effort of pairs of Tree Swallows using nestboxes with old nest material with those nesting in nestboxes where old nests have been removed. Studies of colonially nesting Hirundines (e.g., Brown and Brown 1986, Møller 1990) and seabirds (e.g., Feare 1976) have shown that nest-site re-use by birds may be costly in terms of reproductive success and nestling health (cf. Møller 1989, 1992), however, many studies of hole-nesting birds have not found a significant effect of ectoparasites on their breeding ecology (e.g., Gold and Dahlsten 1983, Roby *et al.* 1992).

I conclude by discussing Møller's (1989, 1992) criticisms in light of my results and those of others, and make recommendations for future research into the ecology of hole-nesting birds and their ectoparasites.

SPECIES STUDIED

Host.--Tree Swallows (Hirundinidae) return to nesting areas around the middle of March each spring to acquire and defend cavities. Territories constitute a 16-20 m diameter circle about a nest-site (Muldal *et al.* 1985). Some pairs often defend two or more cavities, possibly for the entire breeding season (Rendell and Robertson 1989). Pairs are typically monogamous and single-brooded (Leffelaar and Robertson 1986). Females build the nest using dead grass and they line the cup with feathers. Females build alone, although males also bring feathers to the nest. Nest building begins in mid-April, and egg-laying begins in early- to mid-May. Clutches usually of three to seven eggs are laid, followed by 12-14 days of incubation, and 16-21 days during which the nestlings are fed in the cavity. Both parents feed the young (Leffelaar and Robertson 1986). After fledging, young birds remain with their parents for an indefinite period before they migrate south in September or October.

Several types of haematophagous ectoparasites feed on Tree Swallows, but the three types known from my study area are discussed in detail below.

Blow flies.--The blow fly *Protocalliphora sialia* Shannon and Dobroscky (Diptera: Calliphoridae) is found in Tree Swallow nests across North America (Sabrosky *et al.* 1989). They overwinter in crevices in cavities and behind tree bark, and from my observations, rarely in cavity nest material. Adults disperse in spring and enter nest cavities when the hosts have nestlings. Females lay eggs singly or in batches in nest material, typically within a week after the host nestlings hatch. Blow fly eggs hatch in 24 hours whereupon the larvae immediately begin feeding on the nestlings. Each of the first two instars last one to two days during which the small larvae take one or two blood meals. The third and final instar lasts approximately seven days, during which two or three blood meals per day are taken. The pupal stage lasts two to three weeks. Adults emerge in June and July, and may or may not seek mates and hosts in the same season (Hall 1948, Sabrosky *et al.* 1989).

Fowl mites.--Fowl mites (Parasitiformes: Dermanyssidae; Lindquist 1978) reach nests as adults by transport on a bird vector or hatch there. Adults can overwinter in nest material, but most spend their entire life on adult or nestling hosts. They have a short life cycle of five to seven days, and each female may lay two to five eggs, potentially resulting in a rapid, exponential increase in the number of fowl mites in a nest. Eggs hatch in one or two days depending on temperature and humidity, larvae molt into protonymphs in less than a day, protonymphs feed twice and molt into deutonymphs in one to three days, and non-feeding deutonymphs turn to adults in less than a day. Adults reproduce after two blood meals (Sikes and Chamberlain 1954, Baker *et al.* 1956).

Fleas.--Details of the life-history of bird fleas (Siphonaptera: Ceratophyllidae; Holland 1985) are sparse. Fleas are holometabolous insects with a four-stage life cycle. Eggs are laid a few at a time in nest material or on hosts. Development of eggs is asynchronous, and embryogenesis lasts from two to twelve or more days, depending on temperature and humidity. The larvae are free-living and feed on organic material in the nest structure during three instars, but they do not take blood meals from the host. The pupal stage is spent in a silken cocoon. When they emerge, the adults are perfectly formed and ready to feed. They feed exclusively on blood (Lewis *et al.* 1988).

CHAPTER 2

EFFECT OF OLD NEST MATERIAL ON THE NUMBERS OF HAEMATOPHAGOUS ECTOPARASITES IN NESTBOXES OF TREE SWALLOWS

INTRODUCTION

Nestboxes are practical substitutes for tree cavities. They are used during studies of the ecology of hole-nesting birds because nestboxes are accessible, manipulable, and readily accepted for breeding by many of these species. However, Møller (1989, 1992; see also Lindén and Møller 1989) stated that nestbox studies are unrealistic in an important respect. Researchers usually remove old nests from nestboxes at the end of each breeding season, and Møller proposed that by doing so they may reduce the numbers of ectoparasites in nestboxes which feed on the nestlings and adults of hole-nesting species. Higher ectoparasite loads have been shown to reduce reproductive success and nestling health in some species of colonially nesting passerines (Moss and Camin 1970, Brown and Brown 1986, Shields and Crook 1987, Møller 1990, 1991, Chapman and George 1991), colonial seabirds (Feare 1976, Duffy 1983, 1991), and some hole-nesters (Capreol 1983, Clark and Mason 1988, Fauth *et al.* 1991, Richner *et al.* 1991, Winkler 1992). Because ectoparasites can affect reproductive success, Møller suggested that the results from nestbox studies should be regarded with caution because ectoparasites are likely very important in the evolution of life-history strategies in hole-nesters, and that they have been completely disregarded in most nestbox studies. These are important criticisms because much of our knowledge of the traits of avian life-history has been gathered from long-term studies of hole-nesting birds breeding in nestboxes (e.g., van Balen *et al.* 1987, Tinbergen *et al.* 1987).

The hypothesis that ectoparasites are numerous in the cavities of hole-nesting birds where old material is present is the basis of the critiques discussed above, but to the best of my knowledge this hypothesis has never been tested. Many factors other than the presence of old nest material can affect the numbers of ectoparasites in nests. Other arthropods in nests prey on ectoparasites (e.g., the predatory mite, *Cheletomorpha lepidopterorum*, Burtt *et al.* 1991) or parasitize them (e.g., the parasitoid wasp, *Nasonia vitripennis*, Mason 1944, Jones and Turner 1987, Gold and Dahlsten 1989). The numbers of ectoparasites in cavities may be restricted by density-dependent factors, such as the volume of nest material (Whitworth 1976, Pinkowski 1977, Gold and Dahlsten 1989), the availability of hosts (Brown and Brown 1986, Møller 1987a, Shields and Crook 1987), and the number of intra- and interspecific ectoparasites competing for hosts (Burtt *et al.* 1991, Roby *et al.* 1992). Also, cavities undergo significant changes in the characteristics of their microclimate throughout a year (e.g., temperature, freezing and thawing, humidity, and ammonia concentrations, Mertens 1969, 1977, van Balen and Cavé 1970, van Balen 1984, Erbelding-Denk and Trillmich 1990), which could cause mortality, or affect the development of some types of ectoparasites (e.g., generation time in fleas, Holland 1985).

Another important factor affecting the numbers of ectoparasites in the cavities of hole-nesting birds may be the life-cycle of each species of ectoparasite. The *Life-cycle hypothesis* asserts that the life-cycle of a species of ectoparasite influences how numerous it will be in a cavity. Thus, species that depend on nest material for shelter or sustenance outside of the host breeding season (e.g., fleas, Holland 1985; fowl mites, Sikes and Chamberlain 1954, Baker *et al.* 1956) should be more numerous in cavities with old material than in cavities where old material has been removed. Those species that are not dependent on old material outside of the host breeding season (e.g., blow flies, Sabrosky *et al.* 1989), and that disperse away from the natal cavity, should be equally numerous in cavities with and without old nest material.

I examined the numbers of haematophagous bird fleas, fowl mites, and blow flies collected in nestboxes of Tree Swallows. Some nestboxes contained old nest material, and some did not. I test the hypothesis that the number of individuals of an ectoparasite species is the same in nestboxes with and without old nest material, and I examine how other characteristics of a nestbox, such as the amount of nest material, affect the numbers of ectoparasites found there.

METHODS

Study site.--This research was conducted at the Creston Valley Wildlife Management Area (C.V.W.M.A.), southeastern British Columbia (49°05′N, 116°35′W), during 1991 and 1992 (Fig. 1). C.V.W.M.A. is open, wetland habitat divided into shallow ponds by dikes. All dikes are bounded by water (0.5-1.5 m deep) on at least one side, and by either cattail (*Typha latifolia*) or willow (*Salix* spp.) stands. Tree Swallows have bred in approximately 160 nestboxes at C.V.W.M.A. for several years (cf. Wiggins 1990).

Nestboxes were made of cedar or plywood, mounted approximately 1 m off the ground on wooden posts, and provided with metal predator guards. Nestboxes were distributed along dikes and on exposed ground in an unflooded pond. All nestboxes were within 40 m of water during the study, and when water levels rose along the dikes and in ponds due to spring run-off, some nestboxes temporarily stood in 0.5-1 m of water, but none was submerged.

In 1991, nestboxes were distributed in pairs as part of an experiment on nestbox preference in Tree Swallows (Chapter 3), with each nestbox in a pair 3 m apart, and each pair of nestboxes 40 m apart. I refer to a pair of nestboxes as a territory. Seventy-nine territories were established in the marsh. In 1992, the

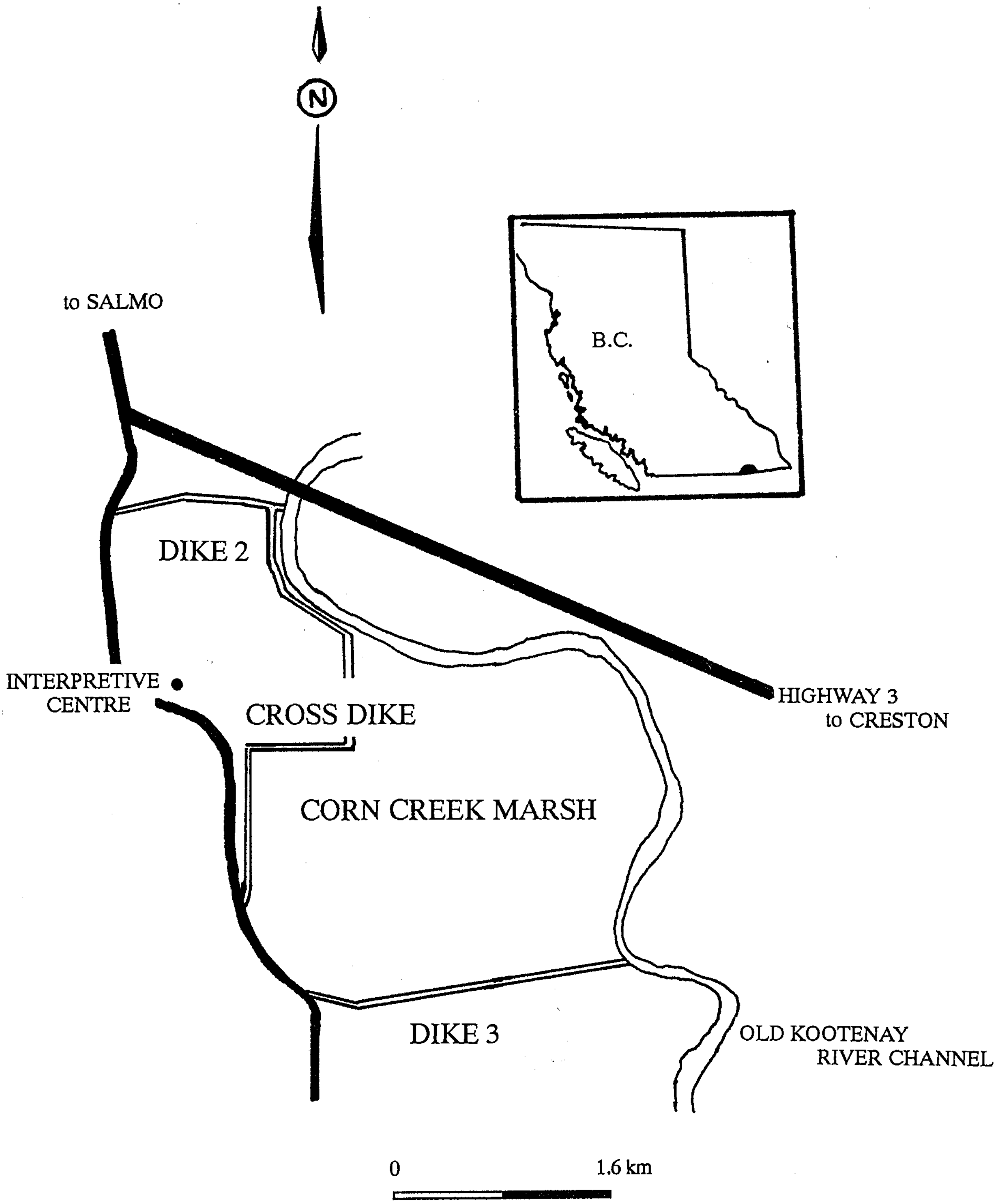

Fig. 1. Map of the study site at the Creston Valley Wildlife Management Area. Nestboxes were arranged along Dikes 2 and 3, the Cross Dike, and in Corn Creek Marsh, in 1991 and 1992.

nestboxes were redistributed. One hundred and twenty-five nestboxes were arranged singly, 30-40 m apart. Tree Swallows occupied all 79 territories in 1991, and 117 of 125 (94%) nestboxes in 1992.

Box-types.--Tree Swallows nested in four box-types during 1991 and 1992: i) clean (C) nestboxes with no old nest material, ii) sham (S, 1991 only) nestboxes which contained old nest material that had been microwaved, iii) clean (CI, 1992 only) nestboxes with inserts that reduced the internal volume of the nestbox, and iv) old (O) nestboxes which contained old nest material. Old nest material was available at C.V.W.M.A. because nestboxes were not cleaned out after the 1990 breeding season.

In 1991, C, S, and O nestboxes were used for experiments. At C nestboxes, old nests were removed and the inside was scraped and swept out with a wire brush and paint peeler to loosen all duff and droppings. Care was taken to clean in the cracks of boxes where possible to kill or flush out hidden parasites. S nestboxes received the same treatment as C nestboxes, except that after cleaning, previously microwaved nests were inserted. To microwave nests I collected 50 old nests from nestboxes at C.V.W.M.A. in February 1991 and took them to Simon Fraser University in separate ZIPLOC® bags. Each nest was sealed in a Look® cooking bag, and microwaved for 5 min at high power in a Toshiba® oven. Nests were then replaced in clean ZIPLOC® bags. To determine the effectiveness of this procedure for killing arthropods, three of the 50 nests, each of which had living arthropods before microwaving, were sifted after microwaving. All of the arthropods in these nests were dead, so I am confident that this procedure killed arthropods in all 50 nests. O nestboxes were not manipulated in any way; the old nest material was left in place and the nestboxes were not cleaned. Nest material used at both S and O box-types showed evidence of occupancy the previous year, such as dead nestlings and droppings. Therefore, any parasites in these nestboxes presumably would have had access to hosts previously, and could have increased in number.

In 1992, C, CI, and O nestboxes were used for experiments. At 15 randomly chosen C nestboxes (CI), I inserted a styrofoam and plywood floor that filled the lower 8 cm of each nestbox. C (including CI nestboxes) and O nestboxes were arranged throughout the marsh as follows: C_1, O_1, O_2, C_2, C_3, O_3,...etc.

Nest switches.--I tried to control for covariation of host phenotype with the box-type used by a female Tree Swallow (Chapter 4). After females settled at a nestbox and built nests I moved old nest material from one nestbox to another. This was done within pairs of nestboxes at randomly chosen territories in 1991, and in 1992, nest switches were made between some O nestboxes and their nearest C neighbour, but CI nestboxes were not disturbed. To give an example from 1992: if a female settled at nestbox C_5, I inserted the O_5 nest material underneath the new C_5 nest material. The C_5 nest was now considered an O nest, and nestbox O_5 now became a C nestbox because I removed the old material from under the new nest, cleaned the nestbox, and put the new material back.

Nest switches were made during nest weighing (Chapter 3), and only when the nests in both box-types involved in a switch were ready to be weighed. Females often built only small nests in S and O nestboxes in 1991 and 1992 (Chapter 3), so nest switches were performed only at those nestboxes where I was sure that nest handling and manipulation would not destroy a new nest structure. In total, nests were switched at 44 of 79 (56%) territories in 1991, and at 14 of 64 (22%) neighbouring C-O pairs in 1992.

Repeated use of nest material.--Because nest material was used and re-used by Tree Swallows from 1990 through to 1992, by 1992 I recognized three types of nestboxes based on the number of times the oldest nest material had been used. The material brought to C and CI boxes was being used for the first time in 1992, the material in some O nestboxes in 1992 had been used only in 1991 and so was being used for the second time, and the material in some O nestboxes had been used consecutively since 1990, and so was being used for the third time. The ability to distinguish these three box-types based on the ages of new and old nest material, and not simply on whether a box was clean or had old material, allowed me to examine how the numbers of the three types of ectoparasites changed with nest re-use.

Estimating the numbers of ectoparasites.--"Hand counts" of adult fowl mites were performed at a nest within 24 hours after the last nestling fledged. I placed my hand in the nest for 10 sec and then estimated the number of mites on my hand and arm, in 10's, 100's & 1000's (Møller 1990). Fowl mites were not found in the Berlese funnel collections (see below), and so the only estimate of their numbers was from "hand counts".

I collected 30 nests in 1991 ($N_C = 11, N_S = 10, N_O = 9$) and 103 nests in 1992 ($N_C = 36, N_{CI} = 13, N_O = 54$) after the mite "hand count", and I stored each in a sealed and marked ZIPLOC® bag. In both years, I sifted through each nest by hand to count the number of adult fleas and blow fly adults, puparia, and third instar larvae. Each nest was placed on a white sheet, and the grass, feathers, and nest duff were separated. All adult fleas, whether they were alive or dead and independent of the age of the material they were collected from in a nest structure, were totalled for each nest. When estimating the numbers of blow flies at nests with old material, I had to distinguish between puparia from the study year, and those from a previous year. To do this, I added only whole puparia with an intact pupa to the number of third instar larvae and newly emerged adults collected in a nest. In both years, the adult fleas I counted were placed in 75% alcohol, while the adult blow flies and puparia were placed in dry containers. For 1991 nests, eleven nests were sifted within one month of collection, while the remaining 19 were frozen briefly and stored until they were sifted in January 1992. All of the 1992 nests were sifted within two months of collection.

Before sifting, each nest in 1992 was dried in modified Berlese funnels (Murphy 1962, Southwood 1966) to flush out live ectoparasites. Each nest was put in a separate plastic funnel that had the stem wrapped in cotton and inserted into a vial of 75% alcohol. Lamps with 60-100 watt bulbs were centered about 10 cm above each nest. The nests were dried out during 24-72 hours. When nest material was too bulky to dry all at once, it was halved and dried, one half after the other, using the same funnel and vial. Once a nest was dry, it was returned to its original bag, and its vial was labelled. The total numbers of fleas and blow flies in nests were tallied by adding those collected from the Berlese funnels to those collected from sifting.

Collection of ectoparasites for identification.--For identification purposes, I collected and preserved blow fly adults, larvae, and puparia, adult fowl mites, and adult fleas according to the methods described in Hall (1948), Beirne (1955), and Lewis *et al.* (1988), respectively.

Volume of nest material.--The volumes of types of nest material in nestboxes were calculated according to methods described in Chapter 3.

Host reproductive output.--Regular checks (every 1-3 days) at Tree Swallow nestboxes enabled me to record the reproductive output and nesting phenology of the host.

Statistical analysis.--To minimize any possible effects of season on the data (cf. Stutchbury and Robertson 1988), I used only those nests where the first Tree Swallow egg was laid before 1 June. Where sample sizes vary between tests, this is due to missing values. Data were tested for normality using Wilk-Shapiro tests (SAS 1985). The results showed that most variables were not normally distributed, so I used nonparametric statistics (SAS 1985, Siegel and Castellan 1988). The power of test statistics were estimated for all statistical tests where no significant difference was found between groups using Cohen (1977) and Siegel and Castellan (1988), and all power values are less than 0.40 unless otherwise stated. The significance level for all statistical tests was 0.05.

I analyzed the total numbers of adult fowl mites, adult fleas and blow flies at nests, and the number of each of these ectoparasites per hatchling at each nest. The latter three variables were calculated by dividing the absolute numbers of each ectoparasite by the number of hatchlings at each nest. The data from 1991 and 1992 were not combined due to different experimental protocols between years, significant differences in host reproductive success and nestling size within nestbox types between years (Chapter 4), and significant differences in the number of mites and fleas at nests between years. All probability values are two-tailed unless otherwise specified.

RESULTS

Frequency in the population

Fowl mites.--Adult fowl mites were observed in 37 of 68 (54%) nestboxes sampled in the population in 1991, but in 1 of 103 (< 1%) nestboxes sampled in 1992. The number of fowl mites at nestboxes ranged from 0-300, and the number of fowl mites per hatchling per nestbox ranged from 0-60, in 1991. Heavy fowl mite infestations were rare in 1991. Only 2 of 68 (2.9%, 1 S and 1 O nestbox) nestboxes sampled in the population exhibited infestations exceeding 100 fowl mites. Neither of these two infestations coincided with events of entire brood death for the host; in fact, young fledged from both nestboxes. The numbers of fowl mites in nestboxes in this study are comparable to those reported in Møller (1987a, 1990), but much less than those reported from European Starling (*Sturnus vulgaris*) nests in Clark (1991).

Fleas.--Adult fleas were observed in 100% of nests collected for sifting in 1991 (N = 30) and 1992 (N = 103). The number of fleas in nestboxes ranged from

4-386 in 1991, and 2-836 in 1992. The highest number of fleas in 1992 was collected from a C nestbox. The number of fleas per hatchling at this nest was 119.4, but despite this number the young fledged successfully.

Blow flies.--Blow flies (= newly emerged adults + intact puparia + third instar larvae) were found in 28 of 30 (93.3%) nests collected for sifting in 1991, and 96 of 103 (93.2%) nests in 1992. The number of blow flies per nest ranged from 0-107 in 1991, and from 0-128 in 1992. The percentage of nests with blow flies at Creston was greater than that in other studies of the same species of blow fly (72%, Rogers *et al.* 1991; 66%, Roby *et al.* 1992; see also Wittmann and Beason 1992). The range in number of blow flies reported for nests in this study are similar to those in Rogers *et al.* (1991) and Wittmann and Beason (1992).

Numbers of ectoparasites

Effect of year.--The median numbers of fowl mites per nest, and fleas per nest, and the median numbers of fowl mites per hatchling per nest, and fleas per hatchling per nest, were significantly different between 1991 and 1992 for all box-types combined (Table 1). Fleas were more common in nests in 1992, and fowl mites were extremely rare that year. The median number of blow flies per nest, and blow flies per hatchling per nest, were not different between 1991 and 1992.

Effect of season.--There were no significant associations between the number of any of the ectoparasite species per nest, or the number of these ectoparasites per hatchling per nest, with the first egg, first hatching, first fledging dates of the hosts, or the date when a nest was collected in either year (Spearman Rank Correlations, all $P > 0.05$ for all box-types combined within a year, $N_{1991} = 30$ nests, $N_{1992} =$ 103 nests).

Effect of other types of ectoparasites.--There were no significant associations between the number of one type of ectoparasite at a nest and that of either of the

Table 1. Numbers of three types of ectoparasites per nest, and the numbers of each type of ectoparasite per hatchling per nest, in nests of Tree Swallows in 1991 and 1992 for all box-types combined. Values are means ± SE (N nests, range).

	Year	
	1991	1992
No. mites**	13.5 ± 6.6	< 1.0
	(65, 0-300)	(103, 0-1)
No. fleas*	57.1 ± 16.4	94.5 ± 12.0
	(30, 4-386)	(103, 2-836)
No. blow flies	34.3 ± 5.8	34.4 ± 2.8
	(30, 0-107)	(103, 0-128)
No. mites per hatchling**	2.8 ± 1.3	< 1.0
	(61, 0-60)	(103, 0-0.2)
No. fleas per hatchling*	10.9 ± 3.1	17.7 ± 2.1
	(30, 0.7-64.3)	(103, 0-119.4)
No. blow flies per hatchling	6.3 ± 1.0	6.6 ± 0.5
	(30, 0-17.8)	(103, 0-25.3)

Medians of the distributions are significantly different between years, * $P < 0.05$, ** $P < 0.0001$, Wilcoxon-Mann-Whitney Test, two-tailed (SAS 1985, Siegel and Castellan 1988).

other two types of ectoparasites at a nest in 1991 or 1992, nor were there any correlations between the number of one type of ectoparasite per hatchling per nest with that of the other types of ectoparasites in a nest (Spearman Rank Correlations, all $P > 0.05$ for all box-types combined within a year, $N_{1991} = 30$ nests, $N_{1992} = 103$ nests).

Effect of box-type.--The median number of fleas per nest (Table 2), and the median number of fleas per hatchling per nest (Table 3), were significantly different between C, S, and O box-types in 1991, and C, CI, and O box-types in 1992. In 1991, fleas were more numerous in O than in S or C nestboxes, and more numerous in S compared to C nestboxes (Table 2, 3). In 1992, fleas were more numerous in O compared to C or CI nestboxes, and more numerous in C compared to CI nestboxes (Table 2, 3).

The median numbers of fowl mites and blow flies per nest (Table 2), and the median numbers of fowl mites and blow flies per hatchling per nest (Table 3), were not significantly different between the three box-types within either year.

Effect of repeated use of nest material.--The median number of fleas per nest, and the median number of fleas per hatchling per nest, were significantly different between box-types where the nest material was being used for the first time, and where the old material was being used for the second or third time (Table 4). Fleas were significantly more numerous in nests where the old nest material was being used for the third time compared with second-use nests, and fleas were more numerous in second-use nests compared with those with new material (Table 4).

The median number of blow flies per nest, and the median number of blow flies per hatchling per nest, did not differ significantly between nestboxes where the nest material was being used for the first time, or where the old material was being used for the second or third time (Table 4).

Effect of the amount of nest material.--The number of fleas per nest, and the

Table 2. Numbers of three types of ectoparasites per nest in different box-types. For values of fowl mites in 1992, see text. Values are means ± SE (N nests, range).

1991	Box-types		
Per nest	Clean	Sham	Old
No. fowl mites	4.2 ± 3.1 (24, 0-75)	17.2 ± 15.0 (20, 0-300)	20.7 ± 14.2 (21, 0-300)
No. fleas*	10.7 ± 1.8^{a} (11, 4-23)	79.4 ± 36.7^{b} (10, 4-386)	89.1 ± 32.5^{c} (9, 7-284)
No. blow flies	50.1 ± 9.3 (11, 0-107)	19.0 ± 8.3 (10, 1-83)	32.0 ± 11.1 (9, 0-92)

1992	Box-types		
Per nest	Clean	Clean/Insert	Old
No. fleas**	93.4 ± 26.6^{a} (36, 2-836)	19.0 ± 6.0^{b} (13, 2-70)	112.0 ± 13.4^{c} (54, 5-396)
No. blow flies	34.9 ± 4.7 (36, 0-123)	40.8 ± 8.4 (13, 4-116)	32.6 ± 3.9 (54, 0-128)

Medians of distributions are different, * $P < 0.005$, ** $P < 0.0001$, Kruskal-Wallis Test, two-tailed, df = 2 (SAS 1985).

Different letters beside means indicate which groups differ from each other, $P < 0.05$, Multiple Comparison Method (Siegel and Castellan 1988).

Table 3. Numbers of three types of ectoparasites per hatchling per nest in different box-types. For values of fowl mites in 1992, see text. Values are means ± SE (N nests, range).

1991	Box-types		
Per hatchling per nest	Clean	Sham	Old
No. fowl mites	0.9 ± 0.7 (22, 0-15)	2.9 ± 2.5 (20, 0-50)	4.9 ± 3.2 (19, 0-60)
No. fleas*	1.9 ± 0.3^{a} (11, 0.7-3.8)	14.6 ± 6.4^{b} (10, 0.7-64.3)	17.7 ± 6.5^{b} (9, 1.4-56.8)
No. blow flies	8.8 ± 1.6 (11, 0-17.8)	3.5 ± 1.4 (10, 0.1-13.8)	6.3 ± 2.1 (9, 0-15.3)

1992	Box-types		
Per hatchling per nest	Clean	Clean/Insert	Old
No. fleas**	17.1 ± 4.4^{a} (36, 0.3-119.4)	3.4 ± 1.0^{b} (13, 0.3-11.5)	21.5 ± 2.6^{c} (54, 1-89.8)
No. blow flies	6.5 ± 0.8 (36, 0-21.2)	8.3 ± 1.8 (13, 0.7-23.2)	6.3 ± 0.7 (54, 0-25.3)

Symbols and statistics are the same for those described in Table 2.

Table 4. Numbers of fleas and blow flies per nest, and the numbers of fleas and blow flies per hatchling per nest, in nestboxes where the material was new (N = 49), and where old material was being used for the second (N = 42), and third time (N = 12), in 1992. Values are means ± SE.

	Nest material		
	New	2nd use	3rd use
No. fleas* per nest	74.8 ± 20.5[a]	100.9 ± 15.5[b]	151.0 ± 23.9[c]
No. blow flies per nest	36.5 ± 4.1	33.8 ± 4.5	28.3 ± 7.9
No. fleas* per hatchling per nest	13.5 ± 3.4[a]	19.3 ± 3.0[b]	29.0 ± 4.1[c]
No. blow flies per hatchling per nest	7.0 ± 0.8	6.4 ± 0.8	6.0 ± 2.1

Medians of distributions are different, * $P < 0.0001$, Kruskal-Wallis Test, two-tailed, df = 2 (SAS 1985).

Different letters beside means indicate which groups differ from each other, $P < 0.05$, Multiple Comparison Method (Siegel and Castellan 1988).

number of fleas per hatchling per nest, were significantly positively correlated with the total volume of nest material (= old + new material, cm^3) in nestboxes in 1991 and 1992 for all box-types combined (1991: No. fleas per nest, Spearman Rank Correlation, $r_S = 0.57$, $N = 30$, $P = 0.001$; No. fleas per hatchling per nest, $r_S = 0.59$, $N = 30$, $P = 0.008$; 1992: No. fleas per nest, $r_S = 0.42$, $N = 103$, $P < 0.0001$; No. fleas per hatchling per nest, $r_S = 0.42$, $N = 103$, $P < 0.0001$). The numbers of fleas per nest, and fleas per hatchling per nest, were significantly negatively correlated with the proportion of the total volume of a nest that was new nest material in both years when all box-types were combined (Fig. 2, 3). Therefore, as the proportion of the total volume of nest material in a nestbox that was new material increased, the number of fleas, and the number of fleas per hatchling per nest, decreased. Within box-types, the numbers of fleas per nest, and fleas per hatchling per nest, were positively correlated with the total volume of nest material in O nestboxes in 1992 (No. fleas per nest, $r_S = 0.31$, $N = 54$, $P = 0.02$; No. fleas per hatchling per nest, $r_S = 0.32$, $N = 54$, $P = 0.02$), but not in 1991. The numbers of fleas were not correlated with the volume of new or old nest material within other box-types in 1991 or 1992.

The numbers of fowl mites per nest, and fowl mites per hatchling per nest, were positively correlated with the total volume of nest material in O nestboxes in 1991 (No. mites per nest, $r_S = 0.46$, $N = 20$, $P = 0.04$; No. mites per hatchling per nest, $r_S = 0.49$, $N = 18$, $P = 0.04$), but not in 1992. The numbers of fowl mites per nest, and fowl mites per hatchling per nest, were not correlated with the total volume of nest material when all box-types were combined in both years, or in C or S nestboxes in 1991, or C or CI nestboxes in 1992. Further, the number of fowl mites was not correlated with the volume of new nest material when all box-types were combined, or analyzed separately, in either year (Spearman Rank Correlations, all $P > 0.05$).

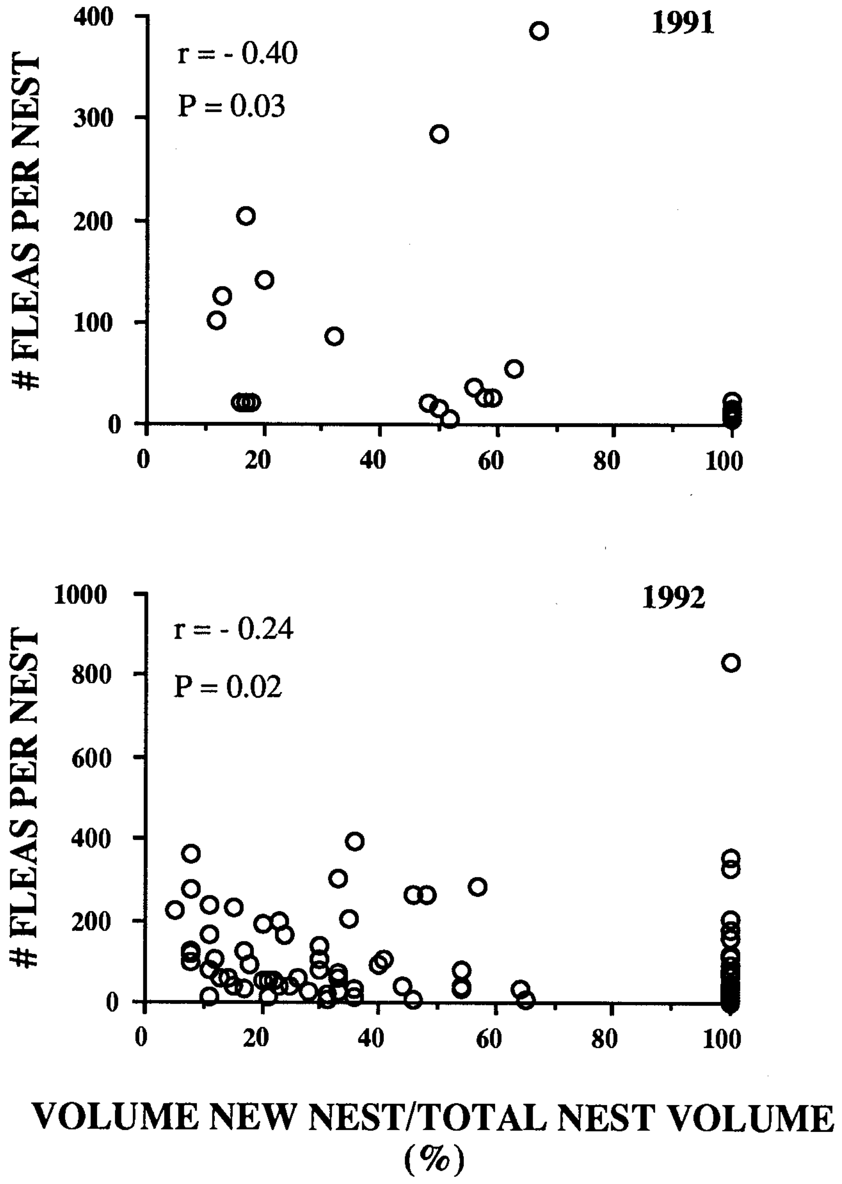

Fig. 2. Plots of the number of fleas per nest and the percentage of the total volume of nest material in a nestbox that is new material. All box-types are combined in 1991 (N = 30) and 1992 (N = 103). r = Spearman rank order correlation coefficient.

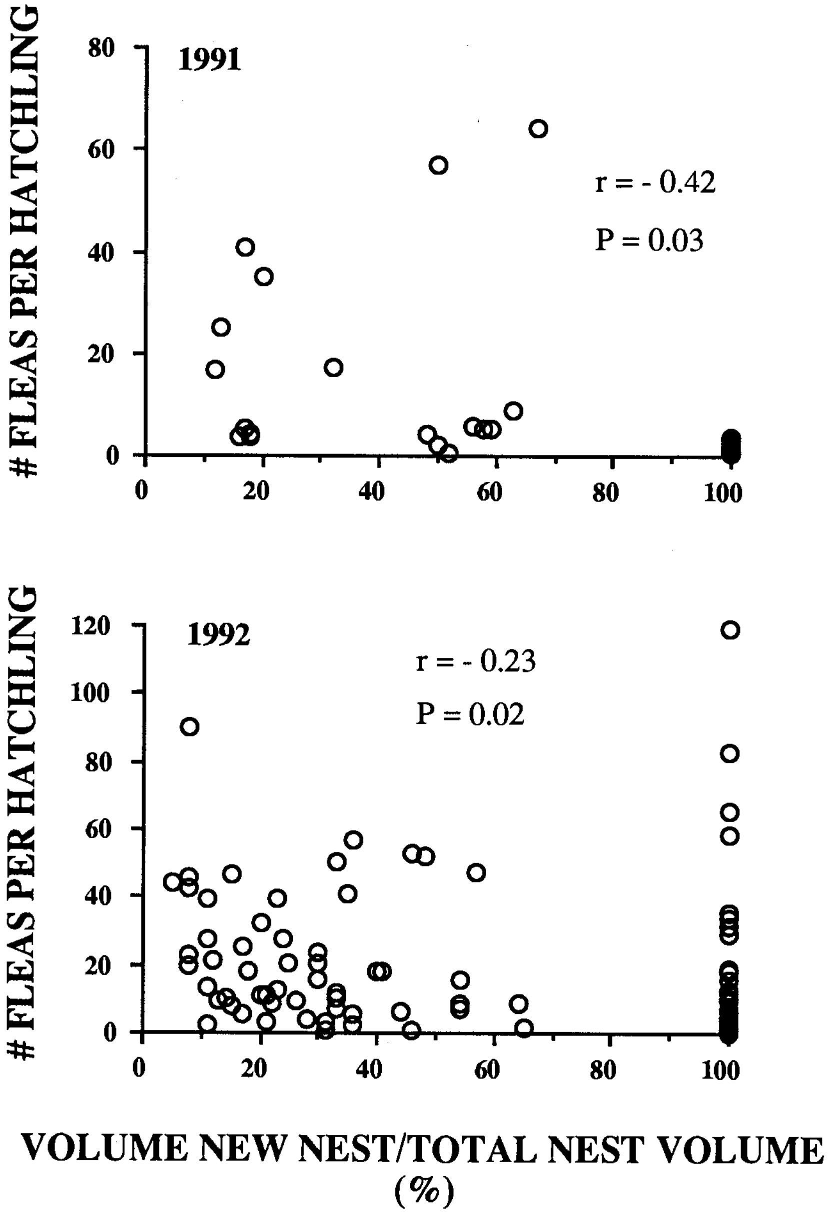

Fig. 3. Plots of the number of fleas per hatchling per nest and the percentage of the total volume of nest material in a nestbox that is new material. All box-types are combined in 1991 (N = 30) and 1992 (N = 103). r = Spearman rank order correlation coefficient.

The numbers of blow flies per nest, and blow flies per hatchling per nest, were not correlated with the total volume of nest material, nor the volume of new nest material in a nestbox when all box-types were combined, or within a box-type, in either year (Spearman Rank Correlations, all $P > 0.05$, $N_{1991} = 30$ nests, $N_{1992} = 103$ nests).

DISCUSSION

The *Life-cycle hypothesis* is based on the assumption that types of ectoparasites whose survival depends on nest material in the absence of the host, such as fleas and fowl mites, should be more common in cavities with old nest material, while other types that do not depend on old nest material outside of the host's breeding season, such as blow flies, should infest cavities randomly regardless of the presence of old nest material. The results of this study generally support the hypothesis. Fleas were more numerous in nestboxes with old nest material (O nestboxes) in contrast to nestboxes where the material was microwaved (S nestboxes), or where old material was removed altogether (C and CI nestboxes). Also, the number of fleas in nestboxes increased with repeated use of nest material, while blow flies were equally common in all box-types. Flea larvae overwinter in old nests, feeding on a variety of organic materials. When the host breeding season begins, the larvae pupate, and the adults begin feeding on the hosts. Blow flies overwinter as adults and seek refuge in cavity crevices and under tree bark during cold periods. Being volant, they are free from being restricted to one cavity, or the nest material inside.

The *Life-cycle hypothesis* is partly supported by my data for fowl mites. Fowl mites were not more numerous in nests with old material than in nests with new material in either 1991 or 1992, but there was a tendency for more mites to be found in S and O nestboxes in 1991. Also, there was a positive correlation between the number of fowl mites and the total volume of nest material in O nestboxes in 1991. In 1992, fowl mites were rare, so factors other than old material must have affected their numbers. Predatory mite species (e.g., Burtt *et al.* 1991) may have increased in number in nestboxes between 1991 and 1992, but it seems unlikely that this could have happened throughout the entire nestbox population. My results do not suggest that fowl mite loads in 1992 could have been limited by the numbers of other types of ectoparasites in nestboxes either because there were no significant associations between one species and another. The major difference between the breeding seasons in 1991 and 1992 was the average temperature during the breeding season. Median monthly temperature was significantly warmer in March, May, and June of 1992 than for the same months in 1991 (Appendix 1). In June 1992, maximum daily temperatures exceeded 30°C over a 9 day period resulting in extreme heat stress for Tree Swallow nestlings, and causing all the young to die at several nests (Chapter 4). It is possible that fowl mites were influenced by high temperatures and high humidities in the nestboxes because the generation time of fowl mites is sensitive to both changes in temperature and humidity (Sikes and Chamberlain 1954, Baker *et al.* 1956).

The amount of material in a nestbox also appeared to influence the numbers of fleas and fowl mites in different box-types. Fleas were more numerous in O nestboxes with more material, suggesting that density-dependent factors such as space limitation can affect their numbers. Larger nests likely have more food for larvae and they may ensure a more stable microclimate for fleas during cold periods, two ways in which the overwintering survival of fleas could be enhanced. Fowl mites were more numerous in O nestboxes with more material in 1991, perhaps for similar reasons to those for flea populations. Whitworth (1976), Pinkowski (1977), and Gold and Dahlsten (1989) all found that the number of blow flies in a nest increased with an increase in nest-size, but this was not observed in this study, nor in two others (Rogers *et al.* 1991, Wittmann and Beason 1992).

The number of fleas and fowl mites were larger than might be expected at S nests in 1991, and C nests in 1992, because these nest-sites had been cleaned, and the nest material microwaved in the case of S nests. These results are probably due in part to the infection process. Both fleas and fowl mites could reinfest cleaned nestboxes via adult hosts. Many Tree Swallows may visit a nestbox during the breeding season (Lombardo 1986, 1987a, b), and this might increase the likelihood of infection at a nest. Also, fleas and fowl mites may have infested S and C nests borne on nest material brought by females. The numbers of fleas and fowl mites in these nests might also have been affected by methods used in this study. Pesticides (e.g., pyrethrin, Møller 1990) were not used at nests so some ectoparasites probably remained in nests after the box-types were cleaned out. Also, the number of fleas that I collected in S and O nests in 1991 may be an overestimate because I could not distinguish between those fleas that were alive in 1991 and those that remained from a previous nest. Nests were processed quickly in 1992, and most fleas collected were alive, so this possible sampling error should not apply to the results of that year.

Conclusion.--The Møller (1989, 1992) hypothesis that ectoparasites will be more numerous in cavities of hole-nesting birds which have old nest material is partly correct, but my results, and those from other studies, show that it is difficult to generalize about how the numbers of types of ectoparasites will change in cavities because there are many factors that can affect their numbers both within and between seasons. One such factor, and perhaps most important, is the degree to which a species of ectoparasite is dependent on nest material for survival during it's life-cycle.

CHAPTER 3

INFLUENCE OF OLD NEST MATERIAL ON NESTBOX SELECTION AND NEST BUILDING IN TREE SWALLOWS

INTRODUCTION

Many characteristics of nesting cavities affect their use and the reproductive success of hole-nesting birds (e.g., Rendell and Robertson 1989, 1990, 1993, Robertson and Rendell 1990). Due to recent critiques of nestbox studies (Møller 1989, 1992, Lindén and Møller 1989), interest has arisen concerning another cavity characteristic, old nest material, and whether or not it affects the natural history of hole-nesting birds. Secondary cavity-nesting birds re-use old cavities because they are incapable of excavating their own tree cavity. However, these species frequently have a choice of cavities (e.g., due to defense of more than one nest-site, Rendell and Robertson 1989; due to a surfeit of local cavities, van Balen *et al.* 1982, Brush 1983, Ingold and Ingold 1984, Peterson and Gauthier 1985, Rendell and Robertson 1989, Waters *et al.* 1990), and they may encounter relatively new and "clean" cavities such as newly excavated woodpecker cavities (Rendell and Robertson 1991). What influence, if any, does old nest material have on the selection and re-use of cavities, and on nest building behaviour in hole-nesting birds? Although they are discussed separately, the hypotheses and predictions mentioned below are not necessarily mutually exclusive.

1. *Ectoparasite avoidance hypothesis.*--Assuming that populations of haematophagous ectoparasites increase in number in cavities that are repeatedly used by birds (Møller 1989, 1992, Chapter 2), and that ectoparasites reduce reproductive success and the health of nestlings (e.g., Fauth *et al.* 1991, Winkler 1992), hole-nesting birds should prefer clean cavities to those with old, infested

material. Also, if hole-nesters can estimate the numbers of ectoparasites in old material, they should choose cavities where old material is present, but ectoparasites are relatively scarce. Alternatively, hole-nesters may show no preference for particular cavities, but build nests with materials that help to deter the ectoparasites from feeding. For example, European Starlings are thought to deter Northern fowl mites (*Ornithonyssus sylviarum*) from feeding through chemical means by lining their nests with specific green plants that have high biological activity (Clark and Mason 1985, 1988, Clark 1991; see also Wimberger 1984), and Tree Swallows may deter mites and lice from feeding because the feathers used to line nest cups act as physical barriers to the movement of ectoparasites (Winkler 1992).

2. *Cavity size hypothesis*.--Regardless of the presence or absence of old nest material, hole-nesters may choose to nest in cavities of a particular size. Cavity size is hypothesized to limit brood and clutch size in hole-nesting birds (e.g., Karlsson and Nilsson 1977, Rendell and Robertson 1993), because overcrowding causes trampling and the death of nestlings due to hyperthermia (Mertens 1969, 1977, van Balen and Cavé 1970, O'Connor 1975, van Balen 1984).

3. *Energy savings hypothesis*.--Assuming that nest building is energetically costly, hole-nesters may save energy by nesting in cavities where old material is already present (cf. Barclay 1988, Pitts 1988, Shields *et al.* 1988). If the existing nest material provides an adequate support structure for the eggs and young, energy saved during nest building could be invested in reproduction.

4. *Time savings hypothesis*.--Nest building takes time, so hole-nesters may save time by choosing cavities where existing nest material provides an adequate support structure. The time that is saved could be devoted to other pursuits, such as feeding.

5. *Predation threat hypothesis*.--Hole-nesters may prefer to nest in cavities with old material because building whole new nests requires more time away from

the cavity and on the ground acquiring nest material. This may increase the likelihood that a bird is taken by avian or mammalian predators.

6. *Nest defence hypothesis*.--By choosing to nest in cavities with old nest material, hole-nesters may be able to spend more time defending their cavity from inter- and intraspecific competitors, rather than nest building.

7. *Insulation hypothesis*.--Old nests may be better insulated (Mertens 1977), and birds may prefer warmer nests early in the breeding season when outside temperatures are cool.

8. *Successful cavity hypothesis*.--Hole-nesters may prefer to nest in cavities with old material if cues indicate that a cavity was successfully used before (cf. Barclay 1988, Shields *et al.* 1988).

In this chapter, I present the results of an investigation into how old nest material influences nestbox selection and nest building in Tree Swallows. I know of only one other study which has investigated either of these topics. Thompson and Neill (1991) found that House Wrens selected nestboxes randomly with respect to the presence or absence of old nest material.

METHODS

Study site.--The study area, the distribution of nestboxes, and the types of nestboxes used are described in detail in Chapter 2.

Host nesting phenology.--Regular checks (every 1-3 days) at nestboxes enabled me to record the nesting phenology of the host. This is described in more detail in Chapter 4.

Nest building.--In 1991 and 1992, I recorded the mass (g) of new nest structures at all box-types once the nest cups were formed, but yet unlined, and before the contents of any nestboxes were switched (Chapters 2). New and old nest materials were easily distinguished, and nest structures were relatively dry when weighed. At 14 of 78 (17.9%) nests in 1991, and 2 of 111 (1.8%) nests in 1992, weighing was done after egg-laying had begun. Nests were weighed in a ZIPLOC® bag with a Pesola® balance (50 g or 300 g balance), then replaced intact. In both years, many nests built on top of old nest material were very light and fragile. I was forced to estimate the mass of these new nest structures because handling them might have destroyed them. Estimates were based on masses of three nests that were weighed despite their small size. Small, fragile nests were scored as weighing either 1 or 5 g.

When I weighed nests, I noted the type (grass, leaves, pine needles, etc.) and freshness (green vs. dead) of new nest material collected by females. I also measured the depth (cm) of new and old nest structures in each nestbox before the settlement of pairs at nestboxes until new nests were completed, and after nest switches were completed (Chapters 2). Using the dimensions of each nestbox and the depth of new and old nests in a nestbox, I calculated the volume of new and old nest structures (cm^3), and cavity size (cm^3), to determine if cavity size affected nest-building. Throughout the remainder of the thesis, cavity size refers to the volume of available cavity space above the nest material.

Nests were collected after a breeding attempt failed or the young had fledged. The number of feathers brought to nestboxes was estimated by counting the rachises in sifted nests (Chapter 2). The total number of feathers included only those that were in the nest cup lining, or the new nest structure. Feathers that were obviously part of an old nest structure were not counted. Feather counts were made for 30 nests in 1991 ($N_C = 18$, $N_S = 8$, $N_O = 4$), and 100 nests in 1992 ($N_C = 34$, N_{CI} (insert boxes, see below) $= 13$, $N_O = 53$).

Nestbox preference experiment.--This experiment was performed using C, S, and O box-types in 1991 when nestboxes were distributed in pairs (Chapter 2). This design provided a choice of nestboxes in which to nest for each pair of Tree

Swallows. On 29 territories, a C nestbox was paired with an O nestbox; on 25 territories, a C nestbox was paired with an S nestbox; and on a further 25 territories, an S nestbox was paired with an O nestbox. The three pair combinations of nestboxes were numbered and arranged sequentially throughout the marsh as follows: CxO_1, CxS_1, SxO_1, CxO_2,...etc. All boxes were in place by 25 March, before the Tree Swallows began settling on territories.

At each territory I scored nestbox preference by observing in which of the two possible nestboxes females built. During regular checks at each territory I measured the depth of the new material in nestboxes, and subjectively assessed cup development and lining, yielding three estimates of which box-type a female preferred. A preference was not obvious until egg-laying at 8 of 78 (10.2%) territories. At one territory a pair of Black-capped Chickadees (*Parus atricapillus*) already occupied one of the nestboxes before Tree Swallows settled at the other nestbox, so this territory was dropped from the analysis.

Insert experiment.--This experiment was conducted in 1992 to examine how cavity size influenced the amount of material brought to nestboxes by females. In 15 randomly chosen C nestboxes (CI), compact styrofoam and a plywood floor overlay were inserted to fill the bottom 8 cm of each nestbox. Therefore, CI nestboxes were clean, but they simulated the smaller cavity size of nestboxes with old nest material. The depth of the inserts approximated the mean depth of old nest material in O nestboxes in 1992 (mean ± SE = 7.4 ± 0.3 cm, N = 58). New nests in CI nestboxes were weighed as described above. Two CI nestboxes were not used by Tree Swallows.

Female age.--In both years, I captured as many nesting females as possible to determine the age distribution of females in the study (72 in 1991, 108 in 1992). Birds were captured by hand, in mist nets, and by using box traps (Stutchbury and Robertson 1986). Captured females received Canadian Wildlife Service aluminum bands and they were painted with unique combinations of non-toxic, acrylic paints at positions along the wing and tail. Females were sexed and aged according to Hussell (1983) and Stutchbury and Robertson (1987). In 1991, females were aged as after-second-year (ASY), and second-year (SY), but recaptures in 1992 allowed me to divide female ages into three classes: SY, ASY (including third-year), and after-third-year birds (ATY, including fourth-year).

Statistical Analysis.--The data were analyzed according to the methods described in Chapter 2. All probability values are two-tailed unless otherwise specified. The nestbox preference data were analyzed using Binomial probability tests (Anonymous 1952). The nest building data were not combined between years due to differences in experimental protocol.

RESULTS

Nestbox preference.--Nestbox use was non-random for all three paired-box combinations (Table 5). C nestboxes were preferred over both S and O nestboxes, and S nestboxes were preferred over O nestboxes.

These results may have been biased because of a variable that I did not control; i.e., the difference in cavity size between box-types. Both S and O nestboxes had old nest material, so cavity size was smaller in these nestboxes compared to C nestboxes. Also, S nestboxes typically had less nest material (at S x O territories: mean depth (cm) ± SE = 6.0 cm ± 0.4, N = 25) than O nestboxes (8.7 cm ± 0.6, N = 25). For each of the three types of territories, I analyzed nestbox preference with respect to cavity size of each nestbox. Tree Swallows significantly more often chose the nestbox with the larger cavity over the one with the smaller cavity (Table 5).

Female age, and presumably experience, did not affect the choice of nest-sites. The numbers of ASY and SY females that chose to nest in C, S, and O nestboxes were not significantly different (Chi Square Test, $X^2 = 0.7$, df = 2, P >

Table 5. Preference of Tree Swallows for A) box-type and B) cavity size at paired-box territories in 1991. Cavity size is compared between the two boxes within each pair at each territory. Box-types are C = clean, S = sham, and O = old.

A)	Preferred box-type			
Territory	Clean	Sham	Old	P[a]
C x S (N = 25)[b]	18	6	-	0.016
C x O (N = 29)	22	-	7	0.006
S x O (N = 25)	-	19	6	0.010

B) Territory	Larger cavity	Smaller cavity	
C x S (N = 25)[b]	18	6	0.016
C x O (N = 29)	22	7	0.006
S x O (N = 25)[c]	17	5	0.012

[a] P values are two-tailed Binomial probabilities (Anonymous 1952).

[b] One territory was excluded because Black-capped Chickadees occupied one nestbox prior to settlement by Tree Swallows.

[c] Three territories were excluded due to tied values.

0.05).

Nest building.--Tree Swallows built nests that included grasses (e.g., Timothy *Phleum pratense* L., Reed Canary *Phalaris arundinacea* L.), feathers, occasionally deer hair, and green moss. Moss was found in 37 of 189 (19.6%, 1991-92 combined) new nests. The actual amount of moss in any single nest was very low (< 1 g wet wt.), and it appeared to be distributed randomly throughout the nest material matrix. In 1991, fresh moss was found in 19 of 40 (47.5%) new nests in C nestboxes, 8 of 25 (32%) new nests in S nestboxes, and 2 of 13 (15.4%) new nests in O nestboxes. In 1992, fresh moss was found in 5 of 53 (9.4%, combining both C and CI nestboxes) new nest in C nestboxes, and 3 of 58 (5.2%) new nests in O nestboxes. I compared the proportion of new nests with and without moss between years irrespective of box-type. Significantly more new nests in 1991 had green moss in them than new nests in 1992 (Chi Square Test, $X^2 = 26.0$, df = 1, $P < 0.05$). Green moss was not found more frequently in any particular box-type in either year (1991: $X^2 = 4.7$, df = 2, $P > 0.05$; 1992: $X^2 = 0.7$, df = 1, $P > 0.05$).

Box-type significantly influenced the median volume and median mass of new nest material brought to nests (Table 6). Females in C nestboxes built significantly larger and heavier new nests than birds that built in either S or O nestboxes in 1991. Nests built in C nestboxes in 1992 were significantly larger and heavier than those built in CI nestboxes, and new nests in CI nestboxes were significantly larger and heavier than those in O nestboxes. Many females building in nestboxes that contained old material brought less than 5 g of grasses to the nest (1991: 16 of 25 S nestboxes (64%), 5 of 13 O nestboxes (38.4%); 1992: 38 of 58 O nestboxes (65.5%)). These individuals merely lined existing material with a thin layer of grass and then added feathers.

To examine how cavity size affected the size of new nests built by females, I correlated the mass and volume of new nest material collected by females with

Table 6. Mass (g) and volume (cm^3) of new nest material gathered, and the number of feathers added to new nest structures by Tree Swallows in 1991 and 1992. Values are means ± SE (N nests, range).

Year	Box-type		
1991	Clean	Sham	Old
Mass*	24.2 ± 1.8^a (40, 10-59)	4.8 ± 1.3^b (25, 1-24)	5.9 ± 1.4^b (13, 1-16)
Volume*	827.1 ± 34.0^a (39, 513-1433)	307.7 ± 54.2^b (22, 109-1102)	428.7 ± 75.4^b (12, 114-1047)
No. feathers	138 ± 8 (18, 84-186)	157 ± 23 (8, 73-286)	241 ± 50 (4, 95-318)
1992	Clean	Clean/Insert	Old
Mass*	26.3 ± 1.3^a (40, 12-50)	16.4 ± 1.4^b (13, 8-22)	6.3 ± 0.7^c (58, 1-25)
Volume*	712.6 ± 25.9^a (39, 456-1323)	581.6 ± 27.5^b (14, 399-772)	287.2 ± 24.9^c (58, 55-798)
No. feathers	139 ± 9 (34, 62-317)	116 ± 11 (13, 61-183)	118 ± 7 (53, 34-278)

Symbols and statistics are the same for those in Table 4.

cavity size in nestboxes chosen by females, using all available data independent of box-type. In both years, the correlations were highly significant (Fig. 4, 5); females built larger nests by mass and volume in larger cavities than in smaller ones.

Female age did not affect the volume or mass of nest material gathered by females in either year of the study (Volume, 1991: Wilcoxon-Mann-Whitney Test, $Z = 0.2$, $P = 0.86$; 1992: Kruskal-Wallis Test, $H = 0.6$, $df = 2$, $P = 0.74$; Mass, 1991: $Z = 0.5$, $P = 0.59$; 1992: $H = 0.4$, $df = 2$, $P = 0.80$).

Although females built larger nests in larger cavities, after new nests were completed cavity size was still significantly greater in C (mean ± SE cm^3 (N) = 1763 ± 37 (37)) nestboxes than in S (1539 ± 62 (19)) and O (1551 ± 67 (12)) nestboxes in 1991 (Kruskal-Wallis Test, $H = 12.0$, $df = 2$, $P = 0.002$), and greater in C (1888 ± 33 (36)) nestboxes than in CI (1205 ± 40 (13)) and O (1515 ± 36 (56)) nestboxes in 1992 ($H = 51.0$, $df = 2$, $P < 0.0001$). After the nest was completed, cavity size was not different between S and O nestboxes in 1991, but was significantly greater in O nestboxes compared to CI nestboxes in 1992 (Multiple Comparison Method, $P < 0.05$, Siegel and Castellan 1988).

Neither box-type (Table 6), nor female age, affected the number of feathers incorporated into new nest structures (Box-type, 1991: Kruskal-Wallis Test, $H = 3.2$, $df = 2$, $P = 0.21$, Power = 0.72; 1992: $H = 3.0$, $df = 2$, $P = 0.23$; Female age, 1991: Wilcoxon-Mann-Whitney Test, $Z = 0.2$, $P = 0.84$; 1992: $H = 2.6$, $df = 2$, $P = 0.28$).

DISCUSSION

Nestbox selection.--The results of this study support two hypotheses concerned with cavity selection by hole-nesting birds: the *Ectoparasite avoidance* and *Cavity size* hypotheses.

Tree Swallows clearly preferred clean nestboxes over those with old nest material, supporting the *Ectoparasite avoidance* hypothesis. It could be interpreted

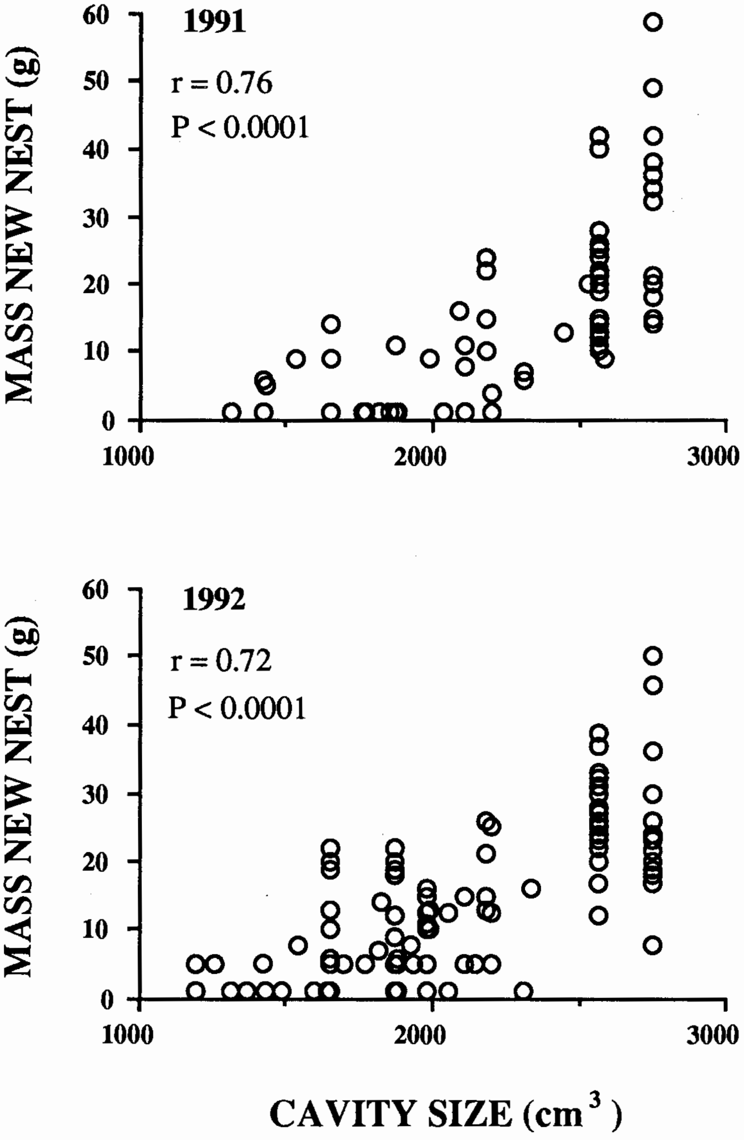

Fig. 4. Plots of the mass of new nest material added to nestboxes and cavity size. All box-types are combined in 1991 (N = 72) and 1992 (N = 111). r = Spearman rank order correlation coefficient.

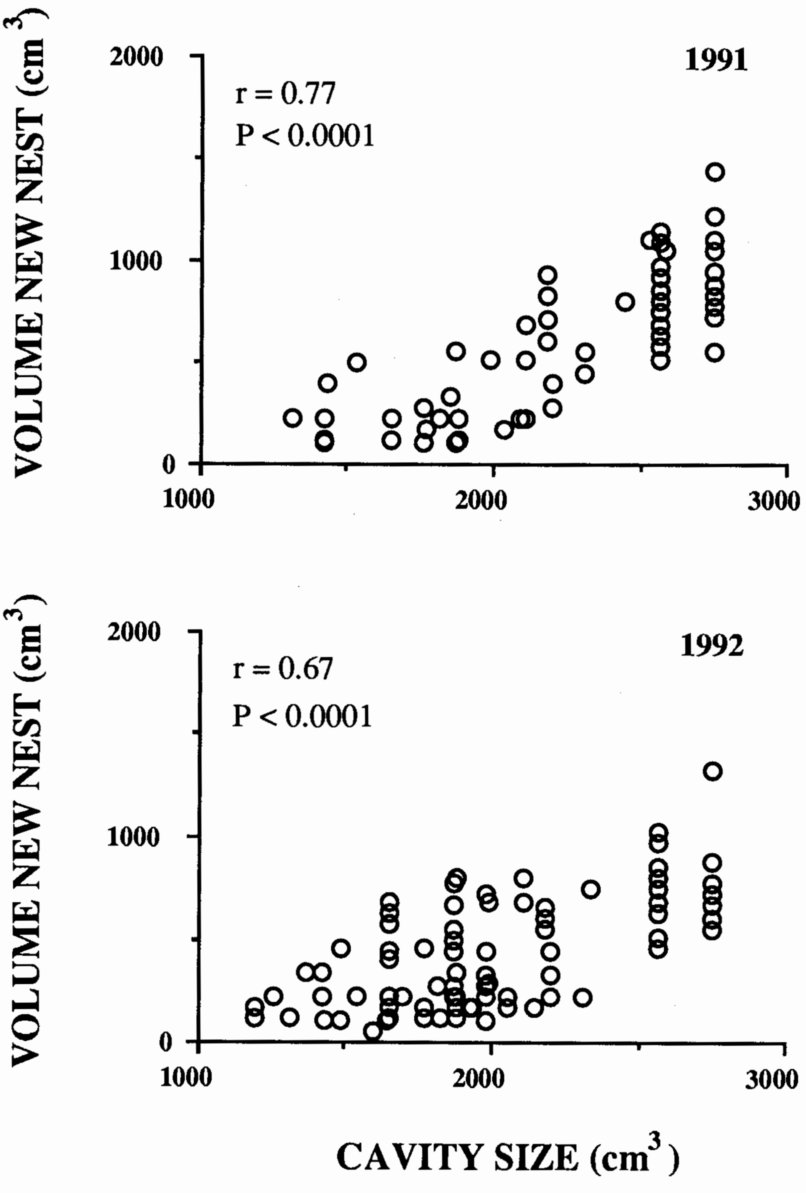

Fig. 5. Plots of the volume of new nest material added to nestboxes and cavity size. All box-types are combined in 1991 (N = 72) and 1992 (N = 111). r = Spearman rank order correlation coefficient.

that they merely avoided nestboxes with old material, but on territories where sham and old box-types were available, they avoided nestboxes with old, unmanipulated nests, suggesting that Tree Swallows discriminated between nestboxes with high and low numbers of ectoparasites (Chapter 2). Other species of Hirundines can discriminate between parasitized and relatively unparasitized nest-sites. Cliff Swallows (*Hirundo pyrrhonota*) and Barn Swallows (*H. rustica*), species whose nests may remain intact over several years, avoid or abandon heavily parasitized old nests and whole colonies and build elsewhere, even for several breeding seasons (Brown and Brown 1986, Emlen 1986, Møller 1987a, 1990, Barclay 1988, Chapman and George 1991, Loye and Carroll 1991). Once parasite numbers decline for lack of a host (Loye and Carroll 1991), these species may return to abandoned colony sites. Apparently, Great Tits (*Parus major*, Richner *et al.* 1991) also avoid nestboxes infested with bird fleas. Analagous to observations of cycling in colony use by colonially nesting Hirundines, if some hole-nesters in the wild avoid cavities because of high ectoparasite loads, this could be an explanation why many recent studies investigating cavity availability for secondary hole-nesters have found numerous, unoccupied cavities in natural populations (van Balen *et al.* 1982, Brush 1983, Ingold and Ingold 1984, Peterson and Gauthier 1985, Rendell and Robertson 1989, Waters *et al.* 1990). One cue to the number of ectoparasites in a cavity could be the presence of ectoparasites at the entrance to a cavity. I observed fleas at the entrances to nestboxes on several occasions in the spring of 1992.

The observed pattern of nestbox selection can also be explained in part by the *Cavity size* hypothesis. Consistent with this hypothesis, Tree Swallows preferred nestboxes with more available space inside, i.e., larger cavities. Lumsden (1986) and Rendell and Robertson (1993) also found that Tree Swallows preferred to nest in larger nestboxes rather than in nestboxes where the internal volume had been experimentally reduced. Other hole-nesting species have exhibited a preference for larger cavities as well (European Starlings, Clobert and Berthet 1983, Trillmich and Hudde 1984; Pied Flycatchers *Ficedula hypoleuca*, Slagsvold 1987; Great Tits, Löhrl 1980, 1986, van Balen 1984). Studies have documented that females lay larger clutches in larger cavities in both nestbox (Löhrl 1973, 1980, Karlsson and Nilsson 1977, van Balen 1984, Gustafsson and Nilsson 1985, Rendell and Robertson 1993) and natural cavity populations (Ludescher 1973, Nilsson 1984, Rendell and Robertson 1989), which suggests that larger cavities may enable birds to rear more young.

Because Tree Swallows consistently preferred cleaner and larger nestboxes, the remaining hypotheses (i.e., *Energy savings*, *Time savings*, *Predation threat*, *Nest defence*, and *Successful cavity*), which all predict that hole-nesting birds should prefer cavities with old material, are not supported by the results. The experiment does not allow me to address the *Insulation hypothesis* because all the data are from nestboxes where clutches were initiated early in the breeding season, and the hypothesis predicts that time of season might affect the preference for cavities with or without old nest material.

For some species of hole-nesters the hypotheses of cavity selection and nest building behaviour described in this chapter may not be relevant due to different behaviours and natural histories. For example, Thompson and Neill (1991) showed that House Wrens selected nestboxes randomly with respect to the presence or absence of old nest material. Unlike Tree Swallows, House Wrens routinely remove old material from cavities, so it seems that the presence of an old nest in a cavity is immaterial for this species.

Nest building.--Tree Swallows exhibited great variability in the size of nests they built due to both box-type and the influence of cavity size. Correlations showed that nest size increased as cavity size increased. Pitts (1988) found that Eastern Bluebirds (*Sialia sialis*) also built significantly larger nests in larger nestboxes.

Larger nests observed in clean and/or larger nestboxes may be needed to ensure a stable platform for the nest-cup and eggs, to provide adequate insulation, or to enable young and adults to leave the nestbox more easily.

Feathers serve an important thermoregulatory function by insulating eggs and nestlings (Capreol 1983, Møller 1984). Winkler (1992) manipulated the number of feathers in nest cups of Tree Swallows and showed that nestlings with more feathers in their nest cups were larger and had fewer ectoparasites (i.e., fowl mites, lice), indicating that feathers serve another adaptive function by deterring ectoparasite feeding. In this study, fleas were more numerous in nests with old material (Chapter 2), and based on Winkler's results, one might expect that birds should have incorporated more feathers into these nests. However, this was not observed, and further, nestling health was not affected (Chapter 4), so my results do not corroborate those in Winkler (1992). Capreol (1983) also found that feathers did not deter the blow fly *Protocalliphora sialia* from feeding on nestling Tree Swallows. Tree Swallows add feathers to the cup lining right up until the nestling stage (Winkler 1992), so it is possible that the birds in my study did not know of the higher flea loads in nests with old material until after the young had hatched, or that flea numbers increased as the nestling stage progressed. However, I dismiss these two explanations because Tree Swallows apparently discriminated between parasitized (O) and relatively unparasitized (S) nests during the nestbox preference experiment, and because there was no significant effect of season on the numbers of the three types of ectoparasites found in nestboxes in this study (Chapter 2). My results differ from those of Winkler (1992) in another manner. He found a negative correlation between the duration of the nestling period and the number of feathers in a nest at hatching in each year of his three year study (significant in one of the three years), suggesting that more feathers in the nest cup enable young to grow faster and fledge earlier. I found no association between the number of feathers in a nest and the duration of the nestling period in 1991, and a significant *positive* correlation between these variables in 1992 (Fig. 6). I suggest that nestling periods were longer for young in nests with more feathers in 1992 because the feathers contributed to the heat stress experienced by nestlings during a heatwave in June of that year, and this heat stress likely slowed growth rates. Feathers decrease the rate of heat loss in nests (Capreol 1983, see also Haftorn 1978), so during warm periods more feathers in a nest may be detrimental because cavity temperatures could be kept dangerously high (cf. Møller 1987b). The mean temperature in June 1992 was almost 6°C warmer than that for June 1991 (Appendix 1), and most of the incidents of entire brood death in 1992 occurred during that month (Chapter 4).

Wimberger (1984) found that the use of green plant material was significantly correlated with nest re-use in North American and European Falconiformes, and he hypothesized that green material lowered the incidence of parasitism for these species. Some Tree Swallows included green moss in new nests, but fresh moss was not found more frequently in any specific box-type, nor was it more common in new nests in 1992 when flea loads were higher than in 1991. I suggest that most of the green moss in nestboxes was carried in while attached to other pieces of grass or feathers, and not for any specific purpose. This contrasts with the behaviour of European Starlings, which weave fresh green plant material from specific plant species (e.g., Wild Carrot *Daucus carota*) into the new nest matrix (Clark and Mason 1985, 1988). The plants used by starlings presumably contain volatile compounds, which act as fumigants that inhibit ectoparasite feeding and enhance host reproductive success (Clark and Mason 1985, 1988, Clark 1991; but see Fauth *et al.* 1991). It is not known to what extent green nest material is incorporated into new nests of other species of hole-nesting birds, nor whether such material serves an adaptive function.

Conclusions.--Tree Swallows avoided nestboxes with old material. This may

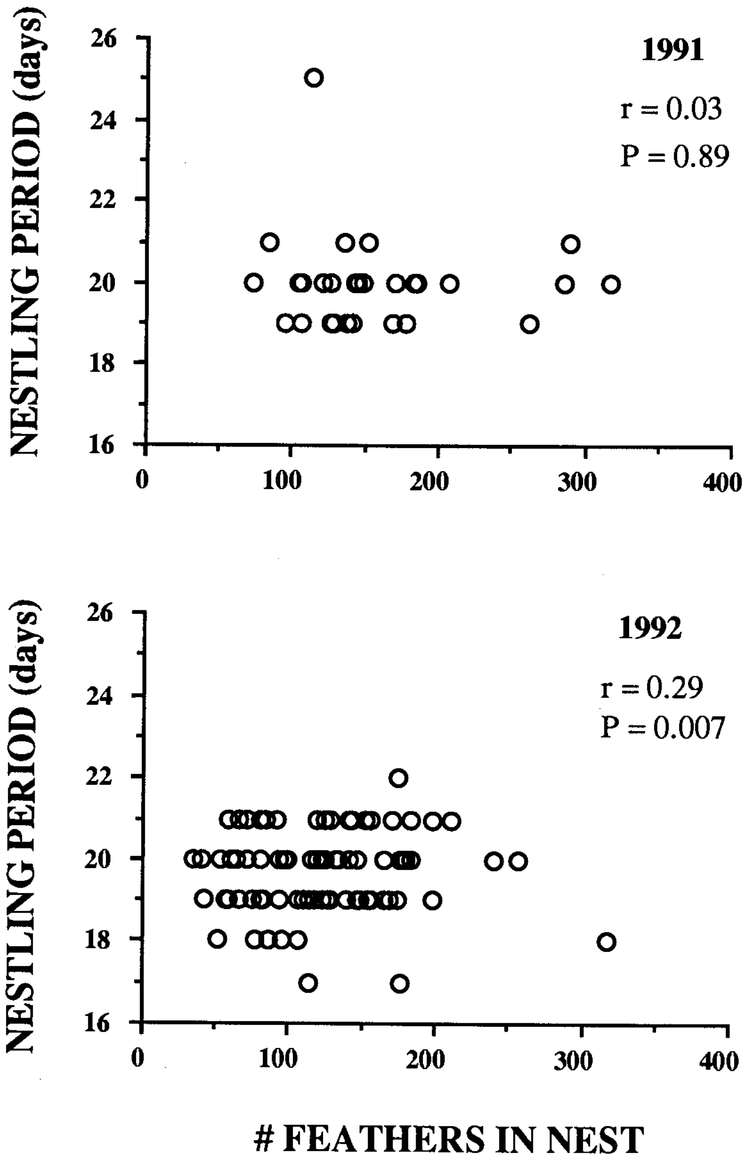

Fig. 6. Plots of the duration of the nestling period and the number of feathers in a new nest. All box-types are combined in 1991 (N = 30) and 1992 (N = 84). r = Spearman rank order correlation coefficient.

be due to the threat of higher ectoparasite loads in such nests, which they can apparently recognize, or also because cavity size in nestboxes containing old nest material is smaller. Further experiments are required to separate the associated characteristics of the presence of old nest material and reduced cavity size on cavity selection in hole-nesters, although in natural cavities these characteristics are probably highly correlated. Tree Swallows built larger nests in larger cavities and it is likely that the observed size of some of the nests in this study, and in other studies of hole-nesters, are an artefact of the size of nestboxes used by researchers. Whether or not nest building by females is energetically costly, e.g., in terms of clutch size, is not known, but if this were the case then cavity size may be another factor that could bias observations of life-history patterns in nestbox studies of birds (cf. Møller 1989, 1992). The number of feathers incorporated into new nest structures did not differ between those pairs using nests with old material and higher numbers of ectoparasites, and those pairs using clean nestboxes, and in fact feathers may have adversely affected nestling growth during warm weather in one year, so my results do not lend support to Winkler's (1992) adaptive hypothesis for feather use in nest lining.

CHAPTER 4

EFFECT OF NEST RE-USE ON REPRODUCTIVE SUCCESS, NESTLING SIZE, AND FEEDING EFFORT IN TREE SWALLOWS

INTRODUCTION

Few studies have examined nest re-use in hole-nesting birds (Thompson and Neill 1991, this study). Most studies concerned with nest re-use have focussed on the costs and benefits of nesting strategies in colonially nesting passerines because they can choose to build a new nest or use an old structure. Secondary-cavity nesters typically re-use old cavities because they cannot excavate their own, but they may still have the opportunity to choose from several different cavities in the spring. Unoccupied natural cavities are abundant in some areas (van Balen *et al.* 1982, Brush 1983, Ingold and Ingold 1984, Peterson and Gauthier 1985, Rendell and Robertson 1989, Waters *et al.* 1990). Tree cavities vary greatly in age and quality (van Balen *et al.* 1982, Rendell and Robertson 1989) and in the number of times that they have been used. The habitat conditions in which tree cavities are found (e.g., on land or over water) vary, and hole-nesters can defend one or more extra cavities giving them a choice of where to nest (Rendell and Robertson 1989, 1991). So, to what extent does nest re-use affect the breeding ecology of hole-nesting birds?

Re-using nests by birds may reduce the time and energy needed to build a new nest (Barclay 1988, Shields *et al.* 1988, but see Chapter 3), but this behaviour has its costs. For example, ectoparasites may be more numerous in cavities with very old nests than in those with newer ones (Brown and Brown 1986, Barclay 1988, Chapman and George 1991, Chapter 2), and higher numbers of ectoparasites in nests have been shown to reduce reproductive success and nestling size and health in some species of colonially nesting passerines (Moss and Camin 1970, Brown and

Brown 1986, Shields and Crook 1987, Møller 1990, 1991, Chapman and George 1991), colonial seabirds (Feare 1976, Duffy 1983, 1991), and hole-nesters (Capreol 1983, Clark and Mason 1988, Fauth *et al.* 1991, Richner *et al.* 1991, Winkler 1992; see also Lindén and Møller 1989, Møller 1989, 1992). Also, to compensate for the possible effects of parasitism, Mason (1944) and Johnson and Albrecht (1993) suggested that parents may incur costs by increasing their nestling feeding effort. This could be done by either increasing the rate of delivery of food (cf. Rogers *et al.* 1991), or by prolonging the nestling period. Previous research has shown that the duration of the nestling period at parasitized nests may be significantly longer than that at relatively unparasitized nests (Shields and Crook 1987, Winkler 1992). A final cost of the repeated use of the same nest cavity is that the addition of nest material by previous occupants reduces cavity size. Studies on hole-nesting birds suggest that smaller cavities limit both brood and clutch size (e.g., Karlsson and Nilsson 1977, Rendell and Robertson 1993) due to space restrictions, and associated thermoregulatory and chemical stresses experienced by nestlings (Mertens 1969, 1977, van Balen and Cavé 1970, O'Connor 1975, van Balen 1984, Erbelding-Denk and Trillmich 1990).

I investigated how nest re-use affects reproductive success, nestling size, and feeding effort in Tree Swallows breeding in nestboxes. I showed in Chapter 2 that flea populations were significantly greater in nestboxes with old nest material, and in Chapter 3 that Tree Swallows clearly avoided nestboxes with old material when given a choice. I predict that reproductive success will be lower, and nestlings will be smaller, for pairs using nests with old nest material because of higher numbers of ectoparasites in these nests and smaller cavity size. If nestling health is worse, and nestling growth rates in nestboxes with old nest material are slower than in clean nestboxes, parents should expend more effort feeding nestlings at nestboxes with old material.

METHODS

Study site.--For a complete description of the study site, the distribution of nestboxes, and the types of nestboxes used in this study, see Chapters 2 and 3.

Nest switches.--In some empirical studies of hole-nesters (e.g., Clobert and Berthet 1983, Trillmich and Hudde 1984) the characteristics of females, their reproductive output, and even their choice of nest-sites may all be correlated; that is, older, experienced, and larger females may settle at larger nestboxes and raise more young. I tried to control for any possible covariation of adult phenotype and reproductive success with the box-type used by a female by switching nests after new nests were built, but yet unlined, and before egg-laying, according to the methods described in Chapter 2.

In both years, immediately after the nest switches were completed, I took measurements of the depth of nest material in each nestbox. Using this value and the known dimensions of every nestbox, I calculated cavity size of every nestbox.

Breeding phenology and reproductive success.--The following measures of reproductive success and breeding phenology were recorded during regular nest checks (every 1-3 days) at 73 nests in 1991 and 105 nests in 1992: first egg date, hatching and fledging dates, clutch size, and the numbers of hatchlings and fledglings. Using the latter three variables I calculated the percentage of eggs that hatched, the percentage of hatchlings that fledged, and the percentage of eggs resulting in fledglings for each nest. First hatching date is equivalent to nestling day (ND) 1, and it is the date when the first nestling hatched. First fledging date is the date when the first nestling left the nest. The nestling period at each nest was calculated as the number of days between the first hatching and first fledging dates.

The outcomes of nesting attempts were divided into four groups: nests where all the young fledged, those where some young fledged, those where the entire brood died, and other. The last group includes nests where one or both members of a pair were evicted from the nest (i.e., turnover), nests that were never used, nests where predation occurred, and those where the nest was abandoned for unknown reasons.

Nestling growth and size.--Nestling size was measured on ND 15 at all nests. At 14 nests ($N_C = 4$, $N_S = 5$, $N_O = 5$) in 1991, and 10 nests ($N_C = 5$ (incl. 3 CI), $N_O = 5$) in 1992, I also measured nestling size on NDs 3, 6, 9, and 12. For these nests, the mass (g) of each nestling was measured on all days, the length (mm) of the ninth primary was measured beginning on ND 9, and flattened wing length (mm) was measured only on ND 15. The measurement of the ninth primary was made from the tip of the outermost primary to where the rachis enters the skin. Each nestling was weighed in a small plastic bag or cardboard tube of known mass using a Pesola® balance (50 g). On ND 15, nestlings were banded with Canadian Wildlife Service aluminum bands. Nestlings were not handled beyond ND 15 to prevent premature fledging.

Feeding rates.--To determine if nestling size and growth rates were the result of different feeding rates at different box-types I recorded the number of feeding trips by males and females during 1/2 h box watches conducted on NDs 3, 9, and 15. These watches were done at the same 24 nestboxes where nestling growth rates were measured. Nestboxes were watched between 0600-1400 h, from 20-75 m away using a stopwatch, 7x50 binoculars and a 15x spotting scope. Each pair was watched at different times each day to control for diurnal variation in insect availability.

Numbers of ectoparasites.--The numbers of ectoparasites in nestboxes were determined by methods described in Chapter 2.

Statistical analysis.--The data were analyzed as described in Chapter 2. All probability values are two-tailed unless otherwise specified.

The data on reproductive success were not combined between years due to the experimental differences, and because several measures of reproductive success and nestling size were significantly different between years. I combined data for all female age classes because there were no significant differences in reproductive success or nestling size between female age classes within box-types and years, and because the female age class distributions did not differ between box-types (1991, Chapter 3; 1992, Chi Square Test, $X^2 = 1.2$, df = 2, $P > 0.05$, Power = 0.50).

Nestling size was compared between box-types using means of the mass, the length of the ninth primary, and the wing length of nestlings on ND 15. To compare growth rates in different boxes, I calculated the means for nestling mass and the length of the ninth primary within broods for the subset of nests sampled throughout the nestling stage. I compared these variables at C, S, and O nestboxes in 1991, and C (incl. 3 CI) and O in 1992, on NDs 3, 6, 9, 12, and 15. All nests were included in this analysis regardless of brood size due to small sample sizes.

Feeding effort by adults was compared between all three box-types in 1991, and C (incl. 3 CI) and O nestboxes in 1992, by comparing the mean number of visits per box, and the mean number of visits per nestling per box, for each watch on ND 3, 9, and 15. Once again, all nests were combined within a box-type regardless of brood size.

RESULTS

Effect of year on reproduction

Nesting phenology.--Median first egg date was not significantly different between years, but median first hatching and median first fledging dates were significantly earlier in 1992 than in 1991 (Table 7). All box-types were combined in this comparison.

Success.--In 1992, median clutch size was smaller than in 1991, and the median number of fledglings fewer, and the median percentage of hatchlings that fledged, and the median percentage of eggs that hatched were lower in 1992

Table 7. Nesting phenology, reproductive success, and nestling size of Tree Swallows in 1991 and 1992 for all box-types combined. Values are means ± SE (N pairs).

	Year	
	1991	1992
First egg date	8 May ± 0.6 (73)	7 May ± 0.6 (105)
First hatching date*	7 June ± 0.6 (66)	4 June ± 0.5 (103)
First fledging date*	27 June ± 0.6 (60)	23 June ± 0.6 (87)
Nestling period (days)	19.9 ± 0.2 (60)	19.6 ± 0.1 (87)
Clutch size*	5.9 ± 0.1 (73)	5.6 ± 0.1 (105)
No. hatchlings	5.4 ± 0.1 (65)	5.3 ± 0.1 (103)
No. fledglings**	4.9 ± 0.2 (63)	3.4 ± 0.2 (103)
% Hatchlings/eggs	92.3 ± 1.6 (65)	93.7 ± 1.2 (103)
% Fledglings/hatchlings**	91.3 ± 3.0 (63)	67.1 ± 3.8 (103)
% Fledglings/eggs**	84.3 ± 3.2 (63)	62.3 ± 3.6 (103)
Nestling mass (g)**	22.2 ± 0.2 (62)	20.6 ± 0.2 (86)
Nestling wing length (mm)**	63.7 ± 0.6 (62)	60.7 ± 0.5 (86)
Nestling ninth primary (mm)**	38.8 ± 0.6 (62)	35.8 ± 0.5 (86)

Medians are significantly different between years, * $P < 0.05$, ** $P < 0.0001$, Wilcoxon-Mann-Whitney Test, two-tailed (SAS 1985, Siegel and Castellan 1988).

than in 1991 for all box-types combined (Table 7). Comparison of these variables for C and O nestboxes, separately, between years, yielded the same results.

Fewer pairs fledged young, and whole broods of more pairs died, in 1992 than in 1991, but the distributions of outcomes of nesting attempts did not differ significantly between years (Table 8). The death of entire broods in 1992 was apparently due to hypo- and hyperthermia. The mean air temperature at C.V.W.M.A. in June 1992 was significantly warmer by 5.7°C than that in June 1991 (Appendix 1). In 1992, 10 of the 16 (62%) instances where whole broods died occurred during 19-27 June, a period of nine consecutive days when the maximum air temperature in the shade exceeded 30°C. On one occasion the temperature in the sunshine was 43°C! During nest checks, nestlings were found panting, a clear sign of heat stress. The remaining deaths in 1992 occurred during a severe rain storm on 13 June when the average daily temperature dropped from 21.5°C to 10°C in one day.

Nestling size.--Median mass was lighter, and wing length and the length of the ninth primary were significantly shorter for nestlings in 1992 than in 1991 for all box-types combined (Table 7). Comparison of these variables within C and O box-types separately, between years, yielded the same results.

Effect of box-type on reproduction

Nesting phenology.--In 1991, nesting phenology was not significantly different between birds using C, S, and O nestboxes (Table 9). In 1992, median first egg date and median first hatching date were significantly different between C, CI, and O nestboxes, but median first fledging date was not. First egg and first hatching dates were earlier for pairs using C nestboxes than for those using CI and O nestboxes, but neither variable was significantly different between pairs using the last two box-types.

Table 8. Outcomes of nesting attempts for Tree Swallows in 1991 and 1992. All box-types are combined within years. Values are percentages of the number of territories for each year. See METHODS for an explanation of the outcome groups.

	Year	
Outcome	1991 (N = 79)	1992 (N = 125)
All young fledged	44.3	30.4
Some young fledged	34.2	39.2
All young died	3.8	12.8
Other	17.7	17.6

Distributions of outcomes are not different between years, Chi Square Test, X^2 = 7.2, df = 3, $P > 0.05$, Power = 0.70.

Table 9. Nesting phenology for pairs of Tree Swallows using different box-types 1991 and 1992. Values are means ± SE in days (N pairs, range in Julian days where 1 June = Julian day 152 in 1991, and 153 in 1992).

Year	Box-type		
1991	Clean	Sham	Old
First egg	20 May ± 0.7 (27, 132-146)	19 May ± 0.8 (23, 130-149)	16 May ± 1.5 (23, 123-151)
First hatching	7 June ± 0.7 (24, 153-164)	7 June ± 0.9 (21, 150-168)	4 June ± 1.4 (21, 144-170)
First fledging	28 June ± 0.6 (22, 175-183)	27 June ± 0.8 (19, 174-188)	25 June ± 1.6 (19, 163-190)
1992	Clean	Clean (Insert)	Old
First** egg	15 May ± 1.0^{a} (37, 123-145)	20 May ± 1.2^{b} (13, 130-145)	18 May ± 0.7^{b} (55, 126-151)
First* hatching	2 June ± 1.0^{a} (36, 141-163)	6 June ± 1.0^{b} (13, 150-162)	4 June ± 0.7^{b} (54, 145-169)
First fledging	21 June ± 1.2 (30, 160-184)	26 June ± 1.1 (12, 169-182)	24 June ± 0.8 (45, 162-190)

* $P < 0.05$, ** $P < 0.01$, otherwise symbols and statistics are the same for those described in Table 6.

The duration of the nestling period did not differ significantly between pairs using any of the box-types in either 1991 (mean ± SE in days (N), C nestboxes = 20.4 ± 0.4 (22), S = 19.6 ± 0.2 (19), O = 19.7 ± 0.2 (19)) or 1992 (C nestboxes = 19.6 ± 0.2 (30), CI = 19.8 ± 0.3 (12), O = 19.5 ± 0.2 (45)).

Success.--Reproductive success was not different for pairs using C, S, and O nestboxes in 1991, or C, CI, and O nestboxes in 1992. Similar proportions of pairs did and did not fledge young between box-types in both years (Table 10). Also, the medians for clutch size, the number of hatchlings, the number of fledglings, the percentage of all eggs that hatched, the percentage of all hatchlings that fledged, and the percentage of all eggs that resulted in fledglings did not differ significantly between pairs using any of the box-types in either year (Table 11, 12). This despite the fact that clutch size was significantly, positively correlated with cavity size in 1991 and 1992 (Fig. 7), and that cavity size was significantly different between box-types each year (1991: Kruskal-Wallis Test, $H = 38.3$, $df = 2$, $P < 0.0001$, mean ± SE (cm^3)(N), C = 1813 ± 49 (28), S = 1381 ± 54 (21), O = 1168 ± 57 (22); 1992: $H = 56.4$, $df = 2$, $P < 0.0001$, C = 1971 ± 47 (37), CI = 1205 ± 40 (13), O = 1431 ± 38 (55)). In both years C nestboxes had significantly more cavity space than the other two box-types. In 1991, cavity size in S nestboxes was significantly larger than in O nestboxes, and in 1992, cavity size was significantly larger in O nestboxes than in CI nestboxes (Multiple Comparsion Method, all $P < 0.05$, Siegel and Castellan 1988).

Nestling size.--Median mass, median wing length, and median length of the ninth primary for nestlings on ND 15 were not significantly different between broods in C, S, and O nestboxes in 1991, and C, CI, and O nestboxes in 1992 (Table 13). Nestling size in C, S, and O nestboxes in 1991 was also compared within broods of five young and within broods of six young between nests, and in 1992, within broods of five young between C, CI, and O nestboxes. There were no significant

Table 10. Outcomes of nesting attempts for pairs of Tree Swallows using different box-types in 1991 and 1992. Values are percentages of the sample size for each box-type, and the sample sizes for each box-type are in brackets. See METHODS for an explanation of the outcome groups.

	1991			1992		
	Clean	Sham	Old	Clean	Clean[a]	Old
Outcome	(28)	(25)	(26)	(49)	(15)	(61)
All young fledged	46.4	44.0	42.3	22.4	33.3	36.1
Some young fledged	35.7	32.0	34.6	38.8	46.7	37.7
All young died	7.1	4.0	0.0	12.2	6.7	14.8
Other	10.7	20.0	23.1	26.5	13.3	11.5

[a] With inserts.

Distributions are not significantly different between box-types within years (1991: Chi Square Test, $X^2 = 0.3$; 1992: $X^2 = 2.3$; df = 2 both years, $P > 0.05$ both years).

Table 11. Clutch size, number of hatchlings, and number of fledglings for pairs of Tree Swallows using different box-types in 1991 and 1992. Values are means ± SE (N pairs, range).

Year	Box-type		
1991	Clean	Sham	Old
Clutch size	6.0 ± 0.2 (27, 4-7)	6.0 ± 0.1 (23, 5-7)	5.8 ± 0.2 (23, 5-8)
No. hatchlings	5.6 ± 0.2 (24, 3-7)	5.5 ± 0.2 (21, 4-7)	5.1 ± 0.3 (20, 3-7)
No. fledglings	4.9 ± 0.4 (24, 0-7)	5.1 ± 0.3 (20, 0-6)	4.7 ± 0.3 (19, 2-7)
1992	Clean	Clean (Insert)	Old
Clutch size	5.8 ± 0.1 (37, 4-7)	5.5 ± 0.2 (13, 5-7)	5.5 ± 0.1 (55, 3-7)
No. hatchlings	5.3 ± 0.2 (36, 2-7)	5.2 ± 0.2 (13, 4-7)	5.3 ± 0.1 (54, 2-7)
No. fledglings	3.4 ± 0.4 (36, 0-7)	4.1 ± 0.5 (13, 0-6)	3.3 ± 0.3 (54, 0-6)

Medians of variables were not different between pairs using different box-types within years, Kruskal-Wallis Tests, one-tailed.

Table 12. Percentages (%) of hatchlings per eggs laid, fledglings per hatchlings, and fledglings per eggs laid for pairs of Tree Swallows using different box-types in 1991 and 1992. Values are means ± SE (N pairs, range).

Year	Box-type		
1991	Clean	Sham	Old
% Hatchlings per eggs	94.2 ± 2.0 (24, 71-100)	92.6 ± 2.2 (21, 67-100)	89.7 ± 4.3 (20, 43-100)
% Fledglings per hatchlings	88.4 ± 5.9 (24, 0-100)	92.6 ± 5.2 (20, 0-100)	93.7 ± 3.9 (19, 33-100)
% Fledglings per eggs	82.9 ± 5.8 (24, 0-100)	86.6 ± 5.2 (20, 0-100)	83.7 ± 5.6 (19, 33-100)
1992	Clean	Clean (Insert)	Old
% Hatchlings per eggs	92.1 ± 2.4 (36, 33-100)	94.6 ± 2.4 (13, 80-100)	94.4 ± 1.5 (54, 50-100)
% Fledglings per hatchlings	66.9 ± 6.5 (36, 0-100)	78.1 ± 9.4 (13, 0-100)	64.6 ± 5.4 (54, 0-100)
% Fledglings per eggs	60.6 ± 6.0 (36, 0-100)	73.8 ± 9.2 (13, 0-100)	60.6 ± 5.1 (54, 0-100)

Medians of variables were not different between pairs using different box-types within years, Kruskal-Wallis Tests, one-tailed.

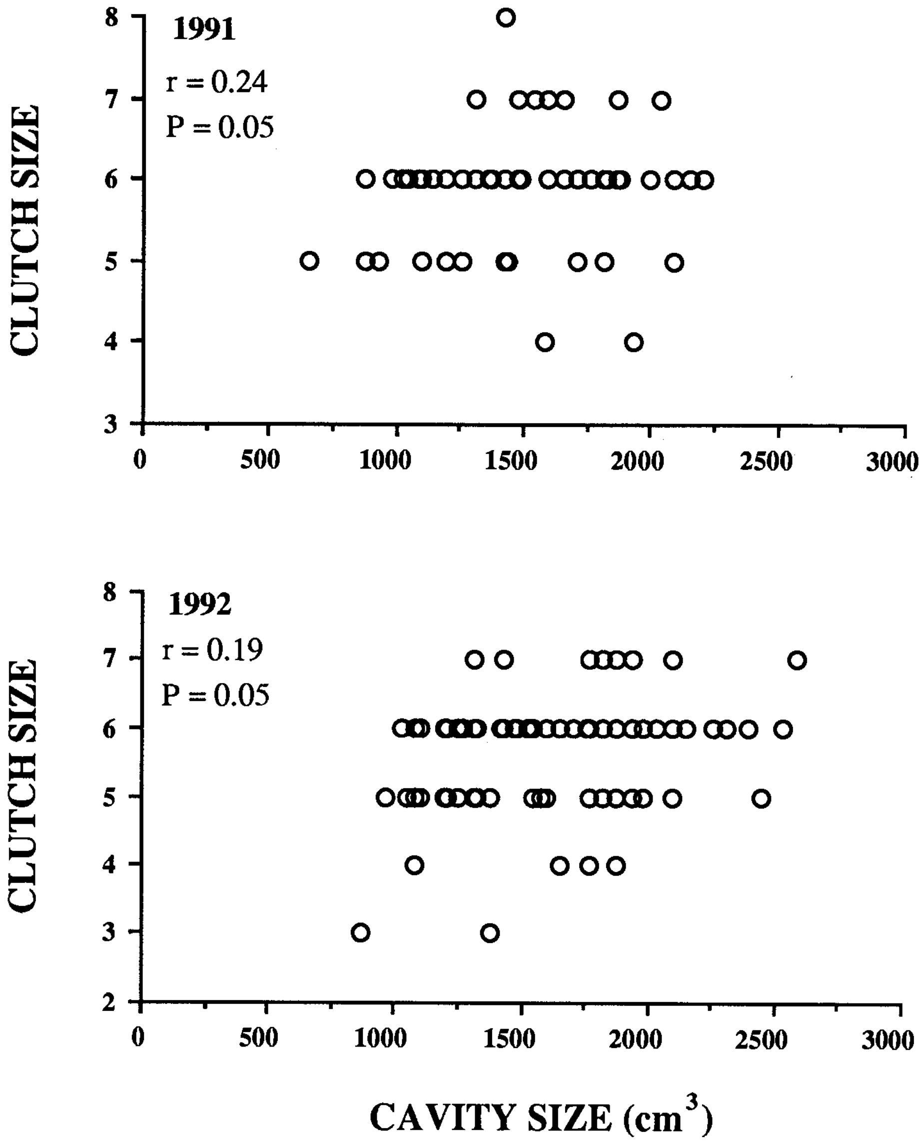

Fig. 7. Plots of clutch size and cavity size. All box-types are combined in 1991 (N = 68) and 1992 (N = 105). r = Spearman rank order correlation coefficient.

Table 13. Mass (g), length of ninth primary (mm), and wing length (mm) for nestlings on ND 15 in different box-types in 1991 and 1992. Values are means ± SE (N broods, range).

Year	Box-type		
1991	Clean	Sham	Old
Mass	22.4 ± 0.4 (23, 17.6-24.9)	22.1 ± 0.2 (20, 19.1-23.4)	22.0 ± 0.3 (19, 17.8-24.1)
Ninth primary	37.7 ± 0.9 (23, 25.5-45.1)	39.9 ± 0.8 (20, 28.4-44.8)	39.1 ± 1.2 (19, 25.2-49.2)
Wing length	62.8 ± 1.1 (23, 47.9-70.1)	64.7 ± 0.8 (20, 53.2-69.9)	63.9 ± 1.3 (19, 50.8-72)
1992	Clean	Clean (Insert)	Old
Mass	20.7 ± 0.4 (31, 17.0-25.3)	20.1 ± 0.5 (11, 16.3-22.5)	20.6 ± 0.3 (44, 16.2-25.2)
Ninth primary	35.8 ± 0.9 (31, 27.0-44.6)	35.1 ± 1.4 (11, 28.8-45.1)	35.9 ± 0.8 (44, 22.7-44.7)
Wing length	60.7 ± 0.9 (31, 51.5-70.2)	60.0 ± 1.4 (11, 53.7-69.4)	60.8 ± 0.7 (44, 44.7-69.8)

Medians of variables were not different between pairs using different box-types within years, Kruskal-Wallis Tests, one-tailed.

differences in median nestling mass, wing length, or the length of the ninth primary within broods of the same size between nestboxes in either year. Tests were not possible for other brood sizes within years because the sample sizes were small.

In 1991, nestlings grew at significantly different rates within broods in C, S, and O boxes between NDs 6 and 12, otherwise growth rates were comparable between broods. Median gain in mass for broods in S nestboxes between NDs 6 and 9 was significantly less than that for broods in C and O nestboxes (Kruskal-Wallis Test, $H = 9.0$, $df = 2$, $P < 0.01$; Multiple Comparison Method, $P < 0.05$, Siegel and Castellan 1988), but was not different between the last two box-types (Fig. 8). Between NDs 9 and 12, the median increase in the length of the ninth primary for broods in C nestboxes was significantly less than that for those in either S or O nestboxes ($H = 9.3$, $df = 2$, $P < 0.01$; Multiple Comparison Method, $P < 0.05$), but the change in median length of the ninth primary did not differ between broods in the last two box-types (Fig. 9). There were no statistical differences between broods in C and O nestboxes for either median gain in nestling mass or median increase in length of the ninth primary between sampling days in 1992 (Fig. 8, 9).

Feeding effort by parents.--Median total number of feeding trips to nests, and the median number of feeding trips per nestling per nest, did not differ between pairs using C, S, and O box-types in 1991, or C and O box-types in 1992, on ND 3, 9, or 15 (Kruskal-Wallis Tests, two-tailed, all $P > 0.05$) (Fig. 10).

Effect of ectoparasites on reproduction

Success.--In 1991 there was a significant negative correlation between the number of fleas per nest (Fig. 11), and the number of fleas per hatchling per nest (Fig. 12), with the duration of the nestling period. This correlation was not observed in 1992 for either measure of number of fleas with the duration of the nestling period (Fig. 11, 12). Also, there were no significant associations between the

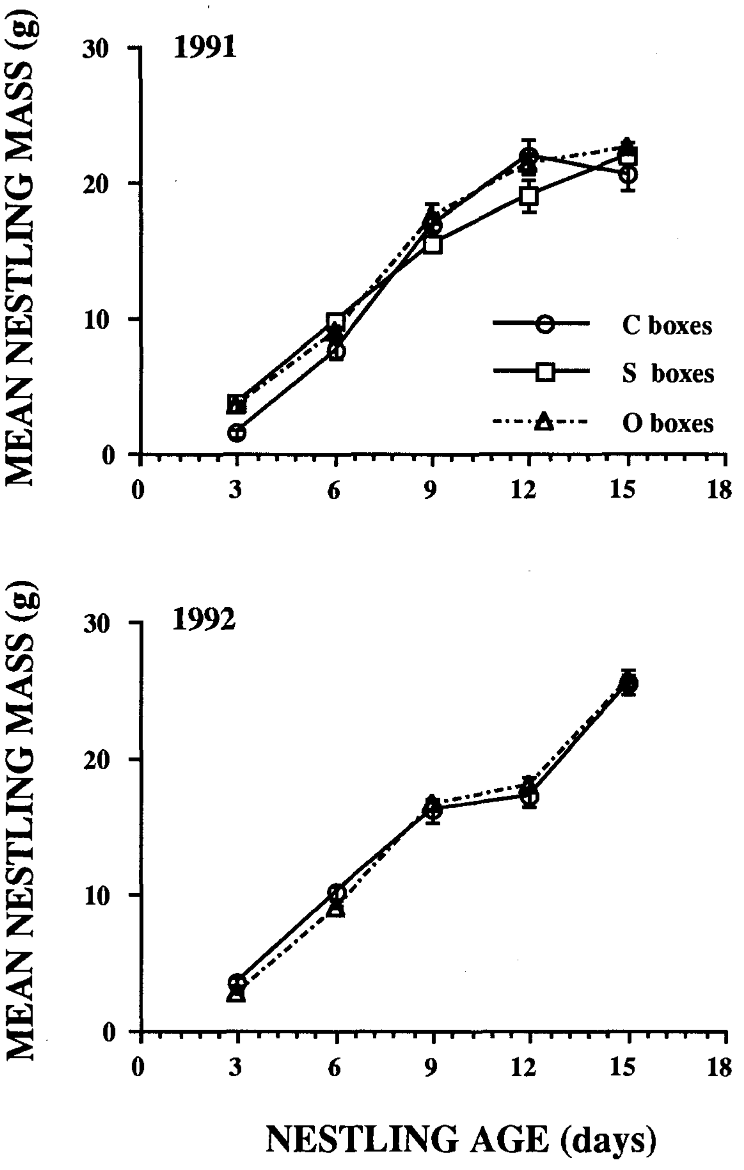

Fig. 8. Plots of mean nestling mass as a function of nestling age at clean (N = 4), sham (N = 5), and old (N = 5) nests in 1991, and clean (N = 5) and old (N = 5) nests in 1992. Bars denote standard error.

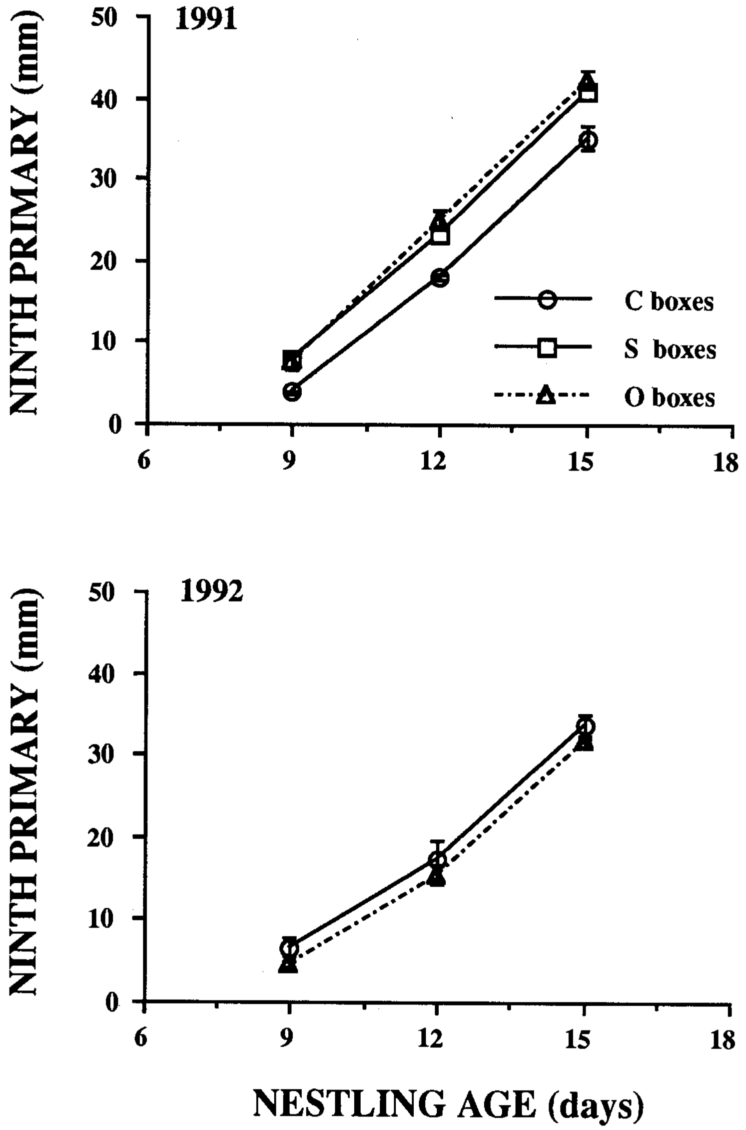

Fig. 9. Plots of mean length of nestling ninth primary as a function of nestling age at clean (N = 4), sham (N = 5), and old (N = 5) nests in 1991, and clean (N = 5) and old (N = 5) nests in 1992. Bars denote standard error.

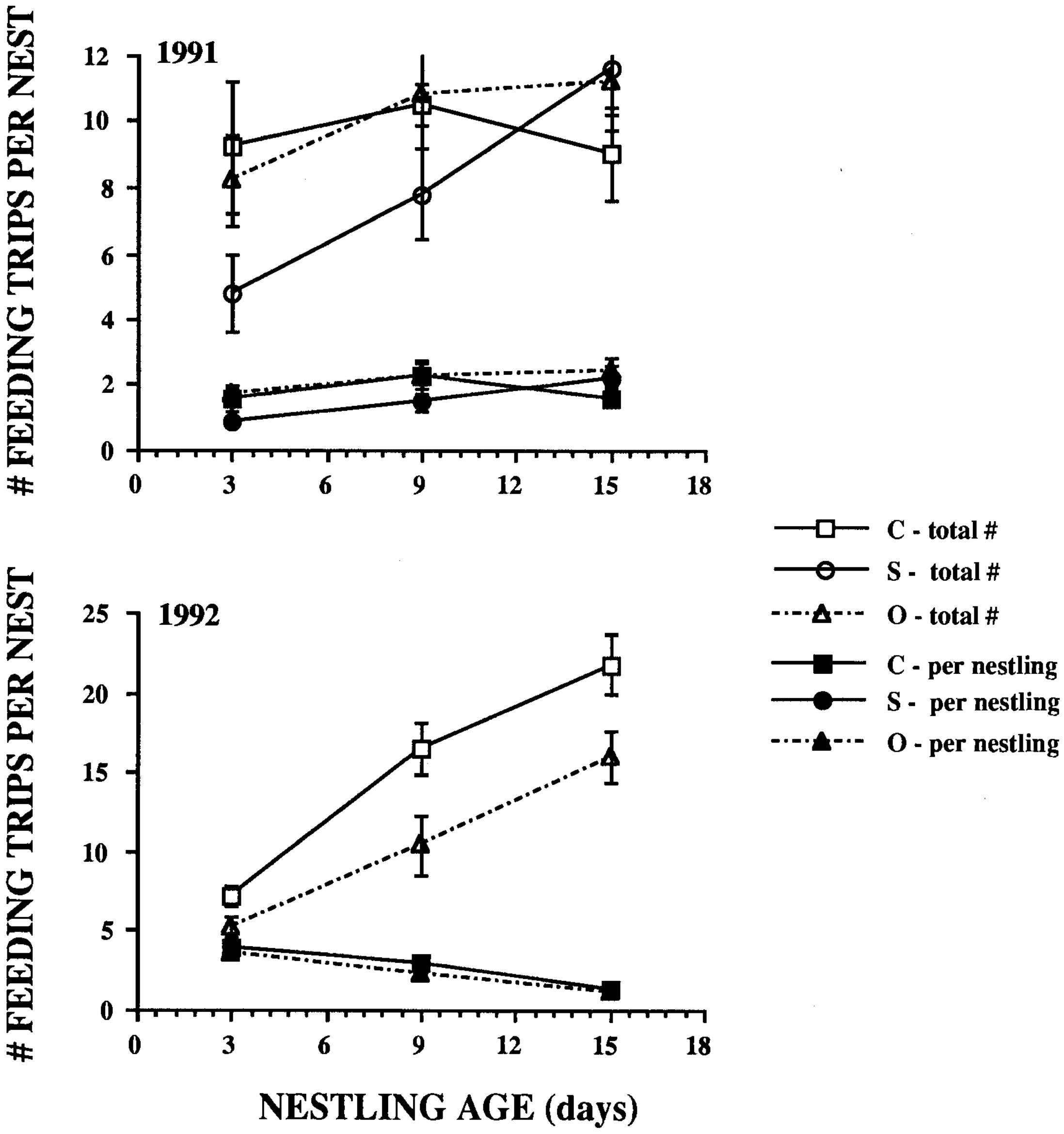

Fig.10. Plot of mean total number of feeding trips per nest, and mean number of feeding trips per nestling per nest, as a function of nestling age at clean (N = 4), sham (N = 5), and old (N = 5) nests in 1991, and clean (N = 5) and old (N = 5) nests in 1992. Bars denote standard error.

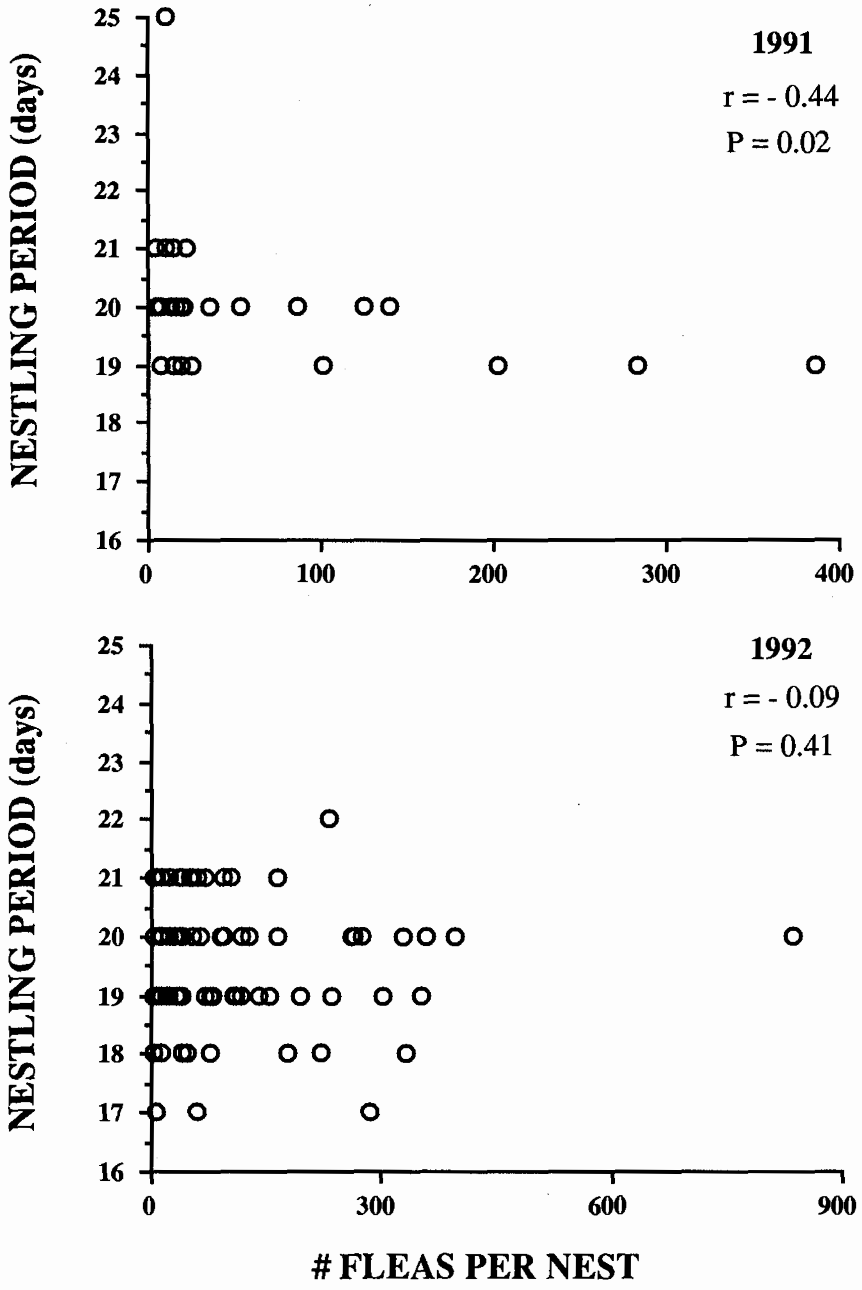

Fig. 11. Plots of the duration of the nestling period and the total number of fleas per nest. All box-types are combined in 1991 (N = 30) and 1992 (N = 87). r = Spearman rank order correlation coefficient.

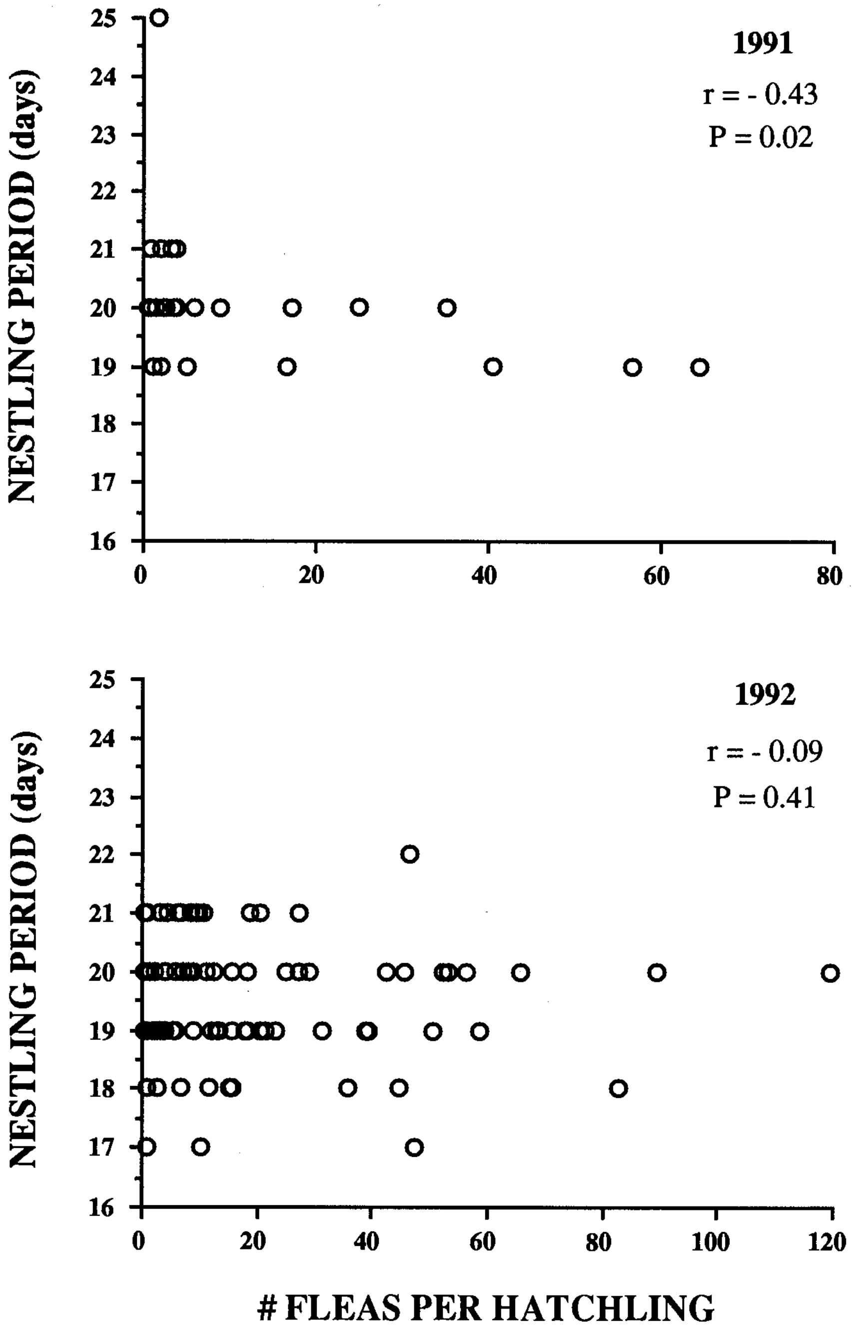

Fig. 12. Plots of the duration of the nestling period and the number of fleas per hatchling per nest. All box-types are combined in 1991 (N = 30) and 1992 (N = 87). r = Spearman rank order correlation coefficient.

number of mites or blow flies per nest, or the number of mites and blow flies per hatchling per nest, with the duration of the nestling period in either year (N_{1991} = 60 nests, N_{1992} = 87 for both mite load variables, N_{1991} = 30, N_{1992} = 87 for both blow fly load variables, Spearman Rank Correlations, all $P > 0.05$).

In 1991, there was a significant negative correlation between clutch size and the mean number of fleas per nest (Spearman Rank Correlation, $r_S = -0.42$, N = 30, P = 0.02). Recognizing that there was also a significant positive association between clutch size and cavity size (Fig. 7), and a negative association between the number of fleas in a nest and cavity size (Chapter 2), I performed partial correlations using these three variables. Under these conditions, clutch size was not significantly negatively correlated with the number of fleas in a nest when controlling for cavity size (Spearman Partial Rank Correlation, $r_S = -0.34$, N = 30, P = 0.07). In 1992 there was no significant association between clutch size and the number of fleas in a nest ($r_S = 0.07$, N = 103, P = 0.46). Also, in both years of the study, there were no significant associations between the numbers of the three types of ectoparasites and the numbers of hatchlings and fledglings, the percentage of eggs laid resulting in hatchlings, the percentage of hatchlings that fledged, or the percentage of eggs that resulted in fledglings.

I compared the numbers of ectoparasites in nests where young fledged with those in which the entire brood died in 1992. All nests were combined. The median numbers of fleas and blow flies per nest, and the median numbers of fleas and blow flies per hatchling per nest, were not different between pairs that fledged young and those that did not (Table 14). Instances where an entire brood died were rare in 1991, so this comparison was only possible using 1992 data (see Table 9), and I compared only numbers of the fleas and blow flies in nests between groups in 1992 because fowl mites were rare in that year (Chapter 2).

Nestling size.--No significant associations were found between the numbers

Table 14. Numbers of fleas and blow flies per nest, and the numbers of fleas and blowflies per hatchling per nest, in nests of Tree Swallows where the young fledged (N = 87) and those where the entire brood died (N = 16), in 1992. Values are means (per nest) ± SE.

	Fledged young	Entire brood loss
No. of fleas	97.6 ± 13.8	76.5 ± 17.8
No. of blow flies	34.7 ± 2.9	32.8 ± 8.9
No. fleas per hatchling	18.6 ± 2.4	12.8 ± 3.2
No. blow flies per hatchling	6.9 ± 0.6	5.4 ± 1.4

Medians were not different between success categories for any variable, Wilcoxon-Mann-Whitney Tests, one-tailed, P > 0.05, Siegel and Castellan 1988).

of fowl mites, fleas, and blow flies, and mean nestling mass, wing length, or the length of the ninth primary on ND 15 in 1991 or 1992 (Spearman Rank Correlations, all $P > 0.05$, 1991: fowl mites, $N = 62$ nests; fleas and blow flies, $N = 30$ nests; 1992: fleas and blow flies, $N = 86$ nests; mites not tested). All box-types were combined in each year.

Feeding effort by parents.--No significant associations were found between the numbers of each of the three types of ectoparasites and the total number of feeding trips, or the number of feeding trips per nestling, on ND 3, 9 or 15 in 1991 or 1992 (Spearman Rank Correlations, all $P > 0.05$, 1991: $N = 14$ nests; 1992: $N = 10$ nests). All box-types were combined in each year.

DISCUSSION

Nest re-use did not affect the breeding success of Tree Swallows within the range of ectoparasite loads and cavity sizes seen in this study, indicating that re-use of cavities is not necessarily a disadvantage to this species. This is despite the fact that the number of fleas was significantly greater in nestboxes with old material (Chapter 2), and that birds using clean nestboxes had the added advantage of a larger cavity on average. All measures of reproductive success and all measured characteristics of nestling size were similar for broods raised in different box-types. The numbers of ectoparasites at nestboxes where the young fledged as compared with those where entire broods died did not indicate that ectoparasites were more numerous at failed nests, and suggests that neither the combined totals of the three ectoparasites in this study, nor each species individually, had a significant, detrimental effect on the reproductive success of Tree Swallows. Some studies have found that a variety of ectoparasites affect the reproductive success of hole-nesters by reducing nestling mass at fledging (European Starling, Fauth *et al.* 1991; Great Tit, Richner *et al.* 1991), nestling growth rate (Tree Swallow, Capreol 1983, Winkler

1992), and nestling survival (Capreol 1983, Richner *et al.* 1991), and by lowering blood haemoglobin in nestlings (European Starling, Clark and Mason 1988, Richner *et al.* 1991). Yet other studies have shown that fleas, blow flies, and fowl mites have little or no significant effect on the reproductive success of hole-nesters (Tree Swallows, Burtt *et al.* 1991, Rogers *et al.* 1991, Roby *et al.* 1992, this study; Eastern Bluebird, Burtt *et al.* 1991, Roby *et al.* 1992, Wittmann and Beason 1992; Western Bluebird, *Sialia mexicanus*, Demas 1989; Mountain and Chestnut-backed Chickadees, *Parus gambeli* and *P. rufescens*, Gold and Dahlsten 1983; House Wren, Eastman *et al.* 1989, Johnson *et al.* 1991, Johnson and Albrecht 1993; European Starling, Christe and Richner 1991, Clark 1991). Møller (1989, 1992; see also Lindén and Møller 1989), in his critiques of nestbox studies, hypothesized that birds re-using old nests have lower reproductive success, but to date, the evidence in support of this hypothesis is equivocal.

The reason that many studies of hole-nesting birds have concluded that ectoparasites have little effect on nesting success could be because hole-nesting species may not have enough ectoparasites to stress the young when compared with high numbers of ectoparasites found at colonies of other passerines (e.g., Brown and Brown 1986, Loye and Carroll 1991). The numbers of ectoparasites in tree cavities may be restricted by their predators (Burtt *et al.* 1991) and parasitoids (Jones and Turner 1987, Gold and Dahlsten 1989). The numbers of ectoparasites may also be restricted by density-dependent relations such as limited volume of nest material (Whitworth 1976, Pinkowski 1977, Gold and Dahlsten 1989, this study Chapter 2; but see Burtt *et al.* 1991, Rogers *et al.* 1991), host availability, and the number of intra- and interspecific ectoparasites competing for hosts (Burtt *et al.* 1991, Roby *et al.* 1992). Furthermore, tree cavities may undergo significant changes in microhabitat conditions that ectoparasites cannot tolerate. Whereas the nests of Barn Swallows and Cliff Swallows are usually sheltered from the weather, natural nest cavities can fill with rain and snow (pers. obs.).

Clark (1991) estimated that Northern fowl mites took 20-90% of the blood volume per nestling from European Starlings, Roby *et al.* (1992) estimated that the blow fly *Protocalliphora sialia* took 13-28% of the total blood volume from Tree Swallows and Eastern Bluebirds, and Johnson and Albrecht (1993) reported that the blow fly *P. parorum* consumed 10-30 g of nestling blood per House Wren brood during the nestling period. However, in all three studies, the ectoparasites in question had little effect on survival, so presumably the parents compensated in some way for this energy stress. Mason (1944) and Johnson and Albrecht (1993) suggested that parents could increase their feeding effort to make up for the cost of ectoparasites feeding on nestlings. Feeding effort could be increased by increasing the feeding rate, or by maintaining the same rate for longer (Shields and Crook 1987, Winkler 1992, but see Møller 1990, Chapman and George 1991, Loye and Carroll 1991, Roby *et al.* 1992). Other studies of Tree Swallows have shown (e.g., Leffelaar and Robertson 1986), or suggested (e.g., Wiggins 1990), that this species can increase feeding effort for short periods of time. My results generally do not support Mason's (1944) and Johnson and Albrecht's (1993) hypotheses, but admittedly the sample sizes are small. Parents at box-types with and without old nests did not differ in the number of feeding trips made to nests. Rogers *et al.* (1991) found no difference in feeding effort between parent Tree Swallows raising young in parasitized and unparasitized nests. The duration of the nestling period was not different between pairs at different box-types, but I found a significant negative correlation between the number of fleas in a nest and the length of the nestling period at 30 nests in 1991, so this result is equivocal. If parents determine how fast to feed on the basis of the health and condition of the young it is possible that the parents in this study did not perceive a need to increase their feeding effort. For the most part, nestling size was not different, and although there were two periods during the nestling cycle in 1991 when the growth rates of young differed, it is not clear that this was due to the effects of parasitism. In fact, the slower growth rates were observed in broods at relatively clean nestboxes (i.e., C and S nestboxes).

Annual differences in the weather affected fledging success and possibly nestling size of Tree Swallows. Instances of entire brood death were rare in 1991, but common in 1992, and apparently due to hypo- and hyperthermia. Possibly the weather and ectoparasites had a synergistic effect on success in Tree Swallows. Many factors affect reproductive success and nestling growth and the cumulative effect of several factors may reduce breeding success in some instances. The combination of significantly more fleas at box-types and higher temperatures in 1992 than in 1991 may have caused the observed differences between years in reproductive success and nestling size, but I caution that this is merely an association and only circumstantial evidence for causation. Moss and Camin (1970) showed that the growth of Purple Martin (*Progne subis*) nestlings at parasitized and unparasitized nests was not different, except under poor weather conditions.

Like Ludescher (1973), Löhrl (1973, 1980), Karlsson and Nilsson (1977), van Balen (1984), Gustafsson and Nilsson (1985), and Rendell and Robertson (1989, 1990, 1993), I found a significant association between clutch size and cavity size, but this did not result in a larger mean clutches for birds in nestboxes with larger cavities (typically C nestboxes). This is likely because the range of cavity sizes in nestboxes in this study were not as great as those in the experimental studies mentioned above (e.g., Rendell and Robertson 1993). Although the effect of cavity size on clutch size is clear, no empirical studies in the wild have shown conclusively that cavity size ultimately reduces brood size and reproductive output in hole-nesting birds.

Conclusions.--Nest re-use evidently did not affect the reproductive success of Tree Swallows in this study, contrary to my hypotheses and Møller (1989, 1992; see also Lindén and Møller 1989). My measurements of reproductive output and nestling size are rough measures of success, and they do not necessarily indicate the likelihood of post-fledging survival, nor recruitment of offspring to the breeding population in subsequent years. Parasitized nestlings in other studies were morphometrically similar to relatively unparasitized young, but some studies showed that the parasitized nestlings sufferred from anaemia (Clark 1991, Richner *et al.* 1991, but see Johnson and Albrecht 1993). Anaemic young must not only replace lost blood, but they also experience an oxygen debt because of low haemoglobin which may have serious consequences for post-fledging survival when they are learning how to fly and forage (Clark 1991). Also, parasitized young may be more likely to contract viral protist and bacterial infections from ectoparasites than unparasitized young (Mason 1944, Duffy 1991, Rogers *et al.* 1991), again with unknown consequences for their survival after fledging. Finally, the approximate power of many of the statistical tests in this study was low, meaning that actual differences in success between broods in different box-types may exist, but were undetectable due to small sample sizes, or small effect sizes (Cohen 1977).

CHAPTER 5

GENERAL CONCLUSIONS

Møller (1989, 1992) noted that researchers typically remove old nest material from nestboxes after each breeding season, and he hypothesized that this introduces an experimental artefact to nestbox studies that calls the validity of results from all such studies into question. He claimed that by removing old nest material from nestboxes researchers reduce the numbers of haematophagous ectoparasites in these nest-sites, and he stated that ectoparasites could have a significant effect on cavity selection, reproductive success, and nestling growth in hole-nesters. Møller concluded that researchers should interpret the results of such studies with caution, and that generalizations should not be applied from studies of birds breeding in nestboxes to those using natural tree holes, or even other species, until ecologists have a better appreciation of the possible costs to hole-nesters associated with breeding in cavities where ectoparasites are numerous.

Møller's critiques have stimulated much recent research and comment on the effects of ectoparasites on the breeding biology and behaviour of hole-nesters, and my study and those of others show that Møller's criticisms are partly justified. Ironically, however, his criticisms are themselves generalizations, and are too broad. He is correct that ectoparasites may be more numerous in cavities with old material, but this applies only to particular kinds of ectoparasites (e.g., fleas). Many factors contribute to the presence and numbers of ectoparasites in nests, including the life-cycle of each species, so the accumulation of old material in a cavity does not necessarily mean that ectoparasites will be common as well. The presence of old material in cavities can affect cavity selection and nest building in hole-nesters (e.g., Tree Swallows), but not all species (e.g., House Wrens). Further, some studies have found that ectoparasites affect the reproductive success and nestling health of hole-nesters, but many other studies have shown that ectoparasites may have little or no significant effect on either of these parameters for these species. At best, the combined results from studies of the effects of ectoparasites on the breeding ecology of hole-nesting birds, and other species for that matter, are equivocal, and there is little opportunity for any generalization from one study to another (Koenig *et al.* 1992).

I do not agree that ecologists should question the validity of all of the previous research conducted in nestbox habitats. Reinterpretation of nestbox studies would be inappropriate in some cases because many nestbox studies were experimental during which the removal of old nests from nestboxes was completely justified for the sake of controlling for factors that may confound experimental results (cf. Møller 1989). Reinterpretation of the results from many long-term studies of life-history may be impractical or impossible due to the unpredictable nature of ectoparasitism and its possible effect on hole-nesting birds. In conclusion, I recommend two avenues of future research by which ecologists could assess the frequency, severity, and costs of ectoparasitism on the breeding ecology of hole-nesting birds. First, although complicated and logistically difficult, simultaneous long-term studies of hole-nesting birds and the ectoparasites in their cavities may contribute to our knowledge of how the numbers of ectoparasites in nests change over time, and how regularly they affect the breeding success of their hosts. Second, to complement such studies, ecologists should develop qualitative and quantitative models of lifetime reproductive success which include parameters estimating the frequency of ectoparasitism and its range of effects on survival and reproductive output in hole-nesting birds.

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Appendix 1. Mean monthly temperature (°C) during August 1990-June 1991, and August 1991-June 1992.

Month	Year	mean ± SE	Year	mean ± SE
August	1990	19.8 ± 0.6	1991	19.9 ± 0.4
September*	1990	16.6 ± 0.3	1991	15.2 ± 0.4
October	1990	6.8 ± 0.5	1991	7.2 ± 1.0
November*	1990	3.4 ± 0.6	1991	1.1 ± 0.7
December*	1990	-6.7 ± 1.4	1991	-1.2 ± 0.6
January*	1991	-4.7 ± 0.9	1992	-0.2 ± 0.5
February	1991	2.9 ± 0.4	1992	2.5 ± 0.4
March*	1991	2.6 ± 0.7	1992	6.5 ± 0.3
April	1991	8.3 ± 0.5	1992	9.3 ± 0.6
May*	1991	12.2 ± 0.4	1992	13.7 ± 0.6
June*	1991	14.7 ± 0.4	1992	19.4 ± 0.8

* Median temperature for a month is significantly different between years, $P < 0.05$, Wilcoxon-Mann-Whitney Tests, two-tailed (SAS 1985).