Bird–Parasite Interactions

ECOLOGY, EVOLUTION, AND BEHAVIOUR

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6 Occurrence and demography of mites of tree swallow, house wren, and eastern bluebird nests

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Introduction

Debate over the evolutionary determinants of avian clutch size has ignored the potential of nest-dwelling, parasitic arthropods to significantly reduce the reproductive success of birds (McKilligan 1987; this volume: Delannoy and Cruz, Chapter 5; Rogers *et al.*, Chapter 7). Parasitic mites (Arthropoda, Arachnida, Acari) occur in bird nests (Hicks 1953, 1959, 1971, 1975; Wilson 1965; Philips and Dindal 1977, 1979; Welch 1977), especially nests sheltered from weather and nests built in cavities (Woodroffe 1953; Moss 1978; Chow *et al.* 1983). Such mites are known to feed on blood, which causes weight loss and mortality of nestlings (Moss and Camin 1970) and may cause desertion of whole broods (Moss 1966).

Little is known about the host–parasite relationship, which can be viewed as a reproductive race between the avian host and its parasitic mite: the bird to hatch and rear the maximum number of young to the optimum weight for postfledging survival and the parasitic mite to efficiently use a temporarily abundant food supply, provided by the nestlings' blood, to raise the maximum number of offspring before the resource fledges. The distribution of nidicolous mites among species of birds is imperfectly known from studies that indicate presence (e.g. Moss 1978), but provide little or no indication of abundance or interaction with other species of nest-dwelling arthropods. The demography of such mites is known only from laboratory studies (e.g. Hastings and Wollkind 1982) and a single study (Phillis 1972) of the population dynamics of *Dermanyssus* spp. in the nests of house sparrows (*Passer domesticus*). Such information is critical to assessing the potential importance of parasitic mites or insects as selection agents in the evolution of clutch size and parental (in this volume: Clark, Chapter 11; Loye and Carroll, Chapter 12; Møller, Chapter 17) and social (Emlen 1986; Shields and Crook 1987) behaviour.

The purpose of this study was to document the distribution of nidicolous mites in three common, cavity-nesting birds: the eastern bluebird (*Sialia sialis*); tree swallow (*Tachycineta bicolor*); and house wren (*Troglodytes aedon*). Further, we sought to evaluate the environmental factors affecting the occurrence and abundance of mites and influencing their demographics. Finally, we looked at possible effects on the reproductive success of the birds.

Methods

Occurrence and distribution

In 1977 16 wooden bluebird houses were placed in Delaware State Park, Delaware County, Ohio. The number of houses was increased subsequently, with 93 available in 1980. Nest boxes were checked every third day during nest construction and incubation and every other day from hatching through departure of the young from the nest. The reproductive status of the occupants was recorded at each check. Eastern bluebirds, tree swallows, and house wrens were the most common occupants (Tuttle 1987), with occasional occupancy by Carolina chickadees (*Parus carolinensis*) and tufted titmice (*P. bicolor*).

In the summer of 1980, we collected invertebrates from 13 eastern bluebird nests, 18 tree swallow nests, and 61 house wren nests taken from the next boxes. The nest was removed intact from its box within 24 h after the young departed. It was tagged, sealed in a plastic bag, and transported to the laboratory where it was placed in a Berlese funnel or, if all funnels were in use, placed in a refrigerator until a funnel was available. All nests were placed in funnels not more than 48 h after removal from the nest box.

The Berlese funnels were of galvanized steel and had a diameter (23.2 cm) and depth (27.9 cm) that accommodated the largest nests without distorting their shape. Before a nest was placed in the funnel, a jar containing a 5 per cent formaldehyde solution was placed beneath the funnel so that the spout of the funnel projected 2–3 cm into the jar without touching any part of the jar or the formaldehyde solution. The funnel was lined with a single layer of cheesecloth to prevent debris from falling into the jar. The nest was removed from the plastic bag, placed on the cheesecloth, and any loose material remaining in the bag was shaken onto the nest. With the nest in place the top of the funnel was closed. The top contained a 60-watt light bulb that heated and dried the nest thereby driving invertebrates down through the nest and into the funnel where they slid into the jar of formaldehyde. Once a day the nest in its cheesecloth was lifted from the funnel and anything clinging to the cloth

was gently brushed into the metal funnel. After 72 h the jar was sealed and the nest was put in a paper bag and frozen. Nests and jars received a code number, but were not labelled with information on the species of bird or its reproductive success. Thus we hoped to avoid biasing our identification and counting of invertebrates.

The volume of the nest was measured by placing the nest in an empty aquarium and pressing it gently into a corner. The height, width, and depth of the nest were measured against the glass sides of the aquarium. Construction materials and the amount of residual faecal material were described briefly.

A sample of mites from each jar was mounted on glass slides and identified as to family under a compound microscope using keys available in Krantz (1978) and McDaniel (1979). Representative specimens were sent to D. E. Johnston at the Acarology Laboratory, Ohio State University for species identification. Following species identification, the contents of each jar were sorted and counted under a dissecting microscope. Insects and spiders were identified as to family using Borror et al. (1976).

Demography

In 1983 20 wooden bluebird houses were placed in Alum Creek State Park, Delaware County, Ohio. By 1987 the number of bluebird houses in the park was 46. In that summer we studied the population dynamics of mites inhabiting tree swallow nests in Alum Creek State Park. Tree swallows were the most numerous species nesting in bird houses in the park (Tuttle 1987). To study the growth dynamics of mite populations in swallow nests, we divided our sample around six collection times within the swallow's reproductive cycle. Nests were collected at 10 days after the last egg was laid, at hatching, 5, 10, or 15 days after hatching, or within 24 h of the nestlings' departure from the nest. Nest boxes were checked every third day until laying began and every other day during laying to determine the day on which the last egg was laid. When the clutch was complete, the nest was assigned a collection time within the reproductive cycle (only the original nest of each pair of swallows was collected). Assignments were random, except that no time was assigned a second nest until all had received one nest, no time was assigned a third until all had two, and so on.

At the time of collection the side of the box was removed, the nest lifted out, the eggs or nestlings placed in a handmade replacement nest, the replacement put in the box, and the box closed. The real nest was sealed in a plastic bag. A few feathers were included in the replacement nest, but as we withdrew from the area, we threw several white feathers

into the air. The swallows immediately caught these and, usually within five minutes, carried the feathers into the nest box. The use of feathers combined with our practice of delaying the first exchange until late in incubation (Burtt and Tuttle 1983) resulted in all swallows accepting the nest exchange.

Arthropods were extracted from the nests as explained above. Few arthropods other than mites were found in these nests and these were not identified or counted.

Statistics

The Spearman rank correlation coefficient (Sokal and Rohlf 1981) was used to evaluate the relationship of mite populations to each other, other arthropod populations, and avian brood size. Regression lines were compared using the small-sample t-test for parallelism (Kleinbaum and Kupper 1978). Because many correlations and comparisons were calculated, alpha was set at 0.01 to reduce the possibility of a type two error. The rate of population growth was estimated from the equation

$$dN/dt = rN. \qquad (6.1)$$

Average population sizes were compared using t-tests (Sokal and Rohlf 1981). Expected proportions of mite species in the nests of each avian species were calculated by assuming that the proportion of each mite species in the nests of each avian species was the same as the proportion of each species of mite in the total population of mites. Chi-square (Sokal and Rohlf 1981) was used to compare expected and observed proportions of mite species. For these few comparisons alpha was set at 0.05.

Results and discussion

Occurrence and distribution

Dermanyssus hirundinis (Fig. 6.1(a)) occurred in all nests of all three avian species (Table 6.1). It has an oval body, long legs, and emerges from the nest material to feed on the blood of nestlings (Moss 1978). *D. hirundinis* may injure nestlings by frequent piercing of the skin, by triggering allergic reactions in the nestlings, by transmitting diseases among nestlings and across generations, or by blood loss (Moss 1966; Krantz 1978). After each feeding the mite returns to the nest material where the female lays about 20 eggs. Most *D. hirundinis, D. americanus,* and *D. prognephilus* emigrate from the nest soon after the nestlings depart, although a few females and nymphs remain behind to overwinter in the nest material (Moss 1966; Phillis 1972).
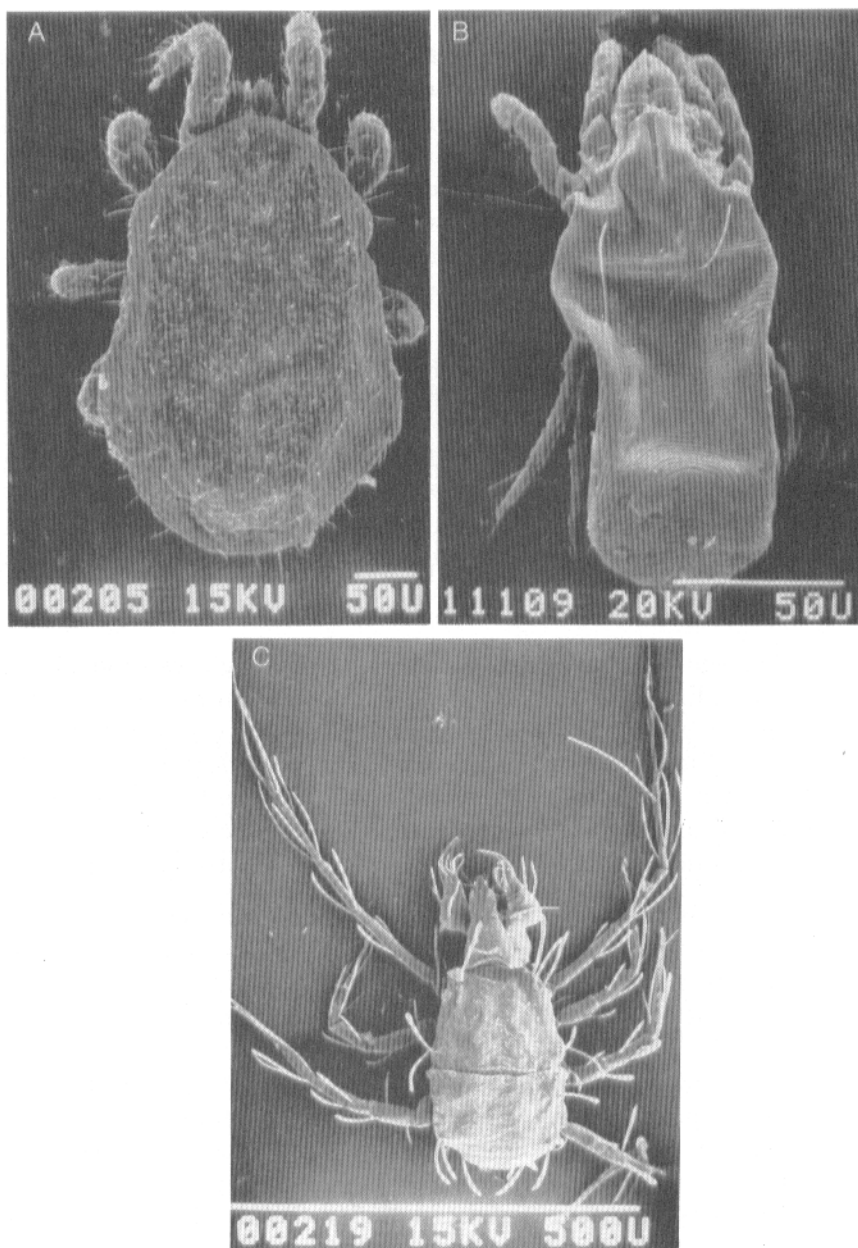
Fig. 6.1. (A) The parasitic mite *Dermanyssus hirundinis;* (B) the scavenging mite *Dermatophagoides evansi;* and (C) the predatory mite *Cheletomorpha lepidopterorum.*

Table 6.1. Mean number of mites/nest ± standard error (range in parentheses)

Avian host species	n (number of nests)	Mites		
		Dermanyssus	Dermatophagoides	Cheletomorpha (in nests where occurred)
Tree swallow	18	9745 ± 978 (1881–16579)	5908 ± 573 (1386–9332)	1206 ± 197 (396–1829)
House wren	61	12675 ± 676 (844–20819)	6714 ± 404 (393–12354)	2622 ± 212 (218–4240)
Eastern bluebird	13	5384 ± 568 (934–8271)	1763 ± 192 (311–3216)	0

Next to *D. gallinae*, which has been found in the nests of 30 species of birds, *D. hirundinis* is the most widespread species of the genus, occurring in the nests of 14 species (Moss *et al.* 1970; Moss 1978). The tree swallow and house wren are among its known hosts, but this is its first known association with the eastern bluebird as reported by Chow *et al.* (1983). *D. hirundinis* may have colonized bluebird nests by overwintering in a box formerly occupied by a swallow or wren and subsequently occupied by a bluebird. However, the number of *D. hirundinis* inhabiting bluebird nests (Table 6.1) suggests that bluebirds are an acceptable host species.

Dermatophagoides evansi (Fig. 6.1(b)) occurred in all nests of all three species of birds (Table 6.1). It was less numerous than *Dermanyssus hirundinis*, but like *Dermanyssus* was most common in nests of the house wren. *Dermatophagoides evansi* belongs to a genus of free-living mites that feed on organic debris and are a common component of house dust where they contribute to human dust allergies (Wharton 1976; Arlian *et al.* 1983). Members of the genus occur on skin, fur, and feathers of mammals and birds and in their nests (Krantz 1978).

Cheletomorpha lepidopterorum (Fig. 6.1(c)), the third species found in our study, belongs to the family Cheyletidae. It has been found in tree bark, organic debris, soil, grain storage, and in association with the *Proxenus* (Noctuidae) moth (Beer and Dailey 1956; Summers and Price 1970; Krantz 1978). *C. lepidopterorum* is a predator capable of capturing and consuming four grain mites per day at 20°C and 80 per cent relative humidity (Krantz 1978). It is known to feed on mites in the families Pyroglyphidae, which includes *Dermatophagoides evansi*, and Laelaptidae, which includes *Dermanyssus hirundinis* (Beer and Dailey 1956).

C. lepidopterorum was the least numerous of the three species of mites (Table 6.1), occurring in 0 of 13 bluebird nests, 6 of 18 (33 per cent) swallow nests, and 30 of 61 (49 per cent) wren nests. In nests colonized
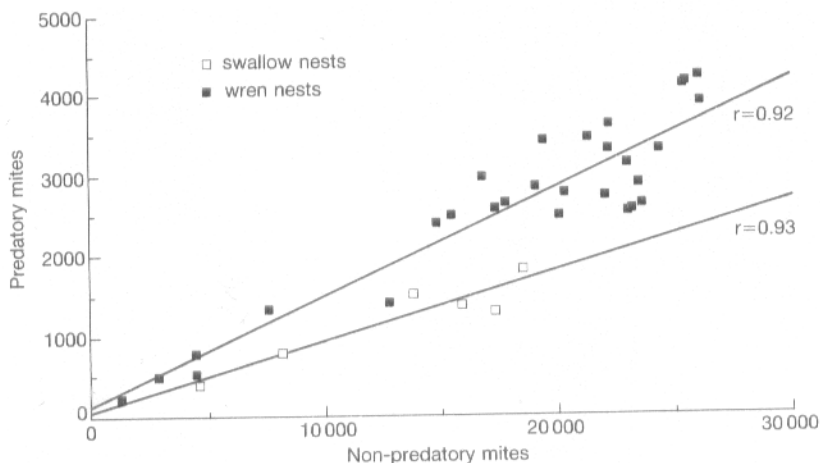
Fig. 6.2. Predatory mites (*Cheletomorpha lepidopterorum*) as a function of the population of non-predatory mites in nests colonized by *Cheletomorpha*. Both populations of mites were counted at fledging of the nestlings.

Fig. 6.3. The proportion of parasitic, scavenging, and predatory mites in nests of swallows, wrens, and bluebirds at the time the nestlings fledged.

by *Cheletomorpha*, its population increased in proportion to the number of non-predatory mites (Fig. 6.2), but always remained the smallest of the three populations of mites (Fig. 6.3). *Cheletomorpha* had little effect on populations of non-predatory mites in tree swallow nests (mean population without *Cheletomorpha*, 16 974; mean population with *Cheletomorpha*, 13 010; $t = 1.29$, $df = 16$, $p > 0.5$) and house wren nests (mean population without *Cheletomorpha*, 20 454; mean population

Table 6.2. Direction of deviation of the observed population of mites from the expected population

Avian host species	Mites		
	Dermanyssus	*Dermatophagoides*	*Cheletomorpha*
Tree swallow	−	+ +	−
House wren	−	−	+ +
Eastern bluebird	+ +	−	−

+ +, 10 000 or more mites than expected; −, 3500–9999 fewer mites than expected where 'expected' is the product of the total number of mites for that bird species and the total number of that species of mite in all nests divided by the total number of mites.

with *Cheletomorpha,* 18 287; $t = 0.31$, $df = 59$, $p > 0.7$). Similar prey availability in nests with and without *Cheletomorpha* suggests that food was not a limiting factor in its distribution, except possibly in the case of bluebirds.

As suggested by the patchy distribution of *Cheletomorpha lepidopterorum,* the number of mites and the relative proportion of each species in the total population depends on the avian host species (Fig. 6.3; $\chi^2 = 17\,590$, $df = 4$, $p < 0.001$). Eastern bluebirds had the fewest mites (Table 6.1) and the highest proportion of *Dermanyssus hirundinis* (Table 6.2, Fig. 6.3), which may have contributed to the failure of *Cheletomorpha* to colonize bluebird nests. *Cheletomorpha* is a 'sit and wait' predator dependent on the movement of its prey, but *Dermanyssus* tends to aggregate low in the nest and remain quiescent between feedings (Davis and Camin 1972). Thus the prey population in bluebird nests is relatively small and inactive and may be less available than prey populations in swallow and wren nests. Tree swallow nests had intermediate numbers of mites (Table 6.1) with a disproportionate number of *Dermatophagoides evansi* (Table 6.2, Fig. 6.3). House wren nests had the most mites (Table 6.1) including a disproportionate number of predators (Table 6.2, Fig. 6.3), which supports the suggestion that prey availability may be the limiting factor in colonization of bluebird nests by *Cheletomorpha*. However, there is no obvious reason why 31 house wren nests with abundant prey and 12 tree swallow nest also with abundant prey contained no predatory mites.

Ecological factors

Distribution of the three species of mites varies with the avian host species. Some of the variation (e.g. the distribution of *C. lepidopterorum*) could derive from interactions among the species of mites, but factors that vary within and among the host species (e.g. distance
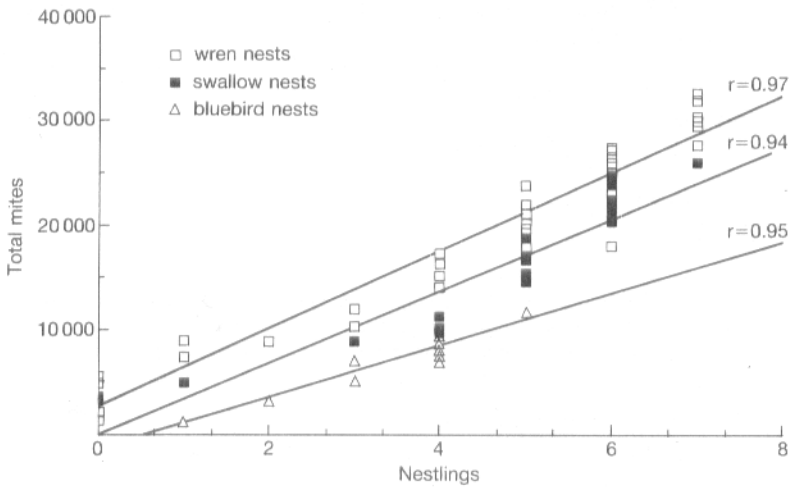
Fig. 6.4. Total population of mites at the time of fledging as a function of the number of nestlings in swallow, wren, and bluebird nests.

between conspecific nests, tendency of avian species to reoccupy nest cavity in subsequent years) may be important determinants of mite populations.

Nestlings per nest

The number of nestlings per nest varied from zero to five in bluebirds and up to seven in tree swallows and house wrens. The combined populations of mites are correlated significantly with the number of nestlings per nest in all three host species (Fig. 6.4). For eastern bluebirds the regression is given by the equation

$$M = 2440\ N - 1297 \tag{6.2}$$

where M is the total number of mites and N is the number of nestlings. The regression for tree swallows is

$$M = 3413\ N + 131 \tag{6.3}$$

and, for house wrens,

$$M = 3694\ N - 2814. \tag{6.4}$$

The slopes are significantly different from each other (small sample t-test for parallelism, wren to swallow: $t = 3375$, $df = 75$, $p < <0.001$; wren to bluebird: $t = 6285$, $df = 70$, $p < <0.001$, swallow to bluebird: $t = 4511$, $df = 27$, $p < <0.001$). As brood size increases, the mite population increases least rapidly in bluebird nests, more rapidly in swallow nests, and most rapidly in wren nests. The increase in mites with increasing

Table 6.3. Correlation coefficients between the number of nestlings and the number of mites for each host species and each species of mite

Avian host species	Mite			
	Dermanyssus	*Dermatophagoides*	*Cheletomorpha*	Total
Tree swallows	0.92	0.92	0.05* 0.93†	0.94
House wrens	0.95	0.82	0.37* 0.92†	097
Eastern bluebird	0.93	0.96	—	0.95

* Based on all nests.
† Based only on nests with *Cheletomorpha*.

numbers of nestlings is rapid, but linear. Thus more nestlings mean more mites, but the number of mites per nestling remains roughly constant.

Taking the species of mites separately, populations of *Dermanyssus hirundinis,* the parasitic mite, are correlated significantly and positively with the number of nestlings per nest (Table 6.3) as are populations of *Dermatophagoides evansi,* the scavenging mite (Table 6.3). Populations of *Cheletomorpha lepidopterorum* are correlated poorly with the number of nestlings per nest (Table 6.3) unless populations of zero are removed from the sample. Thus populations of parasitic and scavenging mites correlate closely with the number of nestlings per nest (Table 6.3), whereas populations of predatory mites correlate closely with the number of nestlings per nest (Table 6.3) and populations of the other mites (Fig. 6.2) when colonization of the nest occurs. Colonization of nests is a limiting factor in the distribution of *Cheletomorpha lepidopterorum.*

Other arthropods

Other arthropods are potential prey, predators, and competitors. In addition to mites, species in one family of spiders and 11 families of insects occurred in the nests of swallows, wrens, and bluebirds. Jumping spiders (Arachnida, Araneae, Salticidae) are small (2–4 mm), predatory spiders that ambush small arthropodan prey. Jumping spiders occurred in most nests and averaged about four per nest in bluebird, swallow, and wren nests. Book lice (Psocoptera, Liposcelidae), which are scavengers, were patchily distributed, but averaged about two per nest. Gall midges (Diptera, Cedidomyiidae), march flies (Diptera, Bibionidae), and fungus gnats (Diptera, Mycetophilidae) all feed on decaying vegetation. All three families occurred in most nests with three to four of each family per nest. Blowflies (Diptera, Calliphoridae, *Protocalliphora* sp.) feed on

living flesh and can be serious parasites of nestling birds (Roberts 1981). They occurred in a few nests with six to seven being found wherever they occurred. We may have underestimated their occurrence since we did not dissect the nests and most of those we found were pupae. Hymenoptera were represented by ants (Formicidae), which prey on smaller arthropods, ichneumon wasps (Ichneumonidae), which parasitize arthropods including blowflies, and chalcid wasps (Perlampidae), which parasitize arthropods including ichneumon wasps. Worker ants occurred in most nests (~ 11 per nest). Since the nest boxes were mounted on greased pipes, the ants were probably carried in on nest materials. Ichneumonids (~ 4 per nest) and chalcids (~ 3 per nest) were patchily distributed. In most cases they occurred in nests with blowflies, but not in all cases, which further suggests that we did not find all the blowflies and our estimate of blowfly occurrence and distribution is low. Flat bark beetles (Coleoptera, Silvanidae), which feed on vegetation, occurred in all wren nests (~ 7 per nest) and patchily in swallow and bluebird nests. House wrens fill the nest box with twigs, which may account for the larger numbers of flat bark beetles in their nests as compared to those of swallows and bluebirds, which use few sticks and more grass. All nests contained some bird lice (Mallophaga, Menoponidae, and Philopteridae, ~ 6 per nest).

Spiders and ants might have preyed on mites. Most of the insects present fed on vegetation and would have interacted minimally with the mites. The blowfly (*Protocalliphora* sp.) may compete with *Dermanyssus hirundinis* for nestling blood, but the blowfly population was so small and patchy that any effect in the present study could not be documented. The combined mite populations were not correlated with any other arthropod population (35 correlation coefficients, $p > 0.01$ in all cases; blowflies in tree swallow nests were too few to calculate a correlation coefficient) nor with the combined population of other arthropods (three correlation coefficients, $p > 0.01$ in all cases).

The nest

Mites live in the nest material. However, the combined mite populations were not correlated with the volume of the host species' nest. Nest volume, within species, is not a determinant of population size among mites inhabiting eastern bluebird, tree swallow, and house wren nests.

Nest structure and materials may·be factors. With only three avian species for comparison the data are sketchy. Bluebird nests are flat and densely woven compared to swallow and wren nests. Thus *Dermanyssus* need move only short distances to feed, but engorged adults and nymphs should find ample shelter in the densely woven vegetation. The more

active *Dermatophagoides* may be somewhat hampered in moving through the nest in search of organic debris (fewer *Dermatophagoides* than expected, Table 6.2) and the predatory *Cheletomorpha* (none in bluebird nests) may be severely restricted in its ability to detect and jump approaching prey in the dense mat of finely woven grasses. As the coarseness of the materials increases, the weave becomes looser and movement easier. Tree swallows have coarser materials and a looser weave than bluebirds and also have more mites. Tree swallow nests have fewer predatory mites than expected (Table 6.2), but some are present and populations of parasitic and scavenging mites are far above those of bluebird nests (Table 6.1). House wren nests have the coarsest materials, the loosest weave, and the most mites with a disproportionate number of predatory mites (Table 6.2). The comparison suggests that the structure of the nest, particularly the type of materials and the tightness of the weave, may be factors in the distribution and abundance of mites.

Bluebird nests had few or no faeces throughout the reproductive cycle and had relatively few scavenging mites (Table 6.1). House wren nests contained substantial deposits of nestling faeces and flakes from feather sheaths and large populations of scavenging mites (Table 6.1), although a smaller proportion than expected (Table 6.2). Tree swallow nests contained large deposits of faecal material and flakes of feather sheaths and disproportionately large populations of scavenging mites (Table 6.2). The population of *Dermatophagoides evansi* appears closely tied to the presence of organic wastes from the nestlings, suggesting that the correlation with nestling number is due to the increasing amount of waste material with increasing brood size.

Timing of avian reproduction

Numbers of mites should increase as the season advances. Not only will the mites in occupied nests reproduce, but mites from early nests will be able to colonize later nests and reproduce again. House wrens initiated their clutches (19 June $\pm$ 25.2 days) significantly later ($F = 20.78$, $df = 2$, 133, $p < 0.01$) than tree swallows (18 May $\pm$ 10.7 days) and eastern bluebirds (28 May $\pm$ 32.8 days) and had significantly larger populations of mites (Table 6.1), as expected. However, tree swallows had much larger populations of mites than eastern bluebirds (Table 6.1), but began laying eggs at about the same time. The data are equivocal. They do not provide strong support for the expectation of more mites in later nests, but they do not refute the expectation. The possibility that mites may influence the timing of reproduction by birds may repay systematic study.

Table 6.4. Population growth (mites/nestling) of *Dermanyssus hirundinis* and *Dermatophagoides evansi* in tree swallow nests during the swallows' reproductive cycle

Swallow's developmental stage	Number of nests	Dermanyssus		Dermatophagoides
		Adult	Nymph	
10 d incubation	7	1.7	3.3	72.2
Hatching	4	0.3	0.1	339.0
5 d nestlings	6	4.4	5.7	254.6
10 d nestlings	7	111.7	81.7	1354.9
15 d nestlings	5	61.8	60.0	2282.7
Postfledging	7	628.3	353.0	3613.9

Demography

During 1987 we studied the population dynamics of *Dermatophagoides evansi* and *Dermanyssus hirundinis* in tree swallow nests. Too few *Cheletomorpha lepidopterorum* were found for analysis. Because the number of mites per nest increases with an increase in the number of nestlings all discussion of demography is adjusted to mites per nestling. The population dynamics of both *Dermatophagoides* and *Dermanyssus* were related to the reproductive cycle of the tree swallow.

The initial population of *Dermatophagoides evansi* measured on the tenth day of incubation was 72.2 mites per nestling (Table 6.4). Between the tenth day of incubation and hatching the population of mites grew rapidly. Prior to hatching an r value (eqn 6.1) of 1.35 gives a close approximation to the growth rate of the mite population. The population appears to stabilize for the first 5 days the nestlings are in the nest and then enters a second growth phase during which r is initially 1.3, but declines to 0.9 as fledging approaches.

The pattern of population growth suggests two distinct growth phases. The first corresponds to an initial period of colonization and exploitation of the detritus to be found in the nest materials and the flakes of material shed by the skin and feathers of the female (only the female incubates). These resources are limited and the number of *Dermatophagoides* reaches carrying capacity about the time of or just prior to hatching of the nestlings. Initially the nestlings add little to the food resources available to *Dermatophagoides*. Newly hatched swallows are small and without feathers. They probably supply little, if any, dead skin or feather material to the nest habitat. Faeces from the nestlings are consumed by the parents throughout this period (Burtt, personal observation). By 10 days after hatching, the feathers of the nestlings are emerging from the sheaths in which they first penetrate the skin. Flakes of material
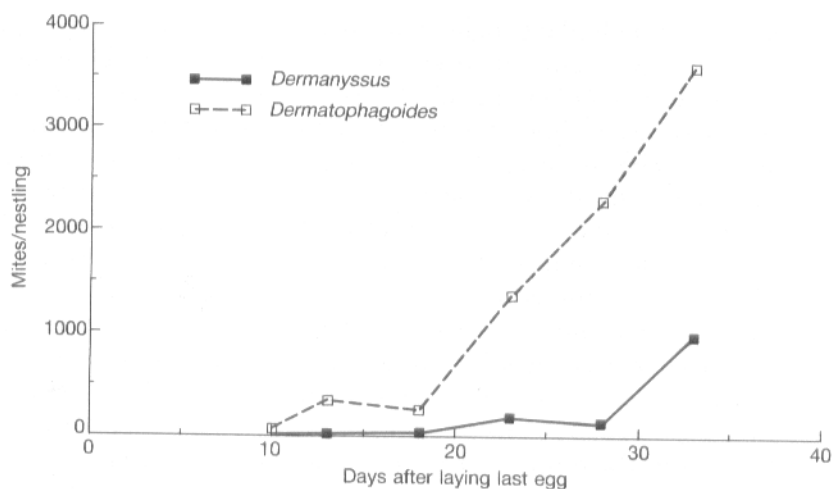
Fig. 6.5. Population growth of *Dermanyssus* and *Dermatophagoides* in relation to the reproductive cycle of the tree swallow.

from the disintegrating sheaths would increase food resources for *Dermatophagoides*. As little as 180 mg of shed skin can sustain large cultures of *D. pteronyssinus* for some months (van Bronswijk and Sinha 1971, cited in Krantz 1978). Deposition of material from growing feathers would increase after 10 days post-hatch as the feathers of nestlings increase their growth rates. Furthermore, after day 10 the parents gradually cease removing nestling faeces from the nest and this source of organic waste would become available to the scavenging *Dermatophagoides*. Despite increasing food resources the rate of growth in the population of *Dermatophagoides* declines from an *r* value of around 1.3 at 10 days after the nestlings hatch to an *r* value of about 0.9 at the time of fledging. The declining growth rate suggests that the population of *Dermatophagoides* is approaching its carrying capacity in the nests of tree swallows.

Few *Dermanyssus hirundinis* are present during incubation (Table 6.4). The population of *Dermanyssus* remains low through the first 5 days of the nestling period and then grows very rapidly for the next 5 days (Fig. 6.5). The population maintains a plateau until the nestlings are 15 days old, whereupon the *Dermanyssus* population grows rapidly until the nestlings fledge. From the fifth day after hatching through fledging of the nestlings the growth rate, *r*, of *Dermanyssus* is close to 1.75.

The population of *Dermanyssus* is substantially lower than that of *Dermatophagoides* during incubation and, unlike the population of *Dermatophagoides*, remains unchanged through the fifth day after hatching of the nestlings. *Dermanyssus* feeds on blood and throughout

incubation only the female swallow is available as a food source. The newly hatched nestlings are not growing feathers and their blood supply may be too far below the skin for *Dermanyssus* to reach. Alternatively, ectothermic nestlings may not attract mites that feed on endothermic animals. The two growth surges evident in Fig. 6.5 may correspond to the development of separate generations of mites. *Dermanyssus prognephilus* has a generation time of 7.3 days at 24°C, 93 per cent relative humidity (Moss 1966). The generation time drops to 5 days at 32°C, 93 per cent relative humidity (Moss 1966). These generation times correspond roughly to the surges in population growth shown in Fig. 6.5. Unlike *Dermatophagoides,* the growth rate of the *Dermanyssus* population is accelerating at the time the nestlings fledge. Phillis (1972) found a similarly rapid population growth for *Dermanyssus* at the time of fledging in the house sparrow. Such rapidly increasing populations of ectoparasites could set a limit on the duration of the nestling period. Furthermore, population increases in the nests of the earliest breeders would provide large numbers of immigrants to the nests of those swallows breeding later in the season or trying to raise a second brood. Such large founding populations would have a much greater potential for population growth than the small founding populations occurring in the present study and might account for the rarity of second broods among tree swallows, the frequent desertion of broods by late-nesting barn swallows (*Hirundo rustica*) noted by Shields and Crook (1987), and the synchrony of breeding and desertion within colonies of cliff swallows (*H. pyrrhonota*) (Emlen 1986; in this volume Loye and Carroll, Chapter 12).

Effect of mites on avian reproductive success

The reproductive success of house wrens was not monitored. Eastern bluebirds laid 53 eggs in the 13 nests from which mites were collected. Forty-five eggs hatched and 45 nestlings fledged. All eight eggs that failed to hatch were infertile. Four additional nests with 12 bluebird eggs were usurped by house wrens, but mites were not collected from these nests. Furthermore, wrens took over the nests soon after the bluebirds began incubation when the mite population would have been very small.

Tree swallows laid 99 eggs in the 18 nests from which mites were collected. Ninety of these eggs hatched, eight were infertile, and one contained a partially developed embryo. Of the 90 hatchlings, 84 fledged. Six nestlings in one nest died from unknown causes, all on the same day. The mite population in the nest was 3420, well below average. Nests were checked every other day and the deaths may have occurred as much as 40 h before they were discovered and the nest collected. This may have given the mites time to disperse, but, even with dispersal, such

a population seems to rule out mites as a cause of death. Five nests were deserted by tree swallows. Four of these, containing 14 eggs, were usurped by house wrens and the fifth, containing 2 eggs, by a house sparrow. Two nests were destroyed by vandals. Mites in these seven nests were not counted. As with the bluebirds, eviction by wrens and sparrows occurred early in the incubation period when mite populations would have been small.

Few nestling deaths occurred and none could be attributed to parasitism by *Dermanyssus hirundinis*. The number of mites increased as the number of nestlings increased, but the increase was arithmetic not geometric. Mites per nestling remained constant and, apparently, within tolerable limits. Moss and Camin (1970) found that purple martin (*Progne subis*) nestlings subject to parasitism by *Dermanyssus progne-philus* were about 7 per cent lighter at fledging than nestlings protected from such parasitism and suggest that such reduced weight may have important implications for survival after fledging. Based on the weight differential Moss and Camin (1970) estimate that parents in nests without mites could have raised an additional nestling. We did not protect nestlings from mites nor did we weigh our nestlings; however, the ubiquity of *Dermanyssus hirundinis* in nests of tree swallows, house wrens, and eastern bluebirds suggests the potential for serious effects on the reproductive success of these species. Replication of Moss and Camin's (1970) experiments are needed for eastern bluebirds, tree swallows, and house wrens particularly in warm, damp years when conditions favour rapid growth of mite populations.

Conclusions

Mites are the most frequent and most numerous of the arthropods inhabiting nests of the eastern bluebird, tree swallow, and house wren at our Ohio study site. In most nests mites also comprise the largest arthropod biomass. The population growth of *Dermanyssus hirundinis*, a parasitic mite, and *Dermatophagoides evansi*, a scavenging mite, is closely tied to the reproductive cycle of the tree swallow, the only species for which we have demographic data. *Dermanyssus* and *Dermatopha-goides* probably overwinter in the nest or nest box. *Cheletomorpha lepidopterorum*, a predator of the other two species, occurred in 33 per cent of tree swallow nests, 49 per cent of house wren nests, and 0 per cent of eastern bluebird nests. It may overwinter in nest boxes with the other species or in bark (Summers and Price 1970; Krantz 1978) and enter nests on twigs used for nest construction by wrens, used occasionally by swallows, and not used by bluebirds. Such a method of colonization

would account for the absence of *C. lepidopterorum* in bluebird nests, their occasional appearance in swallow nests, and their common occurrence in wren nests.

Dermanyssus has an extremely small founding population. Its population growth shows two separate growth phases: one at the time feathers are emerging, which is probably associated with the availability of blood in the feather papillae, and a second growth phase associated with the nestlings reaching their maximum weight. The growth rate of *Dermanyssus* is increasing at the time the nestlings leave the nest. The rapidly increasing population of the parasitic *Dermanyssus* may limit the time the nestlings can remain in the nest, although no mortality attributable to mites was found in this study.

Dermatophagoides has a larger founding population than *Dermanyssus* and its population has an initial growth phase before hatching. A second growth phase begins as the feathers emerge and continues through the departure of the young. This second growth phase begins with rapid growth ($r = 1.3$) that slows toward the time the nestling swallows leave the nest ($r = 0.9$). *Dermatophagoides* feeds on organic debris, which is available during incubation and abundant as the nestlings feather sheaths flake off and the parents stop removing nestling faeces. A growth plateau early in the nestling period suggests that *Dermatophagoides* may have reached a temporary carrying capacity prior to emergence of the nestlings feathers. The decreasing growth rate late in the nestling period suggests that the *Dermatophagoides* population is approaching a second, higher carrying capacity, which it does not reach prior to fledging of the young swallows.

The final populations of *Dermanyssus* and *Dermatophagoides* are larger in nests with more nestlings. The correlation is linear and significant. Nests with faeces and accumulated flakes from feather sheaths have more mites. However, the volume of the nest (i.e. living space for the mites) and the presence of other arthropods have no effect on the population size of *Dermanyssus* and *Dermatophagoides* at fledging of the nestlings.

The presence of *Cheletomorpha lepidopterorum* has little effect on the populations of *Dermanyssus* and *Dermatophagoides*. Bluebirds had relatively few mites and this may account for the failure of *Cheletomorpha* to colonize bluebird nests, but uncolonized wren and swallow nests had the same or more prey than colonized nests. Thus, abundance of prey was not the limiting factor and the occurrence of *Cheletomorpha* in some nests and not others may depend on the difficulty of colonization. Ideas from island biogeography may help explain the distribution of *Cheletomorpha lepidopterorum* among the nests of birds.
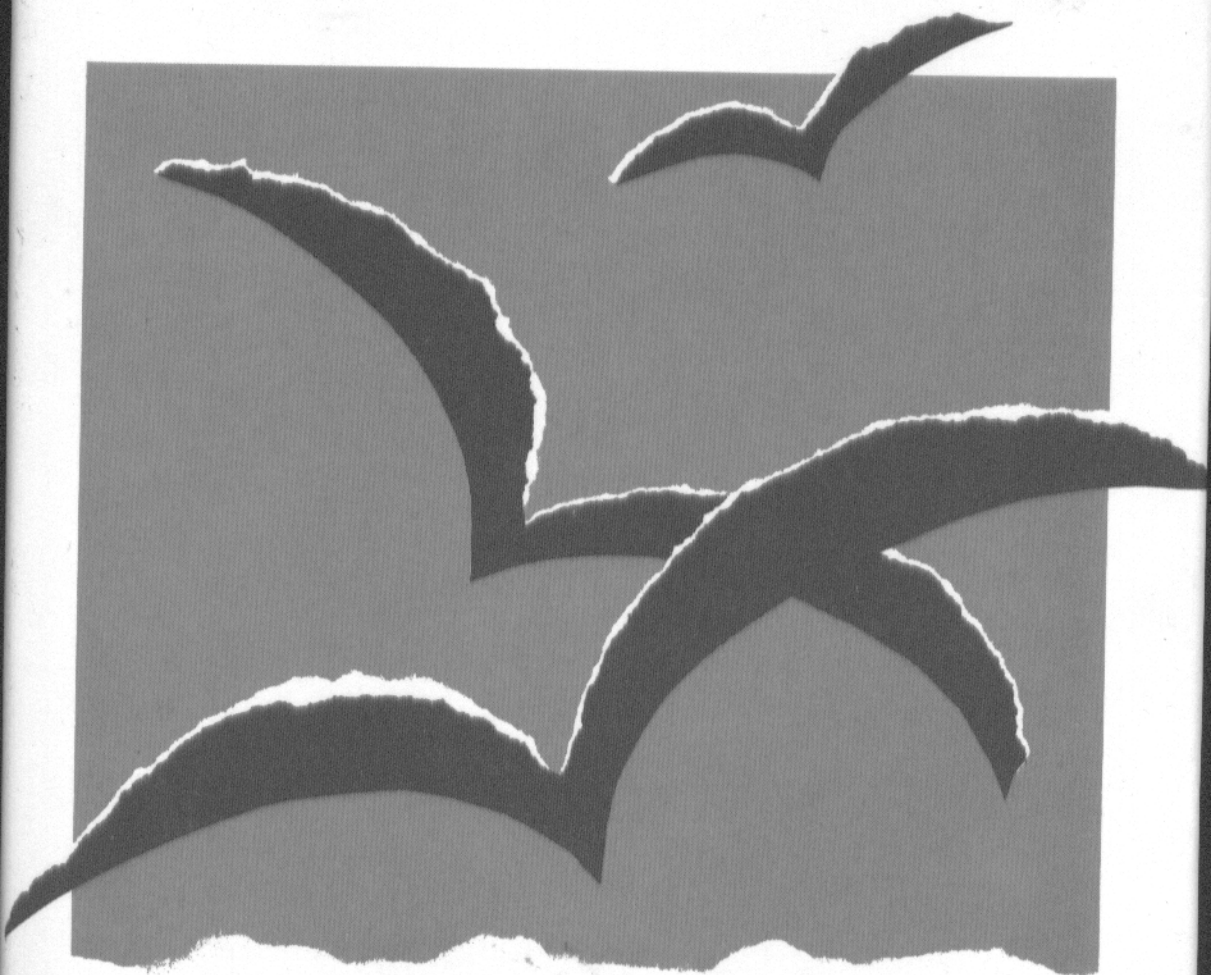
Acknowledgements

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Ecology, Evolution, and Behaviour

Edited by J. E. Loye and M. Zuk