

Effect of biologically active plants used as nest material and the derived benefit to starling nestlings

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Summary. The European starling *Sturnus vulgaris* preferentially incorporates fresh sprigs of particular plant species for use as nesting material. Chemicals found in these plants may act to reduce pathogen and ectoparasite populations normally found in nest environments. The present experiments were performed to test this Nest Protection Hypothesis. In the field, we experimentally determined that wild carrot *Daucus carota*, a plant species preferred as nest material, effectively reduced the number of hematophagous mites found within nests relative to control nests without green vegetation. Chicks from nests containing wild carrot had higher levels of blood hemoglobin than chicks from control nests. However, there were no differences in weight or feather development. In the laboratory, we found that wild carrot and fleabane, *Erigeron philadelphicus*, (also preferred by starlings as nest material) substantially reduced the emergence of feeding instars of mites, while garlic mustard, *Alliaria officinalis*, (commonly available but not preferred) had little effect on the emergence of mites. We infer that preferred plant material may act to inhibit feeding or otherwise delay reproduction of mites, thereby reducing risk of anemia to developing nestlings.

Key words: *Sturnus vulgaris* – Nesting behavior – Ectoparasite – Nest protection hypothesis – Biological control

Increasingly, evidence indicates that heavy infestation of nests by ectoparasites can affect survivorship and fecundity of breeding adult birds. For example, seabirds and swallows abandon breeding colonies following a build-up in ectoparasite populations (Hoogland and Sherman 1976; Duffy 1983). In those cases where breeding persists, high ectoparasite numbers may result in depressed growth of the young, and by implication, a decrease in their long-term, post-fledging survival probabilities (Moss and Camin 1971; Arndt 1985a, b; Brown and Brown 1986). Ectoparasites also can cause physiological stress, thus increasing the risk of opportunistic infection by pathogens, or serve as a direct vector for pernicious forms of pathogens (Hofstad et al. 1984).

Birds have several options to minimize ectoparasite load. One option is the use of nest-sites for only one breeding season. This strategy reduces the time during which ectoparasites can colonize the nest. Birds that re-use nests

or nest-sites incur higher parasite loads relative to species that utilize nests or sites only once (Stoner 1936; Rothschild and Clay 1957; Wasylik 1971; Loye 1985; Barclay 1988). Placement of a nest away from other nests also can reduce the colonization rate by ectoparasites (Brown and Brown 1986).

Neither of the above two options are available to some species (e.g. secondary cavity nesters) for whom nest-sites may be a limiting resource (Hogstad 1975; Brush 1983; Brawn and Balda 1988). In this circumstance, even use of a different site every year does not preclude previous use of that site; thus, escape from parasites may not be possible. Increased nest sanitation and preening may be helpful in reducing ectoparasite load, but additional strategies may be necessary. Such strategies are suggested by the nest protection hypothesis.

Some species of birds incorporate fresh green vegetation into their nest material. Normally, the quantities of material are small relative to the remainder of the structurally supportive dry nest matrix. The naturally occurring defensive chemicals contained in the plants are hypothesized to be toxins (either volatile or contact) which can reduce parasite and pathogen load. Support for the nest protection hypothesis has been anecdotal and speculative (Johnston and Hardy 1962; Sengupta 1981). However, Wimberger (1984) and Clark and Mason (1985) showed that falconiforms and passerines that reused nest-sites across breeding seasons, and by implication, incurred high ectoparasite loads, were more likely to use green plant material in nest construction. In the case of the European starling *Sturnus vulgaris*, the plants used were selected in quantities greater than their proportional availability from the habitat. These same plants were more likely to have antibacterial and insecticidal properties than a random subset of available vegetation.

The objective of the present study was to provide more detailed information on the efficacy of some of the plants used by starlings at reducing ectoparasite infestation of nests. Specifically, we determined how effective wild carrot *Daucus carota* and fleabane *Erigeron philadelphicus*, two plants preferentially utilized by starlings during nest construction, were at limiting the hematophagous mite *Ornithonyssus sylviarum*. Both laboratory and field studies were carried out. A second objective was to assess how the treatment of nests with fresh plant material (and by implication, the manipulation of parasite load) affected the well-being of nestlings. We hope to understand eventually the processes by which starlings acquire this component of nest

building behavior and to elucidate the cues birds use to choose among plants.

Methods

Study site

The nesting colony of starlings was located at the Stroud Water Research Center (SWRC) of the Academy of Natural Sciences of Philadelphia, Avondale, PA. The habitat surrounding SWRC is a mix of lawns, old fields, pastures, and secondary growth deciduous forests. Individual nest boxes used in this study were constructed in 1980 of uniform materials and to uniform dimensions. Such uniformity of nest box construction may be important because there is reason to suspect that larger quantities of green plants are used by starlings nesting in older boxes (Tenovou and Lemmetyinen 1970; L. Clark, unpublished).

Biology of the northern fowl mite

We chose to monitor numbers of the northern fowl mite because this was the most conspicuous ectoparasite occurring at the nest colony over the years. *O. sylviarum* is an ectoparasite which feeds primarily on the blood of birds. *O. sylviarum* can complete a five stage life cycle in 7–14 days, while adult forms are capable of enduring fasts of up to 3–4 months (personal observation). Sykes and Chamberlain (1954) report that eggs are laid on birds or in nest material. After 24 h, nonfeeding, six-legged larva hatch. After an additional 24 h, larva metamorphose into an eight-legged feeding protonymph. All life-history stages of *O. sylviarum* remain in the nest matrix. Feeding forms ascend to the host, feed, then return to the nest matrix. Normally, protonymphs require at least two separate feeding bouts (36 h) before they are fully engorged (0.025 mg blood) and change into a nonfeeding deutonymph stage. After 24 h, deutonymphs give rise to a continuously feeding adult form. Adult females may engorge with 0.041 mg of blood every 1–5 days before laying an average clutch of 2.27 eggs. This life history allows a small founding population to expand to considerable numbers during the 37–40 days starlings are active at the nest (nest construction through fledging of the chicks).

Nest manipulations

We manipulated nests to test the hypothesis that green plants influenced population levels of mites. To control for previous infestation history all boxes were scrapped clean of nest debris during January 1984 and 1985. We daily removed all fresh green plant material from nest-boxes and the dry nest matrix throughout the nest-building season in March and April as an effort to standardize conditions. Further monitoring of the nests' matrix was unnecessary, because once the eggs are laid, addition of green plants to the nest no longer occurs (Clark and Mason 1985).

In 1984 nests were randomly assigned to one of three treatment levels:

1. *Nest replacement (NR)*. The entire dry matrix of nest material was removed and replaced with an equivalent clean mass of dry grass material on –10, –5, 1, 7 and 13 days post-hatching. Starling nests are easily replicated by the

investigator if care is taken to select similar nest material. This treatment served to reduce mite populations throughout the nestling's development.

2. *Plant removal (PR)*. Once fresh plant material was removed these nests received no further treatment. These nests were presumably devoid of putative miticidal or repellent effects of plants (*sensu* Ambasta 1980) and would hypothetically allow mite populations to grow unconstrained.

3. *Plant addition (PA)*. Fresh plant material (5 g) was interwoven into the dry nest matrix at –10, –5, 1, 7 and 13 days post-hatching. Starlings differentially select several herbaceous species for inclusion into the nest relative to available vegetation. Wild carrot was selected because it had the highest preference rating (utilization:availability) of green plants used by starlings breeding in southeastern Pennsylvania (Clark and Mason 1985).

During 1984, 3 nests from each of the 3 treatments were collected in May and June when the nestling occupants were 1, 7, 13 and 19 days of age ($N=72$). Nest materials and debris were placed in a one gallon 'zip-lock' plastic bag and transported to the laboratory. Because feeding stages of *O. sylviarum* demonstrated positive geotaxis, we were able to collect individuals by aspiration at 24 h intervals. After 4–5 days, this method yielded asymptotically fewer mites. Pieces of nest material were then placed in a porcelain pan and washed in 70% ethyl alcohol. The entire nest was washed in an effort to extract as many of the remaining mites as possible. Mites were collected using a bulb pipet. We found that only the protonymph, deutonymph and adult forms could be reliably collected. The eggs were too small to be easily seen and the larva were too small and translucent to be reliably seen, even under stereoscopic magnification and illumination. After collection, mites were sorted according to life history stage. Sorted populations were placed in a centrifuge tube and spun at 2500 rpm for 10 min on a clinical centrifuge. Numbers of mites were determined by comparing volumes of samples to calibrated samples whose numbers and volumes were previously determined. Differences in the log number of mites found in nests were analyzed using a fixed effects analysis of variance model with 3 factors: nest manipulation (3 levels), age of chicks (4 levels) and month hatching occurred (2 levels).

Nestling growth

The growth of chicks from a randomly selected subset of manipulated nests was monitored. During hatching (day 0) nests were adjusted to contain 4 chicks. Only nests containing 4 young throughout 18 days of development were included in the comparison of age-specific growth variables (total number of nests sampled, $N=20$: May-PR=4, June-PR=3; May-PA=4, June-PA=4; May-NR=4, June-NR=1). The order in which chicks from each nest manipulation were weighed was counter-balanced with respect to time of day. Chicks from each treatment group were weighed and measured between 0600–0930 EST on 1–6, 9, 12, 15 and 18 days posthatching. Mass was recorded to the nearest gram using a Pesola scale, while length of the tarsus, 9th primary and 9th primary's sheath were measured to the nearest mm with a ruler.

Comparison of age-specific mass across treatment (3 levels) and month of hatching (2 levels) was carried out using data from chicks aged 6, 12 and 18 days post-hatching

via a three-way analysis of variance with repeated measures. A comparison of growth parameters for mass was made using a two-way analysis of variance, with treatment (3 levels) and month (2 levels) as factors. Average growth curves for each brood were iteratively calculated using all measurement data from individuals by a three parameter logistic model, $W_t = A / \{1 + \exp[-K(t - t_i)]\}$, where W_t is the mass of a chick at age t , A is the asymptotic mass of a chick, K is the growth constant and t_i is the mass of a chick at the inflection of its growth curve (NLIN program of Statistical Analysis System, 1985).

Total 9th primary length and the ratio of feather sheath and total 9th primary length were used as indices of plumage development. Linear measurements of chicks aged 9, 12, 15 and 18 days post-hatching were analyzed using a two-way analysis of variance with repeated measures.

Blood analysis

Because *O. sylviarum* is a blood feeding ectoparasite, heavy parasitism load may be reflected in affected chicks as decreased oxygen transport capabilities (blood hemoglobin content or reduced red cell count). A subset of broods of 4 were collected from the field at 1, 7, 13 and 19 days post-hatching for each of the nest treatment levels, and transported to the laboratory in insulated styrofoam containers. The number of broods sampled for the treatment, PR, was 11; with 2, 4, 3 and 2 broods taken at each of the sampling intervals, respectively. The number of broods sampled for PA and NR treatments was 11 and 9, respectively; with 2, 3, 4 and 2 and 2, 2, 3, and 2 broods taken at each sampling interval, respectively. At the laboratory blood samples were drawn from the brachial vein for analysis. A sample of 330 μ l of blood was collected in heparinized capillary tubes and deep frozen (-50°C) for subsequent analysis.

Total blood hemoglobin was estimated colorimetrically by combining thawed whole blood (20 μ l) with 5.0 ml Drabkin's solution (1.25 g of sodium bicarbonate:potassium ferricyanide:potassium cyanide, 100:20:5 dissolved in 1 l H_2O and 0.5 ml 23-lauryl ether, 30% w/v), and allowing the mixture to stand at 23°C for 15 min. Samples were centrifuged at 3000 rpm for 20 min to precipitate out nuclei, and then decanted to spectrophotometer tubes and compared to a Drabkin's reagent blank using a Spec-20 read at 540 nm. Hemoglobin content of the blood was evaluated by comparing absorbance readings to a cyanmethyhemoglobin standard (human).

A second blood sample was collected in 75 mm micro-capillary tubes and spun at 2500 rpm on a clinical centrifuge for 15 min. Comparison of packed cell volumes (volume of cells/total blood volume) are a reflection of the number of blood cells per unit volume, and as such are a crude indicator of relative oxygen transport capacities of chicks. Chicks were euthanized and deep frozen (-50°C) for subsequent carcass analysis, the results of which are to be reported elsewhere. The effects of treatment (3 levels) and age (4 levels) on blood hemoglobin values were determined using a two-way analysis of covariance, with packed cell volume as the covariate.

Laboratory emergence tests

During 1985, nests were brought into the laboratory in an effort to more closely monitor the effects green plant mate-

rial had on the emergence behavior of mites. Nest boxes were prepared and monitored as they were during the 1984 field season. At 5 days post-hatching, nests were collected ($N=12$), placed in one gallon 'zip-lock' plastic bags, brought to the laboratory and randomly assigned to one of three groups ($N=4$). After thorough mixing of the matrix all nests were divided into halves and the halves were placed into separate 'zip-lock' bags. One half was designated as the untreated control. The remaining, corresponding, half was randomly assigned to one of three plant treatment groups. Those nests were mixed with 5 g of fresh green leaves of either wild carrot, fleabane or garlic mustard *Alliaria officinalis*. In this way each nest served as its own control for the number of mites emerging to feed. Feeding instars were collected as they emerged from the nest matrix. Mites were collected for 13 days after nests were first brought to the lab. The number of mites was quantified as described above. No attempt was made to recover mites from the nest matrix.

Unless otherwise stated, factors in all analyses were found to be homogeneous. Post-hoc comparisons of treatment levels were carried out using the Neuman-Keuls technique with significance values reported at $P \leq 0.05$ (Winer 1971).

Results

Ornithonyssus sylviarum populations in the field

The number of mites collected from nests increased over the course of development of chicks ($F=37.04$, $df=3,48$, $P<0.001$). This pattern did not differ substantially between the first and second breeding attempts in May and June ($F=1.55$, $df=3,48$, $P=0.212$), though more mites were collected from nests during June ($F=72.59$, $df=1,48$, $P<0.001$). The observed pattern of greater numbers of mites associated with development of the young and reuse of old nests is consistent with data reported for other passerines (Wasylik 1971).

Manipulation of the nests strongly affected the number of mites collected ($F=547.19$, $df=2,48$, $P<0.001$). Nests devoid of any fresh plant material (PR) possessed the largest mite populations over the course of development of nestlings, while those nests containing *D. carota* (PA) possessed a significantly lower number of mites. Nest-sites subjected to periodic replacement of nest material (NR) accumulated the fewest number of mites (Fig. 1, $F=7.02$, $df=6,48$, $P<0.001$). Closer inspection of Fig. 1 indicates that addition of *D. carota* did not affect the rate at which mite populations increased relative to the plant removal treatment. Such a pattern suggests that survivorship and fecundity of mites were similar in these two treatments. The lower number of mites in the plant addition treatment may have resulted from a delay in colonization or reproduction of the founding population.

Effect of nest treatments on chicks

The impact of the nest manipulations on the age-specific mass of starling nestlings was negligible ($F=0.17$, $df=45$, $P=0.842$, Fig. 2). Because nest treatments significantly covaried with the densities of mites, we concluded that the fowl mite had no appreciable effect on the age-specific mass of nestlings. Similarly, the overall model for nest manipula-

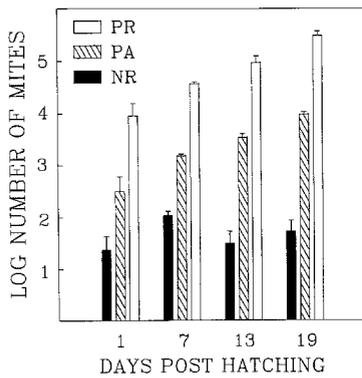


Fig. 1. The mean number of *O. sylviarum* collected from nests during the course of development of starling nestlings. The lettered codes correspond to the type of nest manipulation performed (NR: nest replacement, PA: plant addition, PR: plant removal). The vertical bars correspond to one standard error. The data presented are collapsed over the May and June breeding attempts

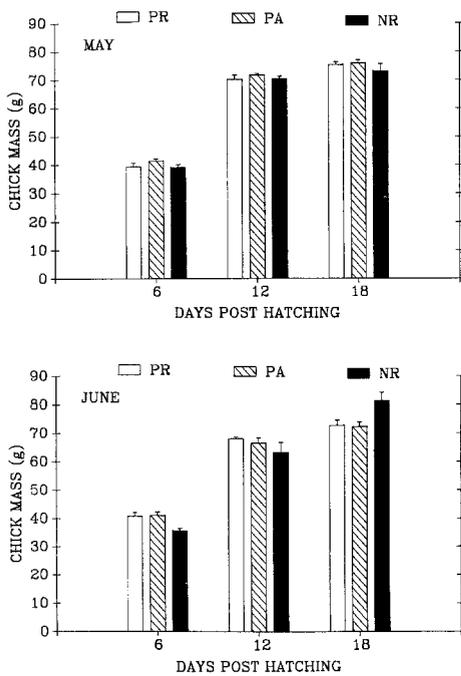


Fig. 2. The mean age-specific mass of chicks reared during the May and June breeding attempts. The lettered codes correspond to the type of nest manipulation (NR: nest replacement, PA: plant addition, PR: plant removal). Vertical bars are one standard error

tion and seasonal effects for the mean asymptotic mass of chicks, the growth constant and inflection of the growth curve well all found to be non-significant ($F=1.10$, $df=5,14$, $P=0.402$; $F=1.39$, $df=5,14$, $P=0.285$; $F=1.51$, $df=5,14$, $P=0.249$, respectively).

Figure 2 shows that the age-specific mass of chicks reared during the first breeding attempt in May differed from their counterparts reared in June ($F=4.75$, $df=2,150$, $P=0.011$). Chicks reared in May were heavier than those reared in June ($F=4.90$, $df=1,75$, $P=0.032$). This is the typical pattern observed for most passerines (O'Connor 1984). A study conducted by Powlesland (1977) in New Zealand on the effects of *O. bursa* on the growth of starling nestlings yielded similar results.

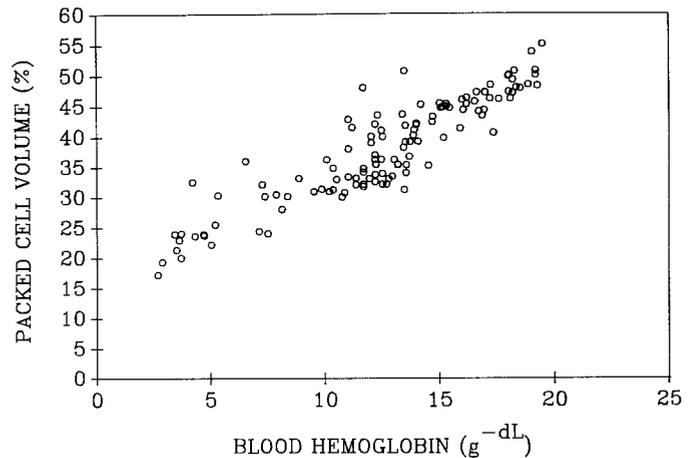


Fig. 3. The relationship between blood hemoglobin content and packed cell volume ($r=0.987$, $P<0.01$, $N=123$)

Ectoparasite load, did not affect the growth and development of the plumage. The age-specific lengths of the 9th primary were similar ($F=0.98$, $df=6,72$, $P=0.442$), revealing no overall treatment effect ($F=1.90$, $df=2,24$, $P=0.171$). Analysis of the ratio of sheath length to total 9th primary length, as an index of maturation of the plumage, yielded similar results. The rate at which feathers emerged from the feather sheaths was similar for all treatments ($F=1.05$, $df=6,72$, $P=0.402$) and showed no overall treatment effects ($F=2.72$, $df=2,24$, $P=0.086$), though there was a trend for chicks from the plant removal treatments to retain their feathers in the sheath for a slightly longer period.

Because fowl mites are hematophagous we considered the possibility that parasite load might affect the blood characteristics of nestlings. The ratio of the volume of red blood cells to plasma volume (packed cell volume) is a conservative physiological character. Even under dehydration chicks maintain blood volume to preserve osmotic balance. Thus PCV, represents a good relative index of the crude oxygen carrying capacity of chicks (Fig. 3). Overall, nestlings reared within each of the three treatments exhibited differences in levels of blood hemoglobin ($F=16.25$, $df=2,110$, $P<0.001$), even after removing the covariate effect of PCV ($F=142.51$, $df=1,110$, $P<0.001$, regression approach). Chicks reared in nests where *D. carota* was incorporated into the nest matrix, and chicks reared in boxes where nests were systematically replaced, maintained higher levels of age-specific blood hemoglobin than those chicks reared in the plant removal treatments (Fig. 4). We infer that the high mite densities associated with the plant removal treatments were sufficient to depress the oxygen carrying potential of nestlings.

Effectiveness of plants against O. sylviarum in the laboratory

The efficacy of treating nest material with green leaves was tested under more controlled conditions in the laboratory. Emergence of feeding instars from nest material was monitored in nests where half the matrix was mixed with green leaves, while the emergence from the remaining untreated matrix was monitored as a control. There was no difference in emergence of feeding instars from nest material treated with the plant *A. officinalis* relative to controls (Fig. 5A;

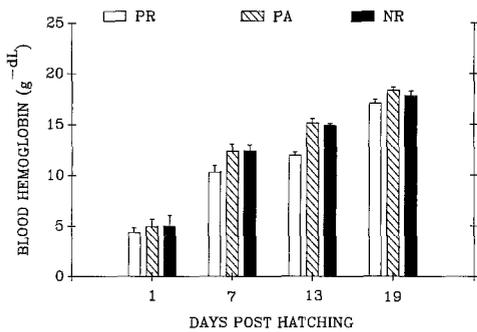


Fig. 4. The mean hemoglobin content of nestlings exposed to the three nest manipulations throughout the course of their development. Treatments were NR: nest replacement, PA: plant addition, PR: plant removal. Vertical bars are one standard error

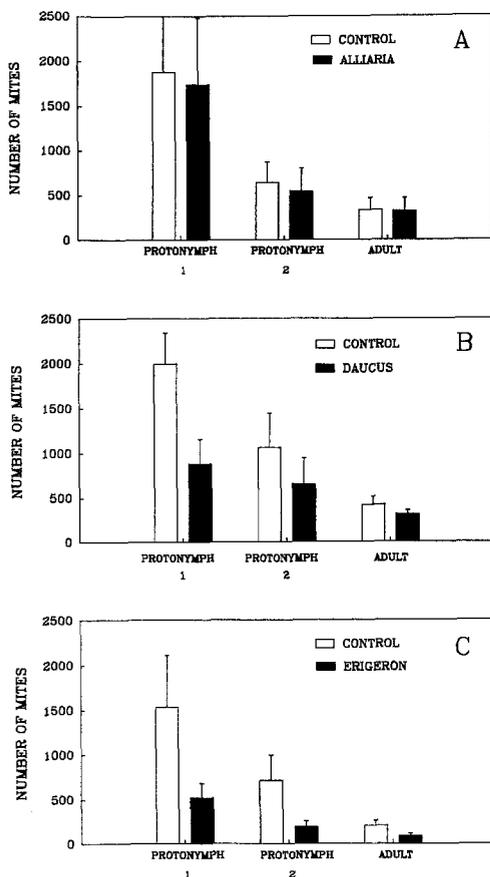


Fig. 5. The mean number of mites emerging from nest material for the halves from each of a set of nests treated with green plant material (solid bars). The open bars represent mean emergence of mites from the untreated, control portion of nests. Vertical bars represent one standard error

$F=0.01$, $df=1,18$, $P=0.924$). Clark and Mason (1985) had previously shown that *A. officinalis* was commonly available during nest construction, but was statistically underutilized by starlings building nests. In contrast, both *D. carota* and *E. philadelphicus* were incorporated into nests in quantities greater than their proportional availability in the habitat. Inspection of Fig. 5B–C illustrates both *D. carota* and *E. philadelphicus* significantly decreased the emergence of feeding instars of mites in the halves of nests treated with plants relative to the untreated controls ($F=6.05$, $df=$

$1,18$, $P=0.023$ and $F=6.08$, $df=1,18$, $P=0.024$, respectively).

Discussion

According to the nest protection hypothesis, plant chemicals found in nest material act to reduce pathogen and ectoparasite populations normally found in nest environments. If the use of green plants by birds is to be considered adaptive several conditions must hold true: (1) parasites and/or pathogens must, directly or indirectly, affect survival and/or fecundity of the breeding adults, (2) plants must in some way decrease the potential detrimental effects of parasites and pathogens, and (3) nest-building behavior must have a genetic basis and birds must preferentially select plant material that reduces parasite and pathogen load. In addition, birds should possess sensory capabilities that permit discrimination among plants.

Do ectoparasites affect survival and reproduction?

There is ample evidence to indicate that ectoparasites influence fecundity and mortality in birds. Our data demonstrate that large infestations by mites result in reduced oxygen carrying capacity of chicks. The extent to which lower hemoglobin levels influence post-fledging survival in starlings remains to be determined, other studies indicate that intensive feeding by *O. sylviarum* on chicks and adults of other species can result in anemia or death of the host (Hofstad et al. 1984). In the domestic fowl *Gallus spp.*, egg production is impaired by 5 to 15 percent as a consequence of mite infestation (DeVaney 1979). Among swallows and thrashers, parasitism by the hematophagous fly *Protocalliphora* can result in poor growth of chicks (Moss and Camin 1971; Arendt 1985a; Brown and Brown 1986; Shields and Crook 1987). Furthermore, high infestations of ectoparasites disrupt breeding efforts by forcing adults to abandon nests (Feare 1976; Duffy 1983). In the case of bird species which typically reuse old nests, large numbers of ectoparasites force adults to delay breeding until new nests are built (Brown and Brown 1986; Barclay 1988). Such delays can influence the probability of successful second breeding efforts (Barclay 1988). Indirectly, hematophagous ectoparasites can act as vectors for avian cholera, fowl pox, viral ornithosis and Newcastle disease, to name but a few documented avian pathogens (Hofstad et al. 1984).

Can plants effectively regulate ectoparasite populations?

There is ample evidence to indicate that metabolites contained within plants can act as toxins to arthropods and pathogens (Frear 1948; Jacobson 1954, 1975; Jacobson and Crosby 1971). Our previous work in the laboratory demonstrated that plants preferred by starlings effectively inhibited bacterial growth and development of the hematophagous louse *Menacanthus* (Clark and Mason 1985). However, the same study also showed that *D. carota*, as well as other plants, had no direct effect on survival of mites, even when the mites were allowed direct contact with the plants. Paradoxically, our present data suggest that *D. carota* effectively reduces mite populations in the field. We conclude that it is unlikely that population control of mites by *D. carota* is affected by lethal doses of toxic compounds. Rather, the significantly lower number of mites found in

nests protected by plants was presumably a result of a delay in the initial colonization of the nest by mites via repellency, inhibition of oviposition, or disruption of the physiological readiness of females to lay eggs.

Because the log number of mites was linearly related to the age of broods (Fig. 1), we were able to project, via regression, the number of mites required to colonize the nests. Nests not protected by plants (PR) needed approximately 100 mites as colonists in order to yield the population observed. Mites colonize nests by leaving the bodies of already infested adults throughout nest-building and incubation (Powlesland 1978). Infestations of 50 to 200 mites are well within the range reported to exist on adults (Boyd 1951; DeVaney et al. 1980). Alternatively, those nests protected by *D. carota* (PA) needed only reduce the colonizing population size to 10–30 mites to yield observed population levels. *D. carota* contains the steroid, β -sitosterol (Duke 1985), which is effective as a repellent and oviposition inhibitor for mites (Ambasta 1980). Coincidentally, β -sitosterol is also found in the leaves of the margosa tree *Azadirachta indica*. Margosa leaves are used in nest-building by house sparrows *Passer domesticus*, much as *D. carota* is used by starlings (Sengupta 1981).

The higher resolution of our laboratory versus our field data on the plant-mite interaction suggest still other biological controls may be exerted on mites. For example, the time course of emergence of mites from the *D. carota* treatment reveals an interesting pattern (Fig. 6). Not only was there a differential emergence of mites from control bags and bags treated with *D. carota*, but also there was a delay in molt associated with treatment by plants.

The major effect of adding either *D. carota* or *E. philadelphicus* to nest material was to decrease the number of mites emerging. Because positive geotaxis is one of the principal behaviors associated with feeding by mites, one plausible interpretation is that these plants contain substances that act to disrupt feeding and behaviors associated with feeding. Such compounds may stimulate inhibitory sensory processes which in turn suppress appropriate orientation behavior (Mustaparta 1984; Stadler 1984).

Many plants contain arthropod juvenile hormone analogs which can delay the transition from one developmental stage to the next (Slama 1979). The emergence of protonymph-1 mites (those never having fed) supports the notion that *D. carota* leaves may contain compounds that delay the molt of mites (Fig. 6). After two days, many of the non-feeding larva from the control half of nests molted to the first feeding protonymph stage, yielding a pulse of mites to be collected as they emerged from the nest matrix. Thereafter, recruitment to the first feeding protonymph stage decreased and a normal exponential decay is emergence was observed (as a consequence of removal sampling). However, the emergence pulse attributable to recruitment in the halves of nests treated with *D. carota* was delayed by two days. No shifts in the emergence of protonymph-2 forms was expected because no molt was involved. The small numbers of adult stages emerging may have obscured any delays attributable to recruitment from the deutonymph stage.

Regardless of the mechanisms involved, any delay or decrease in emergence of mites has two consequences: 1) the *per capita* daily blood loss of chicks is decreased, and 2) without hemolymph, mites would not possess sufficient energy to reproduce. The latter would delay the onset of

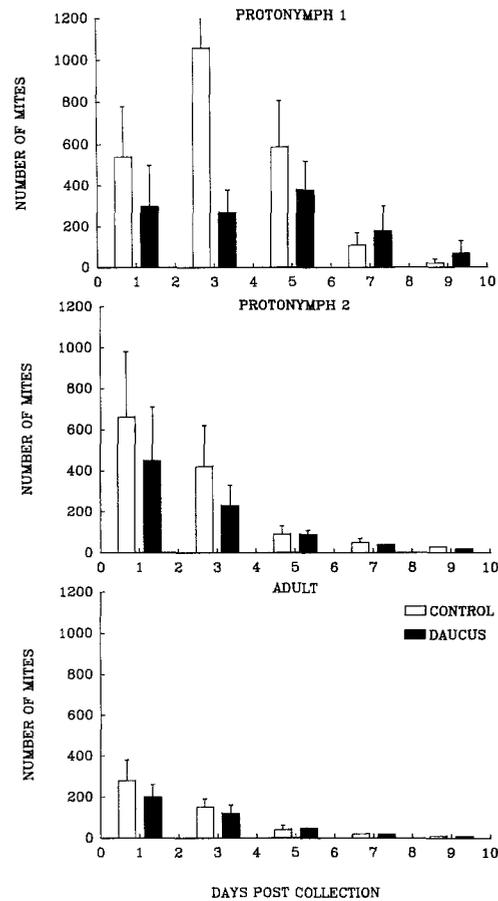


Fig. 6. The time course of the emergence of mites from nests treated with *D. carota* (solid bars) and their corresponding untreated controls (open bars). The vertical bars depict one standard error

population growth of mites until the agents responsible decomposed.

The selection of green plant material

All plants contain secondary metabolites which function as the plants' defense against disease and herbivory. Therefore, a random selection of green plants by birds might be sufficient to chemically protect nests against their own suite of pathogens and parasites. However, in an earlier study we were able to demonstrate that starlings selected some species of plants in quantities greater than their proportional availability in the habitat (Clark and Mason 1985). These preferred plants were more likely to possess antibacterial properties relative to a random subset of plants generally not preferred by starlings. Our present data are consistent with this interpretation. Of the species tested only those species preferred by starlings limited the emergence of mites.

The species of green plants starlings prefer probably change with locale. Birds breeding in England and Ohio seem to show preferences for some plants, but the species involved are not necessarily the same as those preferred in Pennsylvania (P.W. Greg-Smith and R.A. Dolbeer, personal communications). We suspect that starlings use chemical, in addition to visual, cues to differentiate among plants that act as pesticides. Visual cues, such as leaf shape or color, may correlate less well with biologically active properties of plants than do the emitted volatiles. While there

are characteristic chemical differences that do correlate with morphological traits, there is still sufficient chemical variation between individuals to suggest that visual discrimination is an inadequate basis for selection of biologically active leaves (Parks 1974). In our earlier study we were unable to detect any morphological similarity among preferred plants. However, we did observe by gas chromatographic analysis of volatiles that plants preferred by starlings contained more compounds at higher concentrations than a random subset of plants drawn from the environment (Clark and Mason 1985). At the present, we find it unlikely that starlings discriminate among plants based upon specific volatile cues attributable to specific biological activity. Rather, we suggest that starlings use general volatility and chemical complexity as one means of increasing chances of encountering biologically active plant material. Starlings possess the requisite anatomical, physiological and behavioral capacity to perceive and discriminate between plant odors using olfaction (Clark and Mason 1987). Whether they use this capability in the field as a basis for choosing plants remains to be determined.

Acknowledgments. Research support was provided by a grant from the National Geographic Society, 2991-84. We thank K Heinzel for assistance in the field. CA Smeraski was especially helpful for assistance in washing nest material and sorting instars of mites.

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