Use of nest material as insecticidal and anti-pathogenic agents by the European starling

Larry Clark
J Russell Mason

Available at: https://works.bepress.com/larry_clark/117/
Use of nest material as insecticidal and anti-pathogenic agents by the European Starling

L. Clark¹ and J. Russell Mason¹, ²

¹ Monell Chemical Senses Center, 3500 Market Street, Philadelphia PA 19104, USA
² Department of Biology, University of Pennsylvania, Philadelphia PA 19104, USA

Summary. Passerine birds that reuse nest sites face an increased parasite and pathogen load. They also are more likely to use fresh green vegetation during nest construction. The present results demonstrate that at least one passerine, the European Starling: (a) selects a small subset of available plant species for inclusion in nest material; and (b) chooses plants whose volatiles are more likely to inhibit arthropod hatching and bacterial growth relative to a random subset of available vegetation. The results also show that preferred plants possess greater numbers of mono- and sesquiterpenes at higher concentrations relative to a random subset of available plants. These findings strongly suggest that starlings use chemicals in fresh vegetation as fumigants against parasites and pathogens.

Patterns of nest construction

If fresh plants containing chemical compounds act as contact toxicants or natural fumigants, then species tending to nest in previously used sites should be more prone to include fresh plant material into their nests. A review of the natural history literature on nesting behavior and composition of nesting material for 137 passerine birds breeding in eastern North America revealed a significant relationship between nesting mode and the use of green vegetation for nest construction (Bent 1965a–h; Harrison 1975). Passerines nesting in enclosed spaces (e.g. secondary cavity nesters or species using crevices) were more likely to incorporate green plants into their nests, while passerines nesting in open cup nests and characterized by the infrequent reuse of old nest sites were less likely to incorporate green vegetation into their nests ($P < 0.005$, Fig. 1). Notable exceptions occurred. Some secondary cavity nesting species such as nuthatches (e.g. Sitta canadensis and S. carolinensis) did not place fresh plant material into their nests. These species did, however, place pine pitch around their entrance holes or squeeze and rub insects on the surface of the cavity (Bent 1965c).

Given this utilization pattern of nest material among passerines, we set out to address specific questions about the use of nest material in a single species, the European Starling Sturnus vulgaris. We tested three null hypotheses: (1) Starlings randomly select green plants for nest construction from the available vegetation found in the nesting habitat; (2) Plants used by Starlings are not more effective at controlling ectoparasites or pathogenic bacteria than a random subset of vegetation available in the habitat; and, (3) The chemical profiles of volatiles found in plants used by Starlings are not different than profiles of a random subset of vegetation available in the habitat. We focused our analyses on volatile compounds, because the quantity against their own herbivores and pathogens is well established (e.g. Rosenthal and Janzen 1979). Furthermore, extracts and volatiles from a large number of plants are known to be repellent and/or toxic to a variety of arthropods and pathogens (Frear 1948; Jacobson 1954, 1975; Jacobson and Crosby 1971; Secoy and Smith 1983). Therefore, we set out to determine whether or not the pattern of plant use by nesting birds was consistent with the notion that chemical attributes of plants are used to decrease parasite and pathogen load during reproduction.

Long term occupancy of nest sites during a single breeding effort, or over several breeding efforts within a breeding season, increase a bird’s risk of incurring large parasite loads (Stoner 1936; Rothschild and Clay 1957; Wasylik 1971; Smith and Eads 1978; Powlesland 1978; Humphrey-Smith and Moorehouse 1980). Also, because viruses, fungi and bacteria can lie dormant in nest debris and feces for several months, and because they can withstand freezing temperatures (Davies et al. 1971; Hubalek 1978), there is an increased risk of infection to birds breeding at historically active sites. An inability to cope with parasite infestation and/or pathogen infection has led to nest desertion, egg spoilage, and juvenile mortality among several species (Rettger 1913; Neff 1945; Szybalski 1950; Florian and Trussell 1957; Daves et al. 1971; Hoogland and Sherman 1976; Oliphant et al. 1976; Feare 1976; Hitchner 1980; Duffy 1983) and is known to decrease the vigor of nestlings which in turn may diminish their future survivorship probabilities (Moss and Camin 1971; Powlesland 1977; Gold and Dahlsten 1983; Whitman and Bickford 1983).

Many species of birds incorporate fresh vegetation into their nests. One explanation of this behavior is that it is meant to counteract the selective pressure of parasites and pathogens. Chemicals contained in fresh vegetation found in nests may act as repellents, contact toxicants or natural fumigants effective at controlling parasite and/or pathogen populations (Meyers 1922; Johnston and Hardy 1962; Singh 1981; Clark and Mason 1983; Wimberger 1984). The case for plant compounds acting as a chemical defense

Offprint requests to: Larry Clark
of fresh vegetation used in nest construction relative to the dry nest matrix made it seem unlikely plants could serve as contact toxicants for ecto-parasites or pathogens.

Study site. The Starling nesting colony was established in 1971 at the Stroud Water Research Center (SWRC) of the Philadelphia Academy of Natural Sciences, Avondale PA. The habitat lies within the White Clay Creek watershed and is characterized by a patchwork of old fields, secondary growth woodland, and pastureland. The old fields around the research center are maintained via semi-annual mowing. Over the years the size of the colony has ranged from 30 to 100 nest boxes.

Nesting behavior. A detailed account of the nesting behavior of Starlings can be found in Dunnér (1955), Kessel (1957), and Feare (1983). Observations on banded birds at SWRC reveal the following behavioral patterns. Males intermittently visit the nesting area from August to March. Increasing interest in cavity sites is shown by males beginning in December-January. Throughout the late winter months male Starlings spend increasing amounts of time during the mornings in and around one or two nest boxes. At this time males may begin to clear out nest material and debris from the previous season, though this is not always the case (Bent 1965a–h; per. obs.). By March males from the local population are well established at a cavity site, vigorously singing at the nest box in the early morning hours, and defending the nest site against newly arrived young Starlings who are in their first breeding year. These first-year birds are only beginning to establish claim to nest sites in March and April. They are the last birds to occupy available sites.

During March the older males that have established themselves at nest sites begin putting bits of fresh green vegetation into the nest cavity. These bits of vegetation are the tips of new growth of plants and range between 1 and 3 cm in length. The behavior of placing fresh vegetation into the cavity lasts throughout March and into the first week of April. The number of species of plants found in the cavity increases as the availability of vegetation increases. First-year birds follow the same behavior but tend to be less discriminating about which species are laid into the cavity. First year males also tend to place relatively larger amounts of fresh vegetation into the cavity site than older males.

Males initiate nest construction in early April. Nests consist of bulky masses of dried grasses of the previous year’s growth. Woven into the matrix of dried grasses are bits of fresh green plant material. At some point during the early phase of a male’s commitment to a cavity site a female is attracted to the site and/or male. Males then complete nest construction with the aid of a female. Bits of fresh green vegetation are continually added to the nest until the eggs hatch. The behavior of placing fresh plant material into the nest falls off dramatically upon hatching of the eggs. Similar observations on nest building have been reported elsewhere in North America (Kessel 1957), in Finland (Tenovou and Lemmetyinen 1970), and in England (Feare 1983).

Methods

Nest material. We checked nests for green vegetation every three days, from the initial stages of nest building to the hatching of young. We removed nests from the nest box, picked apart the matrix by hand and removed all green vegetation. The green vegetation was labeled and pressed for later identification. The dried nest matrix was reassembled, placed back into the nest box, and a fist was rotated in the nest matrix to form a nest cup. These reconstructed nests resembled natural nests. No birds abandoned their nests as a result of this manipulation.

Vegetation survey. During peak nest building in the last week of April and the first week of May 1984 we sampled the green herbaceous vegetation in plots randomly placed along transects throughout the breeding colony. Areas outside the breeding colony were not sampled because Starlings fly less than 50 m to choose nesting material for their nests (Kessel 1957; Bent 1965h). All above ground stems of green herbaceous plants were counted in each sampling plot. A total of 66 0.5 m$^2$ plots were sampled along 24 transects. Vegetation samples were placed in plastic zip-lock bags, frozen, and stored for subsequent phyto-chemical analysis.

Parasites. Eggs of the louse Menacanthus sp. and adult fowl mites Ornithonyssus sylviarum were collected from adult birds and nests, respectively. Our choice of ectoparasites was dictated by their potential impact on nestling growth and survivorship (e.g. Moss and Camin 1971; Powlesland 1977). The stage of parasite development used for bioassays was constrained by the availability of ectoparasites.

Eggs of the louse were found attached to the base of the feathers on the head and neck of adult birds (see Boyd 1951). These feathers were removed and placed in covered, humidified petri dishes (controls). Experimental treatments consisted of humidified petri dishes with 0.2 grams of plant material. Contact between the eggs on the feathers and plant material did not occur. Dishes were incubated at 30°C ± 1°C, which is within the range of temperature of feathers on live birds (Clark, per. obs.). The viability of the eggs (whether they hatched or not) was checked every other day for eight days. One minus the percentage of eggs that hatched was the effectiveness score for a particular plant. A score of one indicated that a plant was totally
effective at inhibiting or delaying hatching of the Menacanthus eggs. A score of zero meant all eggs hatched and the plant was ineffective at retarding hatching.

Adult fowl mites were collected from infested nest boxes by placing a strip of paper amidst a swarm of mites, allowing the mites to board the paper, then quickly depositing the paper and mites into a vial. In a single experimental treatment 100 adult mites were exposed to the volatiles from fresh leaves. The methods by which mites were handled were similar to those described above.

**Bacteria.** We tested the effectiveness of chemicals contained in leaves at inhibiting bacterial growth for each of four standard strains of bacteria: *Streptococcus aurealis*, *Staphylococcus epidermis*, *Pseudomonas aeruginosa*, and *Escherichia coli*. A nutrient broth inoculated with a single bacterial population was incubated for 24 h in the presence of 1 cm² of sterilized leaf material (the disc). We presumed that any bactericidal compounds in the leaf would diffuse into the nutrient medium and inhibit bacterial growth. Our choice of bacterial strains was based on literature pertaining to the pathogenicity of bacteria (Rettger 1913; Davies et al. 1971).

Leaves were sterilized in a 1:100 dilution of commercial bleach (Chlorox) and sterilized distilled water and subsequently washed in three series of sterilized distilled water baths. This was done to eliminate bacterial and fungal contamination of the leaves, and avoid interactions with the bacterial cultures during the disc diffusion experiments. There were three replications for each plant tested and a control. After a 24 h incubation period the nutrient medium was examined for bacterial growth. Plants were scored as strongly inhibiting bacterial growth (+ + +) if the diameter of the bacteria-free zone around the disc was greater than 1 cm. Plants were scored as effective at inhibiting bacterial growth (+ +) if the bacteria-free zone around the disc was apparent but less than 1 cm. Plants were scored as ineffective if no apparent inhibition of bacterial growth occurred.

We conducted experiments on unsterilized leaves using identical procedures. We carried out similar experiments on mixed populations of bacteria found in nests and cavity sites. Bacteria were collected by swabbing the nest and cavity site with sterilized cotton swabs dipped in sterilized distilled water. Each contaminated swab was transported back to the lab in a sterilized caricature tube. Sterile nutrient medium was innoculated by wiping a contaminated swab on the surface of the nutrient agar. A 1 cm² piece of sterilized leaf was placed on the innoculated nutrient and incubated for 24 h. The experimental and scoring procedures followed were identical to those described above. A similar experiment was carried out on unsterilized leaves.

**Phytochemistry.** The phytochemical analysis of plant volatiles was carried out in consultation with Dr. John Labows, an analytical chemist at the Monell Center. Only large scale patterns of similarity among plants are reported here. A more extensive and detailed analysis of the phytochemistry of plant leaves is forthcoming (L. Clark, J. Labows, and J.R. Mason, unpubl.).

Plant samples were thawed and blotted dry. Five grams of leaf tissue were weighed and placed in a 250 ml flask. Volatiles were collected from the headspace of the flask. The headspace collection was set at 15 min, 37° C, and a flow of 60 ml/min. The volatiles were concentrated on internal absorbent tubes and desorbed automatically to the gas chromatograph (GC) capillary column. Volatiles were also concentrated on absorbent tubes and stored for subsequent gas chromatography/mass spectrometry (GC/MS).

We used a Unacon 810B automatic odor concentrator. Volatiles were concentrated on a trap using a Tenax absorbent. The volatiles were back flushed to a second trap of smaller diameter for further concentration, then to a capillary column of the integral GC unit. The column used was a CP-WAX 30 meter x 0.32 mm heavy-coated fused silica column (Chrompak) and was programmed from 60° (4 min-hold) to 180° at 4°/min. The flow rate was 21 cm/s with hydrogen as the carrier gas. Output from the flame ionization detector was recorded on a SP4100 computing integrator (Spectrophysics). This instrumentation allowed for automatically obtained reproducible GC profiles of the headspace of any sample.

Structural analysis of the components of the sample headspace was done by GC/MS using a Finnegan GC/MS system equipped with a Data General Nova computer system. The system utilized fused silica capillary columns, a specially designed system for desorption of volatiles from Tenax tubes and the 31,000 compound NBS library for mass spectral comparisons.

**Analysis.** Nonparametric tests were used when analyses were based on counts (Conover 1980). Parametric procedures were used when interval data were analyzed (Snedecor and Cochran 1980). Groups analyzed using parametric statistics were tested for homogeneity of variance, and unless otherwise noted, were found to be homogeneous. We used the CLUSTER and TREE routines of the Statistical Analysis System (Sarle 1982) to search for similarities among plants based upon their chemical profiles.

**Results.**

**Plant use.** We recorded 50 herbaceous plant species from a total of 66 sampling plots. An additional 34 herbaceous species were found either by walking through the nesting habitat or by inspection of nest boxes. Because the asymptotic number of plant species found in the habitat was approached after 30 sampling plots (Fig. 2) we concluded that our sampling effort was an adequate description of available vegetation found in the nesting habitat.
A total of 36 nests were censused, and the green vegetation contained within was collected. In all, 38 herbaceous species were recorded from all nests censused, although a small fraction of green vegetation (<5%) from each nest box could not be identified to species.

Based on habitat and nest box sampling efforts we formulated two indices, the mean utilization index ($\bar{U}$) and the mean availability index ($\bar{A}$), for each plant species. We used these to test the hypothesis that green plants used by Starlings were a random sample of available vegetation. The utilization index for a given plant used by Starlings was estimated as

$$\bar{U} = \frac{\sum_{i=1}^{N} \left( \frac{X_{i,k}}{n_i} \right)}{N}$$

the mean percentage of plant $k$ across all nests, where the term $X_{i,k}/n_i$ is the percentage of plant $k$ in nest $i$, $X_{i,k}$ is the number of pieces of plant $k$ in nest $i$, $n_i$ is the total number of pieces of plant in nest $i$, and $N$ is the total number of nests. The availability of a given plant to nesting Starlings was estimated as

$$\bar{A} = \frac{\sum_{j=1}^{P} \left( \frac{X_{j,k}}{p_j} \right)}{P}$$

the mean percentage of plant $k$ across all sample plots, where the term $X_{j,k}/p_j$ is the percentage occurrence of plant $k$ in sample plot $j$, where $X_{j,k}$ is the number of above ground stems of plant $k$ in plot $j$, $p_j$ is the total number of stems in plot $j$, and $P$ is the total number of plots.

Figure 3 is a plot of the utilization of plants by Starlings relative to the availability of plants found in the nesting habitat. The graph is divided into three regions. The diagonal line represents a hypothetical selection scheme by Starlings where plants were selected in proportion to their availability. In general, the region above the line represents a region where plants were selected in numbers greater than their proportional availability (i.e., were preferred by Starlings). The region below the diagonal represents a region where plants were selected for use in nests in numbers less than their proportional availability (i.e., were avoided by Starlings).

The point $(A_k, U_k)$ is only an estimate of the utilization and availability of each plant species. Sampling errors by Starlings (in terms of utilization) and by the investigators (in estimating availability) will tend to increase error in classification of plant species, i.e. whether a plant is preferred (falls in the region above the diagonal line), is selected in proportion to its availability (intersects the diagonal line), or is avoided (falls below the diagonal line). The standard errors about $A_k$ and $U_k$ were used as the major and minor axes of a standard error ellipse about each point. If any part of the error ellipse intersected the diagonal line the plant was scored as being selected in proportion to its availability. If the error ellipse fell fully above the diagonal the plant was scored as preferred, and the plant was scored as avoided if the error ellipse fell fully below the diagonal.

We scored the number of plants occurring in each of the three regions to test the hypothesis that there was no difference in our expectation of occurrence of plant species for each of the three selection schemes. That is to say, any observed differences in the distribution of plants represented chance variation in a random sample from the available pool of plants. Nine species were preferred by Starlings, 34 were selected in proportion to their availability, and 23 were avoided. We concluded that the plants used and preferred were too few to fit into a random selection scheme proposed under the hypothesis (one-tailed Kolmogorov-Smirnoff test, $P < 0.005$).

**Parasites and pathogens.** The results obtained for sterilized vs unsterilized leaves were similar. In general, plants scored as preferred by Starlings were more effective at controlling bacterial growth for the pure laboratory strains of *S. aurea*-lis, *S. epidermis*, and *P. aeroginosa*. No plants were effective against *E. coli* populations (Table 1).

We also cultured native populations of bacteria found in nests in the presence of plant leaves to test the hypothesis that the mean utilization score associated with a plant species effective at inhibiting bacterial growth was the same as the mean utilization score for plant species not effective at controlling bacterial growth (Fig. 4). We found that plants effective at inhibiting bacterial growth had a higher average utilization score (one-tailed $t = 2.06, P < 0.05$).

Volatiles from plants preferred by Starlings were more effective at retarding hatching of *Menacanthus* eggs than volatiles from a random sample of plants that were not preferred (one-tailed $t = 3.39, P < 0.005$; Fig. 5). A similar test for the effectiveness of volatiles against the adult stage of the fowl mite yielded no significant difference between mortality of mites for the two groups of plants. In fact, after three days of exposure to the volatiles, no mites had expired in either group, and after five days of exposure only a few mites from any group had died.
Table 1. Disc diffusion experiments. The effectiveness of unsterilized plant material at inhibiting bacterial growth on a nutrient medium. The symbol ++ represents highly effective plants, + moderately effective plants, blank non-effective plants, and — for plants not tested. See methods and results for a more detailed discussion. The asterisk indicates species of plants classified as preferred by Starlings. Codes are Se Staph epidermis, Pa Pseudomonas aeruginosa, Ec Escherichia coli, Sa Streptococcus aurealia, and NB swabs from nests and nest boxes. Unk 21 is an unidentified plant species.

<table>
<thead>
<tr>
<th>Plant Species</th>
<th>Bacteria Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lamium purpureum*</td>
<td>Se Pa Ec Sa NB</td>
</tr>
<tr>
<td>Daucus carota*</td>
<td>+ +</td>
</tr>
<tr>
<td>Achillea millefolium*</td>
<td>+</td>
</tr>
<tr>
<td>Agrimonia paraflora*</td>
<td>++ ++ ++</td>
</tr>
<tr>
<td>Solidago ulmiflora</td>
<td>+ +</td>
</tr>
<tr>
<td>Solidago rugosa*</td>
<td></td>
</tr>
<tr>
<td>Conium maculatum</td>
<td></td>
</tr>
<tr>
<td>Polemonium reptans</td>
<td></td>
</tr>
<tr>
<td>Glechoma hederacea</td>
<td></td>
</tr>
<tr>
<td>Geum virginianum</td>
<td>+</td>
</tr>
<tr>
<td>Geum canadense</td>
<td></td>
</tr>
<tr>
<td>Taraxacum officinale</td>
<td>+</td>
</tr>
<tr>
<td>Lonicera japonica</td>
<td>+</td>
</tr>
<tr>
<td>Alliaria officinalis</td>
<td>+</td>
</tr>
<tr>
<td>Senecio obvatus</td>
<td>+</td>
</tr>
<tr>
<td>Unk 21</td>
<td></td>
</tr>
<tr>
<td>Viola sp.</td>
<td></td>
</tr>
</tbody>
</table>

Fig. 4. The utilization score of plants used by Starlings as a function of the plant's effectiveness at controlling cultures of bacteria obtained from nests and cavity sites. The horizontal line is the mean, the vertical rectangle is ± standard error, and the vertical line depicts the range. The number above each mean is the sample size.

Similarities of chemical profiles. Plants were assigned two groups. Group 1 was designated as the preferred group, and consisted of: Agrimonia paraflora, Daucus carota, Eriogon sp., and Solidago rugosa. Group 2 was a randomly chosen subset of plants that either were used by Starlings in proportion to their availability or were avoided. The plants in this group were: Potentilla recta, Brassica nigra, Polemonium reptans, Claytonia virginica, and Viola sp. We examined the chemical profiles of the two groups of plants for differences in general volatility and similarity of concentration of chemical compounds.

We recognized the possibility that volatile compounds found in minute concentrations may be biologically important, i.e. toxic to pathogens. Nonetheless, in order to reduce the number of compounds to a manageable level in the initial analysis, we compiled a composite list of all compounds found in all 12 plant species. We eliminated from further consideration those compounds that did not have a concentration of at least 10 percent of the standard for at least one of the 12 species considered. This criterion reduced the number of compounds considered to 26. Within each of the two groups of plants and for each of the 26 compounds we calculated a "chemical score". The chemical score was the number of plants that had a concentration of a given compound greater than 10 percent of the standard. For a given compound, the chemical score had a range of 0 to 6:0 if no plants within that group met the criterion condition and 6 if all plants within that group met the criterion condition. The frequency of these scores (summed across all compounds within each group) is plotted in Fig. 6. If the two groups possessed the same number of compounds meeting the criterion condition, then the two distributions should have been the same. This was not the case (Kolomogorov-Smirnoff two-tailed test, P < 0.01). The plants used by Starlings were characterized by an overall higher volatility in terms of the number of compounds. Similar conclusions were reached with respect to concentration of compounds. Plants preferred by Starlings had higher concentrations of the compounds considered (Wilcoxon matched-pairs test, z = -1.73, P < 0.042).

Simple dissimilarities between the groups and similarities within groups for the chemical constituents were not apparent. Figure 7 presents a cluster analysis of the 26 compounds for the 12 plants considered (3 replications each). The dendrogram did not reveal any clear cut dichotomous relationship between groups I and II for the ordering of individual plants. Using the cubic clustering criterion outlined by Sarle (1982) to evaluate the number of clusters, two results are obtained. First, the distribution tends to be grainy, possibly due to small numbers of observations per plant species and large variability in the chemical pro-
files of plants. Increased sample sizes may clear up this problem. Second, between 6 and 9 clusters are presented as an indication of good groupings (subject to the caution of the first finding). The result is pairs of plants bear close similarity towards one another, and these pairs are usually found within the same group (i.e. preferred or other). But no broader generalization about similarities emerges from this analysis.

Data from the GC/MS analysis indicated that the volatiles contained within plants were largely mono- and sesquiterpenes, e.g. myrcene, α-pinene, and limonene. A more detailed analysis of the chemical composition of plants is pending (Clark, L., J. Labows, and J.R. Mason in prep.).

Discussion

The use of small quantities of fresh vegetation for nest construction has perplexed many biologists, especially in view of the great lengths many birds go to obtain it (i.e. Gibb 1950; Collias and Collias 1984). Several explanations have been offered for the behavior. First, green vegetation may enhance the crypticity of a nest, and thus minimize risk due to predation from visually orienting predators (Skutch 1976). Second, fresh vegetation may reduce the rate of desiccation of eggs (and thereby improve their hatching success) by raising the vapor pressure in the nest environment (Taverner 1933; Sengupta 1968). Unfortunately, no experiments have been carried out to test this hypothesis, nor are there theoretical calculations available to suggest the contributions of leaves at maintaining low vapor deficits within nest cups. Third, the form of a nest matrix may largely be influenced by structural and thermal properties of material conferring survival advantage to chicks (Kern 1984; Kern and Van Riper 1984). Dry material, the primary nest matrix for most species, provides better insulation than damp or fresh vegetation (Mertens 1977). However, many plant defensive compounds are likely to have been leached out, decomposed, or volatilized from dead plant material. A fourth hypothesis, supported by the present experiments is that green plants act as natural fumigants. Birds may be able to capitalize on the defensive attributes of naturally occurring plant chemicals found in fresh vegetation without altering the thermal properties of the nest by weaving small quantities of chemically laden green plants into the matrix. Several lines of evidence indicate birds act in such a manner. For example, Sengupta (1981) reported that House Sparrows Passer domesticus incorporated margosa Azadirachta indica leaves into their nests and that these leaves were used in preference to other available vegetation. Isolated fractions from leaves were not only repellent to arthropods but also inhibited oviposition on treated surfaces. The suspected active chemicals were a steroid, β-sitosterol and the phenolic, quercetion (Ambasta 1980). Similarly, nuthatches frequently smear nest cavities with pine resin (Bent 1965c). Such resins contain a diversity of monoterpenes (e.g., α and β pinene), known for their antiseptic and toxologic properties (Rosenthal and Janzen 1979).

Our own work indicates that the number and quantity of different plant species incorporated into the nest structure is variable. Young, first-year breeding birds are apt to be cosmopolitan in their selection of green plant material. Prior breeding experience, influence of mates on the selection of plant material, and exposure to plants as nestlings, as well as availability of vegetation in the habitat, and random sampling by birds may all influence the composition of nest material. Yet for all the potential sources of variability, there is no question that Starlings prefer only a limited subset of the available vegetation for use in nest construction (Fig. 3). These plants are not randomly selected and they are chosen in numbers greater than their proportional availability in the habitat.

In general, those plants preferred by Starlings were more odorous, i.e. contained more volatile compounds at higher concentrations relative to a random selection of plants not preferred by Starlings. Our initial phytochemical surveys indicated that the preferred plants contained relatively more monoterpenes at higher concentrations than a randomly selected subset of plants chosen in proportion to their availability or avoided (e.g., α & β pinene, myrcene, cymene, ocemene, α-phellandrene, α-terpineol, limonene, δ3-carene, sabine, and terpinolene). At least one of the preferred plants, Solidago rugosa, contained the sesquiterpenes 2-bornyl acetate and farnesol. These compounds have been impli-
cated as potent juvenile hormone analogs (in Rosenthal and Janzen 1979, pp. 684–688). Such compounds generally suppress molting in arthropods. Any such action of compounds on ectoparasites would delay the timing of terminal instars and hence curtail the reproductive capacity of the parasites. As a consequence, the rate of population growth of some arthropods would be severely reduced. Certain ectoparasites, such as the fowl mite, can progress through five instars within a period of seven to fourteen days. The intermediate instars are feeding stages, while the ultimate instar is the reproductive phase. The implied importance of plant derived juvenile hormone analogs can be appreciated when one considers that the per capita blood loss for a brood of four in a heavily infested nest (>50,000 mites) can be 3.5 percent of the daily blood production of chicks (Powlesland 1978).

How Starlings perceive differences among plants to form associations between the chemical properties of plants and effect against parasites and pathogens is unclear. However, because some plant fractions are effective as insecticidal and anti-pathogenic agents there may be a selective premium for Starlings to discriminate among green plants and form associations for effect on the basis of cues of high relevance. Chemical, rather than visual, differences are a likely basis for discrimination because of the high variability of chemical profiles found within plants, even of the same species (Parks 1974). Plants available for use as nest material differ throughout the breeding range of Starlings. The use of morphology (and by implication visual cues) as the sole criterion for plant selection would not guarantee a bird the access to a particular chemical profile. A more efficient and reliable method of choosing plant material would be to use cues (i.e. chemical) that are more directly responsible for insecticidal and anti-pathogenic effects, a notion that suggests further rigorous testing (Clark and Mason, in prep.).

Acknowledgements. This study was funded by Public Health Service NRSA grant # 5 T32 NS07176-05 to the Monell Chemical Senses Laboratory and Janzen 1979, pp. 684–688). Such compounds generally suppress molting in arthropods. Any such action of compounds on ectoparasites would delay the timing of terminal instars and hence curtail the reproductive capacity of the parasites. As a consequence, the rate of population growth of some arthropods would be severely reduced. Certain ectoparasites, such as the fowl mite, can progress through five instars within a period of seven to fourteen days. The intermediate instars are feeding stages, while the ultimate instar is the reproductive phase. The implied importance of plant derived juvenile hormone analogs can be appreciated when one considers that the per capita blood loss for a brood of four in a heavily infested nest (>50,000 mites) can be 3.5 percent of the daily blood production of chicks (Powlesland 1978).

How Starlings perceive differences among plants to form associations between the chemical properties of plants and effect against parasites and pathogens is unclear. However, because some plant fractions are effective as insecticidal and anti-pathogenic agents there may be a selective premium for Starlings to discriminate among green plants and form associations for effect on the basis of cues of high relevance. Chemical, rather than visual, differences are a likely basis for discrimination because of the high variability of chemical profiles found within plants, even of the same species (Parks 1974). Plants available for use as nest material differ throughout the breeding range of Starlings. The use of morphology (and by implication visual cues) as the sole criterion for plant selection would not guarantee a bird the access to a particular chemical profile. A more efficient and reliable method of choosing plant material would be to use cues (i.e. chemical) that are more directly responsible for insecticidal and anti-pathogenic effects, a notion that suggests further rigorous testing (Clark and Mason, in prep.).

Acknowledgements. This study was funded by Public Health Service NRSA grant # 5 T32 NS07176-05 to the Monell Chemical Senses Center and L. Clark. Broad support was also provided by the U.S. Fish and Wildlife Service to J.R. Mason. We thank Dr. J. Labows and S. Aldinger for technical assistance on the phytochemical analysis. C. Smeraski graciously assisted in the field. We thank R. Vannote and the staff of Stroud Water Research Center of the Philadelphia Academy of Natural Sciences for their support. Drs. G. Beauchamp, A.N. Gilbert, and D. Janzen were most helpful in reading an earlier draft of this paper.

References


Bent AC (1965b) Thrushes, Kinglets, and Their Allies. Dover, New York


Bent AC (1965d) Blackbirds, Orioles, Tanagers, and Their Allies. Dover, New York


Dunnet GM (1955) The breeding of the starling Sturnus vulgaris in relation to its food supply. Ibis 97:619–662

Fare C (1976) Desertion and abnormal development in a colony of Sooty Terns Sterna fuscata infested by virus-infected ticks. Ibis 118:112–115


Hitchener SB (1980) Isolation and Identification of Avian Pathogens. Amer Assoc Avian Path College Station, Texas


Mertens JAL (1977) Thermal conditions for successful breeding in Great Tits (Parus major major L). II. Thermal properties of nest and nestboxes and their implication for the range of temperature tolerance of Great Tit broods. Oecologia (Berlin) 28:31–56


Neff JA (1945) Maggot infestation of nestling mourning doves. Condor 47:73–76
Rettger LF (1913) The bacteriology of the hen’s egg with special reference to its freedom from microbe invasion. Bull Conn Univ Storrs Agr Expt Sta 75:187
Skutch AF (1976) Parent Birds and Their Young. Univ Texas Press, Austin
Smith GC, Eads RB (1978) Field observations on the Cliff Swallow, Petrochelidon pyrrhonota (Vieillot), and the swallow bug, Oeciacus vicarius Horvath. J Wash Acad Sci 68:23–26
Stoner D (1936) Studies on the Bank Swallow Riparia riparia (Linnaeus) in the Oneida Lake Region Roosevelt Wildl Annual 4:126–233
Taverner PA (1933) Purple Martins gathering leaves. Auk 50:110–111
Widmann O (1922) Extracts from the diary of Otto Widmann. Trans Acad Sci St Louis 24:1–77

Received November 29, 1984