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Use of California bay foliage by wood rats for possible fumigation of nest-borne ectoparasites

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Studies were conducted to test the hypothesis that dusky-footed wood rats (*Neotoma fuscipes*) place bay leaves (*Umbellularia californica*) on or near the sleeping nest in their stickhouses, with the result that the leaves act as a fumigant against nest-borne ectoparasites. Although many stickhouses were found to contain bay, oak, and toyon leaves, only bay was found significantly more often near the nest than away from the nest. Bay leaves were nibbled in a fashion consistent with the release of fumigating volatiles. Oak leaves, a known food staple, were nibbled in a fashion more consistent with eating. Analysis of the density of ectoparasites in samples of sleeping nest material showed few parasites in most nests, but heavy infestations in a few nests revealed the potential for large numbers of nest-borne ectoparasites. Samples of 1 g of whole and torn leaves of bay, toyon, and oak were incubated with flea larvae in mason jars for 72 h. Torn leaves (to simulate nibbling effects) of bay significantly reduced larval survival to 26% compared to 87–94% survival of larvae incubated with torn oak and toyon leaves. These findings provide evidence that dusky-footed wood rats place bay foliage around the sleeping nest with the effect of reducing their exposure to nest-borne ectoparasites. *Key words:* antiparasite behavior, ectoparasites, *Neotoma fuscipes,* nest fumigation, plant volatiles, *Umbellularia californica,* wood rats. *[Behav Ecol 13:381–385 (2002)]*

There is increasing evidence that ectoparasites can produce fitness costs in hosts, presumably resulting in selection for defensive behaviors against parasites (Hart, 1990, 1992; Lehman, 1993). Rodents that dwell in nests or burrows are particularly susceptible to the buildup of nest-borne ectoparasites because the microclimate of occupied burrows provides a dark, moist, and warm environment, and the year-round presence of the host provides a regular food supply. In addition to grooming, one way of dealing with the threat of nest-borne parasites is to change nest sites, a practice not uncommon in birds (Duffy, 1983; Hart, 1997; Møller, 1990). If an animal can continue to use an old nest, the costs of changing nest sites should be avoided, provided the excessive build-up of ectoparasites can be prevented.

One type of nest protection against ectoparasites in avian species is the use of certain volatile-producing plants woven into the nest matrix. The nest fumigation hypothesis was initially suggested by Wimberger (1984) and was experimentally pursued by Clark and Mason (1985, 1988) in the European starling (*Sturnus vulgaris*). Starlings selected plants that released the most volatiles, and in laboratory tests, volatiles of some plants suppressed the hatching of louse eggs and the development of mites. Plants produce these volatile products to protect against insect herbivores (Langenheim, 1994; Swain, 1977) and pathogenic microorganisms (Deans and Ritchie, 1987; Knobloch et al., 1989).

Exploring the nest fumigation hypothesis in burrowing mammals would be difficult because of the inaccessibility of the nests. Wood rats construct above-ground stickhouses with accessible sleeping nests. Previous investigators (Linsdale and Tevis, 1951; Vestal, 1938) have noted that the folivorous, dusky-footed wood rat (*Neotoma fuscipes*) brings fresh, green foliage into its stickhouse. The presence of foliage in stickhouses has been interpreted as food storage, and the typical foods of *N. fuscipes,* which include oak foliage (*Quercus* spp; Atsatt and Ingram, 1983), were common in the houses that we inspected in preliminary observations. Our preliminary observations also revealed that California bay (laurel; *Umbellularia californica*) was present in many stickhouses in relatively large quantities. This was of interest because *N. fuscipes* is believed not to use bay foliage as a food staple; it eats only blossoms of bay (Cranford, 1977; Linsdale and Tevis, 1951). Our preliminary observations also revealed that rats typically nibble on bay and on toyon (*Heteromeles arbutifolia*), another frequently found plant, as well as on oak leaves.

California bay has a high monoterpenoid content, which is noted for its biocidal activity; correspondingly, bay exhibits little evidence of insect herbivory or disease (Fowells, 1965). The major constituents of volatile oils in the foliage of California bay are 1,8-cineole (19%), which is primarily responsible for the leaves' distinctive odor, and umbellulone (39%), which has been shown to be toxic when fed to laboratory mice (Buttery et al., 1974; MacGregor et al., 1974). Bay leaves are reputed to be effective in repelling fleas from humans and human dwellings (Balls, 1962; Chestnut, 1902), so their presence in stickhouses raises the question of the possible use of bay foliage as a fumigant to control one or more developmental stages of ectoparasites.

There were three aspects to this study. The first dealt with a quantitative description of the location and turnover of leaves within the nest, as well as the pattern of nibbling on bay compared with nibbling on oak and toyon leaves. The second aspect was an analysis of the nest matrix from wood rat houses for types and numbers of ectoparasites. Third, because fleas are known to infest adult wood rats and were usually found in samples of sleeping nest material, an experiment was designed to test the comparative effectiveness of volatiles from bay, oak, and toyon on killing flea larvae.

Study species

Dusky-footed wood rats, or packrats as they are often called, construct durable, above-ground stickhouses using available

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twigs and woody debris from the forest floor. These stickhouses offer protection from the weather and predators. Because of the ever-present threat of predators (Verts and Carraway, 1998), wood rats remain in their stickhouses except for nocturnal excursions for foraging and bringing sprigs of foliage and building materials back to their houses (Vestal, 1938). Radiotelemetry and live-trapping data suggest that wood rats occupy the same stickhouse for several months at a time (Cranford, 1977; Wallen, 1982). Linsdale and Tevis (1951) reported that stickhouses are occupied serially generation after generation and may last a decade or longer. This pattern of stickhouse reuse would suggest a risk of ectoparasite buildup.

METHODS

Study site

The study population was located in Sonoma County, northern California, USA, in a mixed hardwood forest of 80 ha. The forest was located on a predominantly north-facing slope with elevations of 60–150 m above sea level. Most numerous among the trees which made up the closed canopy were California bay, coast live oak (*Q. agrifolia*), and interior live oak (*Q. wislizenii*). Much less numerous among the trees were Douglas fir (*Pseudotsuga menziesii*) and madrone (*Arbutus menziesii*). Common woody plants in the understory were toyon, California hazel (*Corylus cornuta*), and poison oak (*Rhus diversiloba*). The herbaceous layer was dominated by sword fern (*Polystichum munitum*), miner's lettuce (*Monitia perfoliata*), cow parsnip (*Heracleum lanatum*), and false Solomon's seal (*Smilacina racemosa*).

Observations at our study site revealed that stickhouses were nonrandomly distributed in the forest and were found where oak stood alone or where it intermingled with other trees, especially bay and/or toyon. Areas without oak trees contained no stickhouses. Nearly all of the stickhouses were on the ground; the few that were located in the tree canopy (estimated at less than 5%) were not studied. Houses were 1.0–1.5 m in height and 1.5–2.5 m diam at the base and were constructed of decaying sticks and fragments of bark. Some had fronds (fresh and/or dried) of sword fern woven into the structure. Approximately half of the houses were constructed next to, or among, diverging trunks of bay or oak trees; others were free standing or enclosed within poison oak shrubbery. Individual leaves and sprigs of fresh foliage were regularly found throughout the interior of the stickhouses. Sleeping nests were constructed of lichens, mosses, dried grasses, and shredded bark and wood and varied considerably in mass (30–215 g). Nests contain a pocket approximately 8 cm diam. The arrangement, size, and number of chambers and tunnels within stickhouses were variable and similar to that described by previous investigators (Linsdale and Tevis, 1951).

Location, turnover, and pattern of nibbling on leaves

If bay foliage were used by wood rats to control nest-borne ectoparasites, one would predict that this foliage would be found disproportionately near the sleeping nest, compared to other species of foliage used as food. Bay would also be frequently replaced in order to keep levels of volatiles high. Further, because of the containment of volatiles within secretory idioblasts scattered through the bay leaf (Klasapligil, 1951), volatiles would be released more readily if the leaf were cut or broken open by sporadic nibbling. Although rats might nibble on both food staples and bay, the pattern of nibbling should be different between bay and food staples such as oak leaves. A leaf partially consumed as food would be expected to be missing substantial amounts of tissue at one end or from margin to central vein, whereas a leaf damaged to increase release of volatiles would be expected to exhibit torn tissue without much tissue missing. These predictions were explored in this study conducted during the months of June–August 1994 (year 1) and 1995 (year 2).

We inspected chambers through an entrance tunnel with a videostick (a small CCD video camera mounted on the end of an articulating wand; RJ Electronics, Salem, Oregon) introduced through an existing tunnel entrance or a small hole on one side of the stickhouse. In 1994, 34 marked stickhouses were examined to determine the location of foliage types within the chambers. In 1995, 16 additional houses not observed in 1994 were examined to extend the sample. For the purposes of analysis, the two species of oak were combined. The areas within each stickhouse were designated as ''near the nest'' and ''non-nest areas''; leaves located on the rim of the sleeping nest or within 5 cm of the sleeping nest were referred to as ''near the nest.''

We measured turnover of foliage in 1995. Nine houses were each inspected five times at intervals of 2–3 days over a period of 2 weeks. At the time of each inspection, all foliage was removed from the house after noting the location of each item. Individual leaves were distinctively marked with a paper punch and the foliage was then replaced in the same location from which it had been removed. For each reinspection it was possible to assess how much of the foliage present had been added since the previous inspection and thus calculate the proportion of the total foliage that was new. For each house we used the average of these proportions as the estimate of turnover of each plant type.

In 1994, we measured the percentage of houses in which nibbling was observed on any of the three plant types for the 34 stickhouses. We also recorded the pattern of nibbling on each plant species, differentiating between that expected to apply to eating versus that for the release of volatiles.

Ectoparasites in the sleeping nests

We evaluated ectoparasites in sleeping nests in the summers of 1995 (year 2), 1997 (year 4), and 1998 (year 5), inspecting 11, 7, and 10 different nests, respectively, in these years. Complete nests were removed through a small hole in the wall of each stickhouse. The nesting material was immediately placed in a deep plastic bowl, weighed, and then mixed in an attempt to evenly distribute ectoparasites before sampling. A sample of 20–30 g of material was sealed in a plastic bag for extraction of nest-borne ectoparasites. The remaining material was replaced in the nest chamber, and the sticks that had been removed were replaced in the wall. This procedure apparently had no lasting effect on the occupant because a few days later stickhouses were found to contain fresh vegetation, and the sleeping nest's shape had been restored.

Nest material was subjected to a modified Berlese-Tullgren extraction (Southwood, 1978). Two replicate 10 g samples were placed into polypropylene funnels, each containing a 1.7-mm mesh aluminum screen floor to support the sample and each covered with elasticized nylon cloth to prevent escape of ectoparasites. Each funnel was placed 7 cm beneath a 50-W floodlight for 2 days to drive adults and immature forms of ectoparasites from the nest material into the funnel. The spout of each funnel led to a collection tube containing 5 ml of 80% ethyl alcohol preservative. Preserved material in the tube was later passed through filter paper so that we could identify and count ectoparasites. Preliminary trials indicated that no live mobile ectoparasites remained in the nest material after 48 h. We counted mature fleas, flea larvae, and ticks (larval and nymphal stages combined) under a dissecting microscope. Estimated numbers of ectoparasites in the entire nest were calculated on the basis of extrapolation from the proportional weight of the nest samples evaluated. Two genera of fleas (*Orchopeas* sp. and *Anomiopsyllus* sp.) parasitize wood rats (Lindsdale and Davis, 1958). For the purposes of this study, adult and larval fleas of both species were combined.

Effects of leaf volatiles on flea larvae

We used cat fleas (*Ctenocephalides felis*) in this experiment because this is the only species readily available in large numbers. Larvae, rather than eggs or adults, were chosen for the assay because larvae have a soft integument compared to the possibly more protective capsule of eggs and exoskeleton of adults and because larval growth extends over a period of 8–10 days before pupation (Silverman et al., 1981). In nature, larvae in the nest would be exposed to volatiles over this 8- to 10-day period. We tested equal quantities of whole and torn leaves of each of the three plant species regularly found in the stickhouses. Tearing of the leaves was intended to simulate nibbling and increase the release of volatiles.

The experiment (conducted May–June 2000) tested whole and torn leaves from 10 bay trees, 10 oak trees, and 10 toyon trees at our research site. All 30 trees sampled were located in areas with active wood rat stickhouses nearby. The sprigs selected from each tree showed no visible signs of disease. We collected sprigs at 1100–1700 h, placed them in plastic bags, and refrigerated the bags within 2 h of harvest. Cat flea eggs from a commercial supplier (El Lab, Soquel, CA) were collected 24 h after oviposition and arrived in our laboratory the next morning. Eggs were placed in an incubator at 24–26°C with relative humidity maintained at 75–80%. Hatching of eggs into larvae was complete 4 days after their collection by the supplier, at which time we exposed the larvae to the leaves.

Exposure of larvae to leaves occurred in sealed 1-quart mason jars. Each jar lay on its side and contained a 12 × 5 × 3 cm high plastic tray, which held a heap of 80 g of NaCl and 50 g of saturated NaCl solution. This kept the relative humidity inside the jar, once sealed, between 75–80%, countering the tendency of transpiration of the leaves to raise it above optimal level. On the top of the tray was hardware cloth fashioned to remain securely in place and to provide a stable setting for a 60 × 15 mm petri dish containing larvae. Larvae, along with particles of larval food (feces of adult fleas fed blood in a membrane culturing technique), were sprinkled into each dish until the number of larvae was between 20 and 30, the exact number of larvae being recorded for each dish. A piece of 1.7-mm mesh aluminum screen was placed above the dish with larvae, and it was on this screen that 1 g of torn or whole leaves was placed just before the jar was sealed. We used 12 mason jars in assessing each tree; five contained whole leaves, five contained torn leaves, and two contained no foliage and served as controls. Thus each foliage sample was tested with 100–150 larvae. Mason jars were placed in incubators to control temperature between 24° and 27°C. We counted the number of live larvae in the five dishes 3 days later. We determined the total number of larvae that had survived for each plant species under both torn- and whole-leaf conditions on each trial and compared this number to the number originally present. Whole and torn leaves for each plant species were from the same branch, and tearing created leaf fragments 1–2 cm wide. Previous experience with this system revealed that on rare occasions the water content of the foliage sample surpassed the capacity of the salt to regulate the relative humidity, resulting in the larval food particles liquifying, entrapping, and suffocating larvae and invalidating

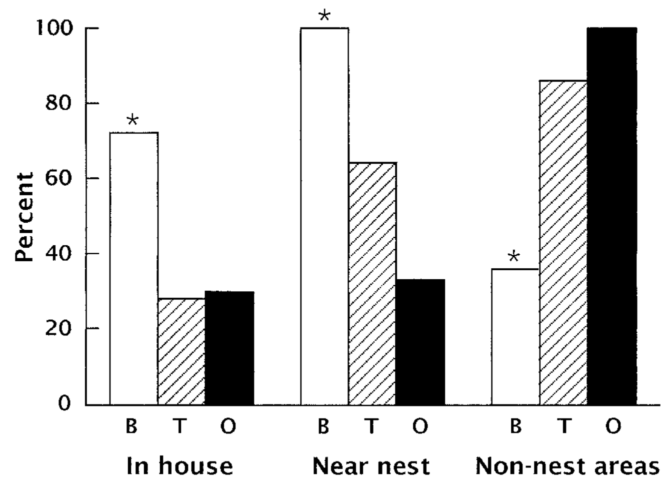

Figure 1
Percentage of stickhouses in which foliage of each of three species of plants were found and the percentage of houses containing each species in which foliage of that species was found near the sleeping nest or in non-nest areas. *Significant difference (in house, $p < .001$; near nest, non-nest areas, $p < .02$). B, bay; T, toyon; O, oak.

the results of that dish. If this occurred in more than two of the five dishes being used to assess a foliage sample, we eliminated data from that tree from the analysis.

RESULTS

Location, turnover, and pattern of nibbling on leaves

Almost all houses contained fresh leaves of one or more of the four species of interest—California bay, interior live oak, coast live oak, and toyon. Poison oak, false Solomon seal, cow parsnip, and miner's lettuce were found infrequently. Toyon usually was found as individual leaves, whereas oak and bay were most often found as sprigs. As illustrated in Figure 1, foliage of bay was found in 72% of the 50 houses, compared to about 30% for toyon and oak. This difference in the occurrence of bay in stickhouses in comparison with toyon and oak was significant ($\chi^2 = 14.24$, df = 2, $p < .001$). Of those houses where foliage of each plant species was found, Figure 1 also shows that bay was much more likely to be found near the nest than toyon or oak ($\chi^2 = 8.78$, df = 2, $p < .02$) and much less likely to be found in non-nest areas than toyon or oak ($\chi^2 = 8.60$, df = 2, $p < .02$).

Bay was nibbled in 43% of houses in which it was found; for toyon and oak the values were 80% and 75%, respectively. Chi-square analysis indicated that differences in the occurrence of nibbling seen in bay, oak, and toyon were not statistically significant. The pattern of nibbling on oak and toyon leaves was of the sort expected for food items, but the pattern of nibbling on bay was not, consisting of individual shallow bites around the margin of the leaf with little tissue removed. Replacement of oak, toyon, and bay foliage within stickhouses was frequent, with a mean turnover of 80% ($n = 9$), 78% ($n = 9$), and 68% ($n = 9$) for oak, toyon, and bay, respectively.

Ectoparasites in the sleeping nest

Agreement between the two 10-g replicates of each of 28 nests was significant for the flea larvae (Spearman correlation coefficient, $r = .56$, $p < .05$) and adult fleas, ($r = .68$, $p < .05$), but not ticks ($r = .39$). Estimates of the number of ectoparasites in the nest were calculated using the mean of the two replicates. Ectoparasite numbers varied considerably between

Table 1
Median (range) of ticks (larvae and nymphs combined), fleas, and flea larvae from sleeping nests in 3 years

Year	*N*	Ticks	Fleas	Flea larvae
1995	11	158 (0–601)	8 (0–63)	57 (12–174)
1997	7	72 (0–411)	0 (0–400)	0 (0–11)
1998	10	319 (78–497)	8 (0–46)	29 (5–223)

years and among stickhouses within a year (Table 1). Median numbers of ectoparasites were lower in 1997 than in the other 2 years. The numbers of parasites at the upper ends of the reported ranges (e.g., 601 ticks; 223 flea larvae) indicate that heavy infestations in the sleeping nest are sometimes realized.

Effects of leaf volatiles on flea larvae

The results of incubating flea larvae with exposure to either torn or whole leaves of each plant species is illustrated in Figure 2. Data from one oak and one toyon were eliminated because of liquification of larval food particles in three of five dishes; thus sample sizes for bay, toyon, and oak are 10, 9, and 9, respectively. A two-way ANOVA conducted on arcsine-transformed data revealed significant factor effects for species ($F = 29.37$, df = 2, 50; $p < .0001$) and leaf condition ($F = 51.65$, df = 1, 50; $p < .0001$) and a significant interaction between factors ($F = 31.54$, df = 2, 50; $p < .0001$). Inspection of Figure 2 indicates that torn bay leaves with a survival of 26.4% were responsible for the significant factor and interaction effects. Mean survival rates for other leaf types ranged from 87.6 to 94.4%. Mean survival rate for jars containing no foliage ($n = 60$) was 94.9%.

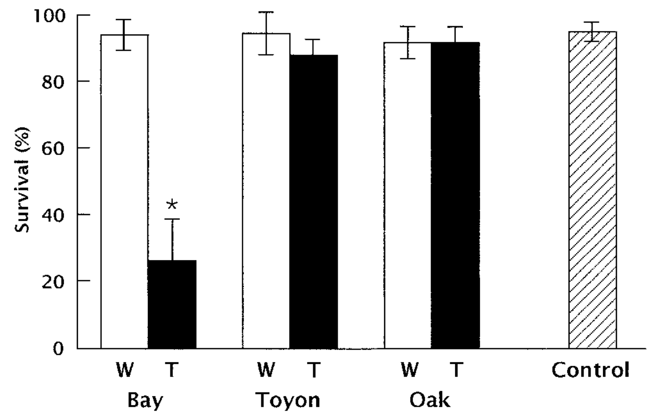

Figure 2
Mean (± 95% confidence interval) percentage of flea larvae surviving after a 3-day incubation with whole (W) or torn (T) leaves of bay, oak, or toyon or without foliage. *Significant difference ($p < .0001$).

DISCUSSION

Wood rat nests, like those of other rodents, harbor ectoparasites. Examination of the ectoparasite density of the sleeping nest matrix revealed that the majority of wood rat nests contained developmental stages of fleas and ticks. Although considerable variability in numbers of ectoparasites was found between individual sleeping nests and between years (some nests with few and some with large numbers of parasites), the potential clearly exists for a major buildup of ectoparasites. It is possible that, in spite of the swiftness and care with which nest material was sampled, the methodology underestimated the numbers of parasites present. Disturbance of the nest may have caused adult fleas or larvae of ticks and fleas to move away, or parasites may have dropped out of the nest when it was removed from the stickhouse. Additionally, the extraction procedure may have killed some mobile parasites that remained in the nest matrix.

If the methodology did reveal a good estimate, then the relatively few ectoparasites found in many nests suggests that the parasite defense behaviors of wood rats may be effective in controlling the number of parasites. The use of bay leaves on or near the nest was the parasite defensive behavior addressed in the present study. Bay leaves are known to produce volatiles toxic to ectoparasites. Our observation of the placement of bay leaves in disproportionate proximity to the sleeping nests, compared with bay placement in other parts of the stickhouse, stands in contrast to no indication for selective placement of toyon and oak near the sleeping nest and is consistent with the role of bay being used as a fumigant against nest-borne ectoparasites.

There was a substantial turnover of bay leaves within 2–3 days, a behavior which could maintain concentration of released volatiles. The pattern of nibbling on bay leaves, typically as small lacerations sporadically along the margin of the leaf, was not suggestive of use of bay for food but did suggest a function in releasing volatiles. The nibbling of oak, a known food staple (see below), involved removal of large sections of the leaf, as would be associated with eating. Whether wood rats eat any small parts of bay leaf that are removed is not clear.

The most convincing finding in favor of the nest fumigation hypothesis was the experiment on incubation of bay, toyon, and oak leaves with flea larvae. In this experiment, in which leaves of all three species were torn to simulate nibbling (and facilitate the release of biocidal volatiles), torn bay significantly reduced survival of flea larvae to 26.4%, compared with the 87.6–94.4% survival seen after incubation with torn oak leaves, torn toyon leaves, or control. Incubation with whole bay, toyon, or oak did not reduce survival of larvae compared with control. Nest fumigation, as a behavior that reduces nest-borne ectoparasites, provides a means by which the wood rats may continue to occupy a house for several seasons, a well-known phenomenon. Flea larvae may forage on plant debris in the nest, so it is possible that if nest-borne larvae consume old, decaying fragments of bay leaves, this may also kill some larvae. We did not test this possibility.

With regard to the presence of oak leaves in the stickhouses, it is well known that oak is used as food and is cached in the stickhouses. In laboratory studies, the dusky-footed wood rat has been shown to thrive on oak and acorns in spite of its high tannin content (Attsatt and Ingram, 1983), and our findings support the use of oak as a food staple. Oak was replaced every 2–3 days, and we found clear signs of oak leaves being eaten (in a different fashion than the nibbling on bay). The frequent finding of toyon leaves in stickhouses is not readily explained because the plant has not been studied as a food staple, and yet there was no evidence of it being toxic to flea larvae.

The prospect of the use of bay by wood rats for nest fumigation raises a number of compelling questions. One is whether the use of plants by preparturient and post-parturient female rats with pups may differ from that of males. Another question is the degree to which such use of plants for defense against nest-borne ectoparasites may be characteristic of other species of wood rats that live in different geographical areas with different plants available to them. Of interest in this regard is the presence of plant species of the genera *Juniperus* and *Artemesia* in the den sites of *N. cinerea* (Smith, 1997).

Some junipers are reputed to be effective in the control of fleas and mites (Huddle, 1936), and some members of the genus *Artemesia* are effective against ixodid ticks (Jacobson, 1975). A related question is the degree to which burrowing rodents or lagomorphs might also use plants with fumigating properties. Finally, if the nest fumigation hypothesis is true, there is a question of whether bay may be used regularly on a prophylactic basis or whether the wood rats, sensing a build-up of nest-borne ectoparasites, elect to use plants at the most appropriate times.

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