the Spot-winged Falconet may not benefit the Monk Parakeet in such a manner.

We are grateful to A. Gómez Durán and J. C. Vera (INTA) for granting us the use of the fieldwork areas, to N. Arguello and M. Nores for their assistance in the identification of food remains, and to J. Navarro for his help in the field. This work was supported by a grant from the Subsecretaria de Ciencia y Tecnología (SUBCYT) of Argentina.

LITERATURE CITED

DEAN, A. 1971. Notes on *Spiziapteryx circumcinctus*. Ibis 113: 101-102.

HOY, G. 1980. Notas nidobiológicas del noroeste argentino. II. Physis (Buenos Aires), Secc. C, 39 (96): 63-66.

MACLEAN, G. L. 1973. The Sociable Weaver, part 4: predators, parasites and symbionts. Ostrich 44: 241-253.

STRANECK, R., & G. VASINA. 1982. Unusual behaviour of the Spot-winged Falconet (*Spiziapteryx circumcinctus*). Raptor Res. 16: 25-26.

Received 7 July 1983, accepted 21 February 1984.

The Use of Green Plant Material in Bird Nests to Avoid Ectoparasites

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Certain birds characteristically place green plant material in their nests. This greenery is not part of the nest structure proper but is placed haphazardly around the edges or inside the nest. The birds replenish the sprays of green material, often daily, during incubation and the nestling period (Brown and Amadon 1968, Beebe 1976, pers. obs.).

I hypothesize that the plants are placed in the nests to repel or actually kill avian ectoparasites. Plant material may repel or kill ectoparasites because of the secondary compounds it contains. Secondary compounds often function as insect repellents in plants (Levin 1971). The compounds work as olfactory repellents, toxins, or juvenile hormone analogues to deter insects. If the parasite-repellent hypothesis is correct, the plant species chosen should be aromatically repellent, because avian ectoparasites do not ingest these leaves.

The aromatic compounds of plants are hydrocarbons, mainly monoterpenes and isoprene (Rasmussen 1972). In general, trees and long-lived shrubs emit the greatest volume of volatile compounds, whereas annuals emit the lowest volume of these compounds (Rasmussen 1972). Plant volatiles are used as a defense against herbivores but are also used by insects to locate their host plant (Freeland 1980). It has been established that volatile plant compounds can disrupt olfaction in insects by masking the particular chemical cue that the insect uses to find a host (Tahvanainen and Root 1972). If this is true of host-plant location, it may also be true of host-animal location. If my hypothesis is correct, then nest greenery would function in these manners.

There is evidence that infestations of ectoparasites causes nestling mortality in and nest desertion by birds (Webster 1944, Neff 1945, Fitch et al. 1946, Moss and Camin 1970, Feare 1976, Wheelwright and Boersma 1979). In general, the increased mortality due to ectoparasites is caused by the loss of blood, which weakens the host, by viral disease, or by disease caused by noxious endoparasites for which arthropod parasites are vectors (Herman 1955). The groups of ectoparasites most responsible for mortality are dipterans, fleas, ticks, and mites (Herman 1955).

Three predictions follow from the hypothesis that the use of nest greenery evolved to inhibit infestations of ectoparasites. (1) Birds that reuse their nests over successive years should be more prone to the use of foliage than birds that build a new nest each year. Nest reuse is implicated because hippoboscid fly larvae overwinter in nests and emerge about the time the eggs hatch (Bequaert 1953). The larvae are large relative to their hosts. Thus, it does not take many of them to weaken their host significantly. A number of endoparasitic diseases also are transmitted by hippoboscids and simuliid flies (Herman 1955). (2) The incidence of foliage use among birds that prey on higher vertebrates (birds and mammals) should be greater than that among birds that prey on lower vertebrates, because higher vertebrates often harbor large flea populations, as well as some dipterans, ticks, and mites. Parasite transmission occurs when mammals are taken by birds; owls have been found infested with rodent fleas (Rothschild and Clay 1952). (3) The types of greenery used in the nest should be high in volatile secondary compounds.

I used the order Falconiformes in order to test the first two predictions because of the variability in greenery use, nesting habits, and food preferences that members of this order exhibit. To get the most accurate and consistent data base about relative frequency of greenery use for this comparative study, I

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used the original data slips associated with the egg sets of North American raptors housed at the Western Foundation of Vertebrate Zoology and at the University of Washington Museum. Information on European Falconiformes was taken from Harrison (1975), because European egg collectors were remiss in describing nest contents. Data about food habits for North American Falconiformes were taken from Snyder and Wiley (1976). A comparable data base does not exist for European Falconiformes. I could not test Prediction 3, because the egg collectors often failed to specify on the data slips what type of greenery was used. When greenery was identified, however, it invariably was either from trees or shrubs, never from herbaceous species, although highly aromatic herbs exist. Falconiformes that do not build nests (e.g. *Falco*, some *Cathartes*), were not included, because such birds do not make choices about nest material. Nest reuse denotes a regular tendency for a species to reuse their nest and should not be construed as a clear-cut either/or situation.

An immediate problem was determining which egg collectors were likely to mention the presence of greenery in nests. Some collectors left only meager notes about nest materials and contents. I used the data from those collectors who mentioned greenery at least once to calculate the frequency of greenery use by each species. Species that were noted to use greenery on 50% of the data slips qualified as greenery users. Cooper's Hawks (*Accipiter cooperii*) and Bald Eagles (*Haliaeetus leucocephalus*) were the only exceptions to this rule. J. McNutt (pers. comm.) observed that 29 of the 32 Cooper's Hawk nests he watched in the San Juan Islands contained green conifer sprigs that were often replenished. F. W. Preston (pers. comm.) has also found that Cooper's Hawks use greenery. Newton (1979) and A. Hanson (pers. comm.) detail extensive use of decorative nest greenery by Bald Eagles. Neither of these species was recorded to use greenery by 50% of the egg collectors. This suggests that egg collectors were likely to overlook greenery use in their notes. Thus, my decision to categorize birds as greenery users is a conservative one.

I chose species as the unit under investigation, because the multispecific genera usually contain species representing all of the behaviors being correlated. This demonstrates that phylogenetic history does not constrain greenery use and that species can be considered as independent units for the purposes of this study. Significance was determined using the Fisher 2×2 Contingency Test and the Chi-square statistic.

Greenery use is significantly correlated with nest reuse in North American and European Falconiformes, a correlation that supports the first prediction. Of the 28 species that use greenery, 22 reuse their nests, whereas only 8 of 20 species that use no greenery also reuse their nests ($\chi^2 = 8.281$, $P < 0.005$). The trend becomes even more striking when one considers the large number of Passeriformes that build new nests yearly and use no greenery. Among passerines that reuse their nests, European Starlings (*Sturnus vulgaris*; pers. obs.), Purple Martins (*Progne subis*; A. S. Gaunt pers. comm.), and American Crows (*Corvus brachyrhynchos*; P. Arcese pers. comm.) have been reported to place fresh greenery or the highly aromatic inner bark of western red cedar (*Thuja plicata*) in their nests.

Contrary to Prediction 2, prey type is not correlated with greenery use. Of the 15 species that use greenery, only 8 have diets consisting of greater than 25% higher vertebrates, whereas 5 of 8 species that use no greenery also have diets that consist of greater than 25% higher vertebrates (Fisher Exact $P = 0.51$). This may be because parasite transmission is not common between predator and prey, because the parasites that are transmitted are not virulent to the new host, or because greenery volatiles are not effective against the relevant ectoparasites.

Greenery use varies geographically within a species. For instance, greenery was mentioned by collectors of Red-tailed Hawk (*Buteo jamaicensis*) eggs in 10% of the nests in the Pacific Northwest ($n = 10$), in 65% of the nests in the Southwest ($n = 23$), in 67% of the nests in the Northeast ($n = 20$), in 23% of the nests in Missouri ($n = 30$), and in 62% of the nests in California ($n = 55$). F. W. Preston (pers. comm.) has observed that all of the *Buteo* nests that he has looked at in the Northeast contain nest greenery. This discrepancy is probably due to the patchy data collection of the oologists. The regional differences also may be related to the availability of suitable plant species, time of leafing, or regional abundances of ectoparasites. The low incidence of greenery use in the Northwest is evidence that the availability of suitable plant species and time of leafing make little difference in whether or not greenery is used, because conifers are the predominant trees in the Northwest. They are aromatic and used in other parts of the country where they are available.

The ectoparasite-repellent-greenery hypothesis provides the most compelling and generalizable explanation for the widespread use of greenery in bird's nests. A number of other hypotheses have been postulated. (1) Greenery serves as a means of nest sanitation by covering debris in the nest. (2) It advertises nest occupancy. (3) It helps maintain humidity in the nest. (4) It serves to shade the nestlings (Bush and Gehlbach 1979). Newton (1979) discusses the first three possibilities.

The sanitation hypothesis fails to explain why the material used is invariably green, is brought to the nest before the nest is soiled, and is often placed haphazardly around the nest rim. The use of greenery to indicate nest occupancy does not explain why it is still brought after there are eggs or nestlings present. The nest-occupancy hypothesis may apply to Golden Eagles (*Aquila chrysaetos*), which place greenery in all the nests within their territory throughout the year in Washington (they maintain

TABLE 1. Tabulation of traits used in testing predictions: nest reuse, nest-greenery use, and diet composition (higher vertebrates refers to birds and mammals). Taxonomic order after Morony et al. (1975).

Species	Nest reuse	Greenery use	Diet >25% higher vertebrates
Osprey (*Pandion haliaetus*)	+	−	−
Honey Buzzard (*Pernis apivorus*)	−	−	
American Swallow-tailed Kite (*Elanoides forficatus*)	−	−	−
White-tailed Kite (*Elanus leucurus*)	−	−	+
Black-shouldered Kite (*E. caeruleus*)	−	−	
Snail Kite (*Rostrhamus sociabilis*)	−	+	−
Mississippi Kite (*Ictinia mississippiensis*)	−	+	−
Black Kite (*Milvus migrans*)	+	−	
Red Kite (*M. milvus*)	−	−	
Pallas's Sea-Eagle (*Haliaeetus leucoryphus*)	+	+	
Bald Eagle (*H. leucocephalus*)	+	+	−
White-tailed Eagle (*H. albicilla*)	+	+	
Egyptian Vulture (*Neophron percnopterus*)	+	−	
Lammergeier (*Gypaetus barbatus*)	+	−	
Lappet-faced Vulture (*Torgos tracheliotus*)	−	−	
Cinereous Vulture (*Aegypius monachus*)	+	+	
Short-toed Eagle (*Circaetus gallicus*)	−	+	
Marsh Harrier (*Circus aeruginosus*)	−	−	
Northern Harrier (*C. cyaneus*)	−	−	+
Pallid Harrier (*C. macrourus*)	−	−	
Montagu's Harrier (*C. pygargus*)	−	−	
Dark Chanting Goshawk (*Melierax metabates*)	−	−	
Northern Goshawk (*Accipiter gentilis*)	+	+	+
European Sparrowhawk (*A. nisus*)	−	+	
Sharp-shinned Hawk (*A. striatus*)	−	−	+
Levant Sparrowhawk (*A. brevipes*)	−	+	
Shikra (*A. badius*)	−	+	
Cooper's Hawk (*A. cooperii*)	+	+	+
Common Black-Hawk (*Buteogallus anthracinus*)	+	+	−
Harris' Hawk (*Parabuteo unicinctus*)	+	+	+
Gray Hawk (*Buteo nitidus*)	+	+	+
Red-shouldered Hawk (*B. lineatus*)	+	+	−
Broad-winged Hawk (*B. platypterus*)	+	+	−
Short-tailed Hawk (*B. brachyurus*)	+	+	+
Swainson's Hawk (*B. swainsoni*)	+	+	−
White-tailed Hawk (*B. albicaudatus*)	+	−	−
Zone-tailed Hawk (*B. albonotatus*)	+	+	+
Red-tailed Hawk (*B. jamaicensis*)	+	+	+
Common Buzzard (*B. buteo*)	+	+	
Rough-legged Hawk (*B. lagopus*)	+	−	+
Long-legged Buzzard (*B. rufinus*)	+	−	
Ferruginous Hawk (*B. regalis*)	+	−	+
Lesser Spotted Eagle (*Aquila pomarina*)	+	+	
Greater Spotted Eagle (*A. clanga*)	+	+	
Tawny Eagle (*A. rapax*)	−	−	
Imperial Eagle (*A. heliaca*)	+	+	
Golden Eagle (*A. chrysaetos*)	+	+	+
Bonelli's Eagle (*Hieraaetus fasciatus*)	+	+	
Booted Eagle (*H. pennatus*)	+	+	

alternative nests on a territory; N. V. Marr pers. comm.). Resident birds may use greenery to keep ectoparasite populations low year round. Further support for the territory-occupancy hypothesis would be the observation of greenery placed on the nest by migratory species after territory establishment and before egg laying.

The humidity-maintenance theory does not explain the fact that the behavior is as common in rainforests and maritime climates as it is in dry ones. The shade hypothesis does not explain the presence of greenery in cavity nests or in the nests of forest birds nesting beneath the canopy or why the material used to shade should be green. There is no indication of fresh sprays being positioned in the nests of open-dwelling birds in a manner that would shade eggs or nestlings during the hottest part of the day, when the behavior would be most beneficial. All of the above hypotheses lack the generality sufficient to explain the widespread occurrence of the trait in the variety of climates, habitats, and circumstances where it appears, unless greenery is used for many different reasons by different species.

This indirect test is weak support for the hypothesis that birds place greenery around their nests to lower the incidence of ectoparasites to which they are host, and it should be interpreted cautiously. Clearly, field tests are needed to demonstrate conclusively whether or not greenery actually repels or kills ectoparasites. In order to test the hypothesis, one could manipulate greenery presence experimentally and then compare fledging success from the two treatments. Simply counting ectoparasites in the nest and on the nestlings may be meaningless, because flying insects may account for a significant portion of the mortality incurred by the young birds from the ectoparasites.

I thank D. Boersma, G. Butcher, D. H. Janzen, D. Paulson, F. W. Preston, R. and V. Rausch, D. Rhoades, S. Rohwer, and N. Wheelwright for discussion, commenting on earlier drafts of the paper, or providing me with valuable information. Data were collected at the Western Foundation of Vertebrate Zoology with the help of L. Kiff and at the University of Washington State Museum. This project was supported in part by a Josselyn Van Tyne Memorial Award from the American Ornithologists' Union.

Literature Cited

BEEBE, F. L. 1976. Hawks, falcons and falconry. Saanichton, British Columbia, Hancock House Publ. Ltd.

BEQUEART, J. C. 1953. The Hippoboscidae or louse-flies (Diptera) of mammals and birds, part 1. Entomol. Amer. 32: 1-209.

BROWN, L., & A. AMADON. 1968. Eagles, hawks and falcons of the world. New York, McGraw-Hill Book Co.

BUSH, M. E., & F. R. GEHLBACH. 1979. Broad-winged Hawk nest in central Texas: geographic record and novel aspects of reproduction. Texas Ornithol. Soc. 11: 41-43.

FEARE, C. J. 1976. Desertion and abnormal development in a colony of Sooty Terns, *Sterna fuscata*, infested by virus infected ticks. Ibis 118: 112-115.

FITCH, H. S., F. SWENSON, & D. F. TILLOTSON. 1946. Behavior and food habits of the Red-tailed Hawk. Condor 48: 205-237.

FREELAND, W. J. 1980. Insect flight times and atmospheric hydrocarbons. Amer. Natur. 116: 736-742.

HARRISON, C. 1975. A field guide to nests, eggs and nestlings of British and European birds. Boston, Massachusetts, Demeter Press Inc.

HERMAN, C. M. 1955. Diseases of birds. Pp. 450-467 *in* Recent studies in avian biology (A. Wolfson, Ed.). Urbana, Illinois, Univ. Illinois Press.

LEVIN, D. A. 1971. Plant phenolics: an ecological perspective. Amer. Natur. 105: 157-181.

MORONY, J. J., JR., W. J. BOCK, & J. FARRAND, JR. 1975. Reference list of the birds of the world. New York, Amer. Mus. Nat. Hist.

MOSS, W. W., & J. H. CAMIN. 1970. Nest parasitism, productivity, and clutch size in Purple Martins. Science 168: 1000-1002.

NEFF, J. A. 1945. Maggot infestation of nestling Mourning Doves. Condor 47: 73-76.

NEWTON, I. 1979. Population ecology of raptors. Vermillion, South Dakota, Buteo Books.

RASMUSSEN, R. A. 1972. What do the hydrocarbons from trees contribute to air pollution? J. Air Pollution Control Assoc. 22: 537-543.

ROTHSCHILD, M., & T. CLAY. 1952. Fleas, flukes and cuckoos. New York, Philosophical Library.

SNYDER, N. F. R., & J. W. WILEY. 1976. Sexual size dimorphism in hawks and owls of North America. Ornithol. Monogr. 20: 1-96.

TAHVANAINEN, J. O., & R. B. ROOT. 1972. The influence of vegetational diversity on the population ecology of a specialized herbivore *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). Oecologia 10: 321-346.

WEBSTER, H. 1944. A survey of the Prairie Falcon in Colorado. Auk 61: 609-616.

WHEELWRIGHT, N. T., & P. D. BOERSMA. 1979. Egg chilling and the thermal environment of the Fork-tailed Storm Petrel, *Oceanodroma furcata*, nest. Physiol. Zool. 52: 231-239.

Received 5 July 1983, accepted 28 February 1984.