

Ectoparasite Behavior and Its Effects on Avian Nest Site Selection

J. E. LOYE AND S. P. CARROLL

Department of Entomology, University of California, Davis, CA 95616

Ann. Entomol. Soc. Am. 91(2): 159–163 (1998)

ABSTRACT In planning conservation efforts for birds, nest-site quality must be considered. An important but neglected aspect of nest-site quality is the presence of ectoparasites; these may cause birds to reject or abandon nests. Here, we present published and unpublished data showing the importance of ectoparasites, particularly blood-feeding arthropods.

KEY WORDS ectoparasite, blood-feeding, bird, biodiversity, conservation biology, habitat

CONSERVATION OF ANY organism is grounded in the maintenance of appropriate habitat for feeding, finding mates, and raising young. At one extreme, many animals will abandon sites of poor quality, a behavior that becomes a management problem for species in areas of limited habitat choice. Neglected in the evaluation of habitat quality for vertebrates of concern is their community of invertebrates (e.g., ectoparasites). Among such ectoparasites are blood-feeding arthropods that shelter both on vertebrate food resources and within host-associated microenvironments such as nests (Marshall 1982, Clayton and Moore 1997). The behavior of these ectoparasites should be considered in the planning of avian conservation programs, because the availability of clean and safe nesting sites is a vital determinant of offspring survival and thus an important component of habitat quality. An understudied aspect of nest site quality is the role of ectoparasite presence in causing birds to reject or abandon their nests (see references in Loye and Carroll 1995). Here I discuss both published and unpublished findings illustrating the importance of insect behavior in effecting habitat quality for birds.

I review evidence for the interaction of ectoparasite behavior with behavior and survival in birds and briefly present findings from my ongoing research on increasing parasite success in locating active bird nest sites.

Parasites are among the most abundant of organisms and are, by definition, harmful to their hosts (Askew 1971, Price 1980, Anderson and May 1982). Insect parasites may accommodate host biology in many ways, such as the timing of development and specialized host finding and oviposition behaviors (Foster 1969; Marshall 1982; Winterstein and Raitt 1983; Loye 1985a, b; Larimore 1987; Burt et al. 1991; Saumier et al. 1991). Reciprocal behavioral and physiological responses in birds may directly reduce the impact of parasites; the responses include increased preening (Clayton 1990), stereotyped "tremble-thrust" attacks

on flies by adult birds in the nest (Hartshorne 1962), increased food consumption (Conners 1987), increased maternal provisioning of nestlings with food (Perrins 1965), the incorporation of insecticidal leaves into nests (Clark and Mason 1988, Clark 1991), anting behavior (Ehrlich et al. 1988, Clayton and Wolfe 1993), nest and nestling abandonment (Duffy 1983, Clayton and Moore 1997), and avoidance of nesting sites with abundant parasites (Chapman 1973; Emlen 1985; Brown and Brown 1986, 1996; Mollar 1989; Loye and Carroll 1991; see also Richner et al. 1993). The energetic and reproductive costs of these responses provide strong inferential evidence that parasitism is expensive to the host in terms of energy loss or mortality, both in contemporary and evolutionary time, although this has not been frequently quantified. These costs must be considered in conservation management.

Because blood-feeding arthropods spend much of their energy searching for hosts, the choice for breeding birds of where to nest may be the 1st line of defense against bites and stings. Birds may avoid parasite-infested nest sites, eliminate the parasites, or learn to avoid recruiting parasites (Hart 1990). A clean, safe shelter should be preferred by hosts and could be termed a nest of "high quality." In colonially nesting birds such as cliff swallows, *Hirundo pyrrhonota* Vieillot, choice nest sites of high quality has been observed: groups avoided colonies with large numbers of cimicid bugs or ticks (Emlen 1985; Brown and Brown 1986, 1996; Loye and Carroll 1991; Chapman and George 1991). Similarly, semicolonial barn swallows may avoid mite-ridden nests (Moller 1987). Even after the initiation of nesting, intense parasitism may precipitate the mass desertion of colony sites, leaving nestlings to die and forsaking an entire season's breeding efforts.

In contrast to colonial birds, solitary birds are best known as hosts of larval blow flies (Hicks 1959). Bennett and Whitworth (1991b) studied the nests of 4,668

solitary birds of 72 species; every species sampled had some blowfly parasitism. Volant adults make blowflies more difficult to avoid than flightless parasites, and drawing conclusions from the literature about health effects of these parasites on solitary birds is challenging. Johnson and Albrecht (1993) noted that studies on ectoparasite infestation of nests often fail to report the rate and abundance of parasites, the number of chicks per nest, and even the species of parasite. The effects on host mass vary widely, and cause may be confused with effect (e.g., parasites found on a small or weak chick are regarded as responsible for the demise of an animal that may have been previously unhealthy and thus vulnerable to parasitism). The observed effects of parasite presence on bird behavior is marked but in contrast to colonial birds, parasitism of solitary nesters is understudied.

Behavioral differences in movement, dispersal, and oviposition of ectoparasites can lead to high variation in the observed effects on different bird populations. Because many endangered bird species are solitary nesters, the interactions of blood-feeding insects with their hosts is of great relevance in conservation management programs. Nest abandonment because of parasite population growth has been observed, particularly late in the bird breeding season (Moss and Camin 1974, Pinkowski 1977, Duffy 1983, Loye and Regan 1991). And Moller (1989) predicts greater mortality by predation of parasitized hosts. If a bird population is already stressed by habitat alteration or reduction, the pattern of ectoparasite nest locating behavior and the subsequent host response may be critical to host survival. Yet, little is known about the behavior of blood-feeding insects with respect to nest location, oviposition, and dispersal.

I have found no published studies that specifically address the topic of ectoparasite location of hosts and its effect on avian communities; therefore, I use as an example unpublished data from a system using hole nesting birds in boxes in Carmel Valley, California. The particular value of this system lies in the availability of a community of several species of bird hosts used by just 1 taxon of nest-associated ectoparasites, the larvae of flies of the genus *Protocalliphora*. The presence or absence of fly larvae gives a good indication of fly nest location success over time. The pilot study was carried out at Rana Creek Ranch, Rancho San Carlo, Hastings Reservation in Carmel Valley, California (1991–1995). Fly larvae were found in nest boxes used by western bluebirds, *Sialia mexicana* Swainson; tree swallows, *Tachycineta bicolor* Vieillot; violet-green swallows, *T. thalassina* Swainson; ash-throated flycatchers, *Myiarchus cinerascens* Lawrence; and house wrens, *Troglodytes aedon* Vieillot. One of the most basic observations in this system was of the apparent variation in host location success by the flies. The infestation rates of *Protocalliphora sialia* (Shannon & Dobrosky) in the nests of the most abundant hosts, western bluebirds, varied year to year as well as within seasons. The mean number of parasites per nest in Carmel Valley ranged from 11 ± 7.8 to 43.3 ± 31.9 during a 9-yr period (Table 1).

Table 1. Variation in infestation of western bluebird nests at 3 sites on Monterey Peninsula in California

| Year | No. nests | No. infested (%) | Mean no. \pm SD pupae/nest | Range |
|-------------------|-----------|------------------|------------------------------|-------|
| 1986 ^a | 51 | 25 (49) | 43.3 \pm 31.9 | 6–121 |
| 1987 ^a | 65 | 22 (34) | 28.8 \pm 20.1 | 2–76 |
| 1991 | 17 | 4 (24) | 11.0 \pm 7.8 | 2–25 |
| 1992 | 106 | 21 (20) | 28.8 \pm 40.0 | 1–162 |
| 1993 | 172 | 34 (20) | 26.2 \pm 19.3 | 1–65 |
| 1994 | 247 | 54 (22) | 16.3 \pm 12.0 | 1–40 |

Boxes 1986, 1987, 1991 $n = 369$; 1992 $n = 569$; 1993 $n = 1069$.
^a From Demas (1989).

The parasitic protocalliphorid flies locate hosts and oviposit repeatedly during March to July, the birds' breeding season. The larvae are blood-feeding and grow to maturity within the 21 d that the bluebirds develop to fledging. Fly populations increase over the season because new adults emerge to reproduce while older adults persist (Bennett and Whitworth 1991a). A high rate of reproductive philopatry in flies is suggested by experiments in which cavity nests from which all flies were removed took years to regain original infestation rates, although other source nests were as close as several hundred meters (Bennett and Whitworth 1991b). Thus, even though many nests of temperate birds are parasitized by *P. sialia*, indicating that flies are mobile, individual flies may move relatively short distances. Variation in infestation rates in nests may be related to nest locating ability of the flies as well as absolute fly population size.

Host location strategies of flies may have important implication for the conservation of birds. For instance, when a system of bird boxes is installed, fly parasites may increase in the nests over the years as they did from 1991 to 1993 (Table 1). Accordingly, although at first, low rates of fly infestation may permit unhampered fledging of the 1st broods in a season, subsequent use of the same nest or adjacent sites may greatly reduce nesting success (Bennett and Whitworth 1991b). An example of the range of variation in the number of nests infested is seen in Table 1 where as many as 50% of the nests checked were infested in 1986, but after a wet, rainy winter in 1987 the infestation was 24% and only 17 nests were used of 369 boxes available for nesting. An "additive effect" (Powesland 1977; cf., Anderson and May 1982), in which host population growth rate is depressed below that of parasite-free conditions, could occur after several good winters. This may have occurred in 1986, when Demas (1989) found measurable negative effects of parasitism on growth and development in nestling bluebirds. This could ultimately provide a constraint to further breeding.

The route to the nest site used by flying ectoparasites is an important consideration in nest site preference studies. For example, studies of mosquito vectors of disease (MacDonald 1957, Harwood and James 1979) indicate that they travel on air currents created by roads and open trails. Mosquitoes use birds and

other arboreal vertebrate hosts for food and serve as an excellent example of dipteran use of space. In addition, the edge-induced increase in biodiversity includes the intrusion of more vertebrate predators and nest parasites along edges created by road-building and other habitat fragmentation activities (Gates and Gysel 1978, Martin 1988, Moller 1988, Ratti and Reese 1988). Habitat fragmentation may provide "flyways," which can both increase opportunities for host location and limit habitat, leading to higher rates of nest reuse or nesting density of individuals (Loye and Carroll 1995). Both of these factors may lead to a net increase in nest parasitism.

An increase in nest parasitism would be predicted if natural nest sites for birds are particularly constrained, because they are in limited habitats. Although long-term data on nest ectoparasite establishment are not yet available, the potential of parasite buildup in fragmented habitats with limited nest site choices is indicated by the uniquely high infestation rates of the *Philornis* (Meinert) sp. flies on the pearly-eyed thrasher, *Margarops fuscatus* Viellot, in a tropical fragmented habitats in Puerto Rico (Arendt 1985a, b). In contrast, the infestation rates by *Philornis* sp. are much lower in nest boxes in Costa Rica (Young 1993), where habitat is more abundant.

Additional nest site limitation for birds is caused when parasitized nests are rejected. The parasite-caused nest avoidance hypothesis was tested by Barclay (1988), who used unquantified numbers of mites in barn swallow nests and found both significant avoidance of parasitized nests significant and use of unparasitized nests. This avoidance behavior indicates that parasites are detected in advance of nesting by birds.

Many solitary hole-nesting birds are territorial (reviewed in Ehrlich et al. 1988) and reuse nest sites in their territory. This behavior could lead to greater food resource predictability for host seeking flies. For birds, previously used boxes would signify a preferred territory and might be reused in preference to unused boxes, which could signify a territory of lower quality. The use of previously built nests by birds was examined by Thompson and Neill (1991), who found that winter wrens, *Troglodytes troglodytes*, preferred using old nests to building new ones. This may indicate that territory is more important than the reduced quality of nests contaminated by feces or parasites under normal circumstances. However, if parasites have increased success in locating nests they become more numerous. If any nest in a nest box or if natural cavity signals an enhanced potential for parasitism, then sites used the previous year may be avoided by birds. Lack of information about the behavior of nest parasites limits conclusions in this case.

A knowledge of protocalliphorid fly site tenacity and locally limited host-seeking patterns could be used to predict patterns of bird reuse of nests over several years (Martin 1988). However, if ectoparasitic insects behave with philopatry toward their natal nests, then they could be selective agents driving nest switching in bird hosts. For instance, in Carmel Valley,

I examined ectoparasite presence and nest reuse in territorial, hole-nesting ash-throated flycatchers, western bluebirds, and tree swallows. These hosts build "dummy" nests that they do not use in the vicinity of the nest they do use for breeding. The maintenance of the nests in the boxes provided an opportunity to examine nesting decisions between years. I found that all 3 species of birds used more new nests than old, in contrast to the wrens studied by Thompson and Neill (1991). Reuse patterns between 1992 and 1993 (the 1st and 2nd yr of box establishment) did not show a significant avoidance by birds of old nests or of dummy nests. At the 2 sites in Carmel Valley (Rancho San Carlos and Rana Creek Ranch), 47% of the nests ($n = 271$) were reused, with use of 50% of 52 dummy nests and only $\approx 30\%$ (26 of 62) of previously used nests. However, in 1994, after 3 yr of colony establishment, parasite avoidance was a significant factor in nest site selection ($\chi^2 = 36$, $P > 0.0001$, $df = 1$, $n = 71$ nests of western bluebird, ash-throated flycatcher, and tree swallow). A significant pattern was also found in bluebird nests examined alone ($n = 55$, $\chi^2 = 22.67$, $df = 1$, $P > 0.001$). This suggests that a build-up of parasites will cause nest avoidance. Over time, fly populations spread and increase as they disperse from nest to nest in the environment.

Two points arise from the study of parasitic fly nest location behavior. One is that the potential for nest site choice by parasites can influence the long-term well-being of vertebrate hosts. Second is that long-term study of these parasite-host systems is necessary because important effects of ectoparasites on hosts can be difficult to detect. During the initial period of study in California (1991–1993), no trends in avoidance of old nests with *P. siala* were detected. Yet by 1994, after 4 yr of box availability, a clear effect of parasitism was detected. Both the paucity of infested nests and the high variance in numbers of parasites indicate that *P. siala* parasitism could be an unpredictable selective event, of importance when high parasitism coincides with abiotic challenges (e.g., negative effects of drought on the food insects of birds). In Carmel Valley, in a newly installed system of boxes, the numbers of birds and parasites have increased each year, a pattern that demands a long-term study with access to large numbers of nests. To study changes in any ectoparasite infestation, the nests must be left in the boxes from year to year. Different reliable methods of parasite retrieval for counts, followed by replacement or manipulation within the nests, are needed and must be tailored to the life history strategies of each arthropod group. For instance, the behavior of maggots that migrate to enclosed spaces to pupate can be used to sample pupae by inserting corrugated cardboard squares under the nests.

If nest sites are limited and there has been a documented increase in bird populations (as is the case with western bluebirds [Tate and Tate 1982, Ehrlich et al. 1988]), then we can predict that fewer options for these nesting choices will occur in the forest islands that are created by development. The importance of tree-holes and bird boxes as shelter and food

sources for arthropods is little known. And, to design a successful conservation program for hole-nesting birds, knowledge of parasite location of and impact on nest site quality as well as availability is necessary. Host nest use may be predictable from studies of parasite behavior. This will be especially important in cases where nest site limitation leads to greater search efficiency by the parasites, and thus greater rates of reinfestation (Loye and Carroll 1995).

When we attempt to conserve a habitat for birds we also need to consider the requirements for choice of parasite-free nesting habitat and the behavior of the parasites in locating hosts within the configuration of the area. Until we understand how the ectoparasites themselves select nest sites we have no way of managing parasitism in order to provide good habitat for threatened vertebrates.

Acknowledgments

Many thanks to the scientists of Hastings Reservation: Janis Dickinson, Walt Koenig, Mark Stromberg; and research assistants, Laurel Moore, Geoff Pease, Chris Chang, Ron Kim, Aaron Gabbe, Ian Hannah, and Andy Rosser. Thanks also to the owners and staff at Rana Creek Ranch, particularly Brian Heneks, and Rancho San Carlos and to Hugh Dingle and Bob Washino at U.C. Davis. Scott Carroll, Buck Carroll-Loye and Minnow Carroll-Loye worked hard to make this research possible. Special thanks go to T. Whitworth for insect identification and for invaluable advice.

References

- Anderson, R. M., and R. M. May. [eds.] 1982. Population biology of infectious diseases. Springer, Berlin.
- Arendt, W. J. 1985a. *Philornis* ectoparasitism of pearly-eyed thrashers. II. Effects on adults and reproduction. *Auk* 102: 281–292.
- 1985b. *Philornis* ectoparasitism of pearly-eyed thrashers. I. Impact of growth and development of nestlings. *Auk* 102: 270–280.
- Askew, R. R. 1971. Parasitic insects. Elsevier, New York.
- Barclay, R.M.R. 1988. Variation in the costs, benefits, and frequency of nest reuse by barn swallows (*Hirundo rustica*). *Auk* 105: 53–60.
- Bennett, G. F., and T. Whitworth. 1991a. Studies on the life history of some species of *Protocalliphora*. (Diptera: Calliphoridae). *Can. J. Zool.* 69: 2048–2058.
- 1991b. Host, nest and ecological relationships of species of *Protocalliphora*. *Can. J. Zool.* 70: 51–61.
- Brown, C., and M. B. Brown. 1986. Ectoparasitism as a cost of coloniality in Cliff Swallows (*Hirundo pyrrhonota*). *Ecology* 67: 1206–1218.
1996. Coloniality in the cliff swallow: effect of groups size on social behavior. University of Chicago Press, Chicago, IL.
- Burt, E. H., Jr., W. Chow, and G. A. Babbitt. 1991. Distribution and ecology of mites living in birds' nests, pp. 104–122. *In* J. E. Loye and M. Zuk [eds.], *Ecology, behavior and evolution of bird-parasite interactions*. Oxford University Press, Oxford.
- Chapman, B. R. 1973. The effects of nest ectoparasites on cliff swallow populations. Ph.D. dissertation, Texas Technical University, Lubbock.
- Chapman, B. R., and J. E. George. 1991. The effects of ectoparasites on cliff swallow growth and survival, pp. 69–92. *In* J. E. Loye and M. Zuk [eds.], *Ecology, behavior and evolution of bird-parasite interactions*. Oxford University Press, Oxford.
- Clark, L. 1991. The nest protection hypothesis: the adaptive use of plant secondary compounds by European starlings, pp. 205–221. *In* J. E. Loye and M. Zuk [eds.], *Ecology, behavior and evolution of bird-parasite interactions*. Oxford University Press, Oxford.
- Clark, L., and J. R. Mason. 1988. Effect of biologically active plants used as nest material and the derived benefit to starling nestlings. *Oecologia (Berl.)* 77: 174–180.
- Clayton, D. 1990. Mate choice in experimentally parasitized rock doves: lousy males lose. *Am. Zool.* 30: 251–262.
- Clayton, D., and J. Moore [eds.]. 1997. Host-parasite evolution: general principles and avian models. Oxford University Press, Oxford.
- Clayton, D., and N. D. Wolfe. 1993. The adaptive significance of self-medication. *Trends Ecol. Evol.* 8(2): 60–63.
- Connors, V. A. 1987. Analysis of the cost of infection by *Plagiorhynchus cylindraceus* (Acanthocephala) in the European starling (*Sturnus vulgaris*). Ph.D. dissertation, University of Nebraska, Lincoln.
- Demas, V. P. 1989. Effects of parasitism by blowfly larvae *Protocalliphora sialia* (Diptera: Calliphoridae) on western bluebird (*Sialia mexicana*) nestlings. M.S. thesis, University of Florida, Gainesville.
- Dingle, H., S. P. Carroll, and J. E. Loye. 1997. Behavior, conservation and 99% of the world's biodiversity: is our ignorance really bliss? pp. 72–92. *In* J. Clemmons and R. Buckholz [eds.], *Behavior and conservation biology*. Academic, New York.
- Duffy, D. C. 1983. The ecology of tick parasitism on densely nesting Peruvian seabirds. *Ecology* 64: 110–119.
- Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1986. The adaptive significance of anting. *Auk* 103: 835.
1988. *The birder's handbook*. Simon and Schuster, New York.
- Emlen, J. T. 1985. Responses of breeding cliff swallows to nidicolous parasite infestations. *Condor* 88: 110–111.
- Foster, M. S. 1969. Synchronous life-cycles in the orange-crowned warbler and its mallophagan parasites. *Ecology* 50: 315–323.
- Gaston, K. J., T. R. New, and M. J. Samways. 1993. Perspectives on insect conservation. Intercept, Andover, U.K.
- Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59: 871–883.
- Hagan, III, J. M., and D. W. Johnston [eds.], 1992. *Ecology and conservation of neotropical migrant landbirds*. Smithsonian Institution Press, Washington, DC.
- Hart, B. L. 1990. Behavioral adaptations to pathogens and parasites: five strategies. *Neurosci. Biobehav. Rev.* 14: 273–294. Pergamon, New York.
- Hartshorne, J. M. 1962. Behavior of the eastern bluebird at the nest. *Living Bird* 131–149.
- Harwood, R. F., and M. T. James. 1979. *Entomology in human and animal health*, 7th ed. MacMillan, New York.
- Hicks, E. A. 1959. Check-list and bibliography on the occurrence of insects in birds' nests. Iowa State College Press, Ames.
- Johnson, L. S., and D. J. Albrecht. 1993. Effects of haematophagous ectoparasites on nestling house wrens, *Troglodytes aedon*: who pays the cost of parasitism? *Oikos* 66: 255–262.
- Larimore, R. W. 1987. Synchrony of cliff swallow nesting and development of the tick, *Ixodes baergi*. *Southwest. Nat.* 32: 121–126.

- Loye, J. E. 1985a. The life history and ecology of the cliff swallow bug, *Oeciacus vicarius* (Hemiptera: Cimicidae). Cah. ORSTOM Ser. Med. Parasitol. 23: 133-139.
- 1985b. Host effects on feeding and survival of the polyphagous cliff swallow bug, *Oeciacus vicarius* (Cimicidae: Hemiptera). Bull. Soc. Vector Ecol. 10: 7-13.
- Loye, J. E., and S. P. Carroll. 1991. The effect of nest ectoparasite abundance on cliff swallow colony site selection, nestling development, and departure time, pp. 222-241. In J. E. Loye, and M. Zuk [eds.], Ecology, behavior and evolution of bird-parasite interactions. Oxford University Press, Oxford.
1995. Birds, bugs and blood: avian parasitism and conservation. Trends Ecol. Evol. 10: 232-235.
- Loye, J. E., and T. W. Regan. 1991. The cliff swallow bug *Oeciacus vicarius* (Hemiptera: Cimicidae) in Florida: ectoparasite implications for hole-nesting birds. Med. Vet. Entomol. 5: 511-513.
- MacDonald, G. 1957. The epidemiology and control of Malaria. Oxford University Press, Oxford.
- Marshall, A. 1982. The ecology of ectoparasitic insects. Academic, London.
- Martin, T. E. 1988. Habitat and area effects on forest bird assemblages: is not predation an influence? Ecology 69: 74-84.
- Moller, A. P. 1987. Advantages and disadvantages of coloniality in the swallow, *Hirundo rustica*. Anim. Behav. 35: 819-832.
1988. Nest predation and nest site choice in passerine birds in habitat patches of different sizes: a study of magpies and black birds. Oikos 53: 215-221.
1989. Parasites, predators and nest boxes: facts and artefacts in nest box studies of birds? Oikos 56: 421-423.
- Moss, W. W., and J. H. Camin. 1970. Nest parasitism, productivity, and clutch size in Purple Martins. Science (Wash. D.C.) 168: 1000-1003.
- Perrins, C. M. 1965. Population fluctuations and clutch size in the great tit, *Parus major* L. J. Anim. Ecol. 34: 601-647.
- Pinkowski, B. C. 1977. Blowfly parasitism of eastern bluebirds in natural and artificial nest sites. J. Wildlife Manage. 41: 272-276.
- Powesland, R. G. 1977. Effects of the haematophagous mite *Ornithonyssus bursa* on nestling starlings in New Zealand. N.Z. J. Zool. 4: 85-94.
- Price, P. 1980. Evolutionary biology of parasites. Princeton University Press, Princeton, NJ.
- Ratti, J. T., and K. P. Reese. 1988. Preliminary test of the ecological trap hypothesis. J. Wildl. Manage. 52: 484-491.
- Richner, H., A. Oppliger, and P. Christe. 1993. Effect of an ectoparasite on reproduction in great tits. J. Anim. Ecol. 62: 703-710.
- Saumier, M. D., M. E. Rau, and D. M. Bird. 1991. Behavioural changes in breeding American kestrels infected with *Trichinella pseudospiralis*, pp. 290-316. In J. E. Loye and M. Zuk [eds.], Ecology, behavior and evolution of bird-parasite interactions. Oxford University Press, Oxford.
- Slobodkin, L. B., and A. Rapoport. 1974. An optimal strategy of evolution. Q. Rev. Biol. 49: 181-200.
- Soule, M. E. 1986. Conservation biology. Sinauer, Sunderland, MA.
- Tate, J., Jr., and D. J. Tate. 1982. the blue-list for 1982. Am. Birds. 36: 126-135.
- Thompson, C. F., and A. J. Neill. 1991. House wrens do not prefer clean nest boxes. Anim. Behav. 42: 1022-1024.
- Whitworth, T. L. 1992. Pathogenicity of larval *Protocalliphora* (Diptera: Calliphoridae) parasitizing nestling birds. Can. J. Zool. 70: 2184-2191.
- Winterstein, S. R., and R. J. Raitt. 1983. Nestling growth and development and the breeding ecology of the Beechey jay. Wilson Bull. 95: 256-268.
- Young, B. E. 1993. Effects of the parasitic botfly *Philornis carinatus* on nestling house wrens, *Troglodytes aedon*, in Costa Rica. Oecologia (Berl.) 93: 256-262.

Received for publication 14 August 1997; accepted 5 November 1997.