

- SAUER, J. R., AND S. DROEGE. 1992. Geographical patterns in population trends of Neotropical migrants in North America, p. 30–68. *In* J. M. Hagan III and D. W. Johnston [EDS.], *Ecology and conservation of Neotropical migrant landbirds*. Smithsonian Inst. Press, Washington, DC.
- SCHMIDT, K. A., AND C. J. WHELAN. 1999. The relative impacts of nest predation and brood parasitism on seasonal fecundity in songbirds. *Conserv. Biol.* 13:46–57.
- WOODWORTH, B. 1999. Modeling population dynamics of a songbird exposed to parasitism and predation and evaluating management options. *Conserv. Biol.* 13:67–76.

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ROOST SITE SELECTION OF GREAT HORNED OWLS IN RELATION TO BLACK FLY ACTIVITY: AN ANTI-PARASITE BEHAVIOR?¹

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Abstract. We document a shift in roosting behavior of Great Horned Owls (*Bubo virginianus*) from winter and late spring to summer. During summer, Great Horned Owls roosted near the ground or exposed on open ground, whereas they chose concealed perches at mid-canopy level for the rest of the year as typical for forest owls. This shift of roosting behavior coincided with the emergence of ornithophilic black flies, which transmit avian malaria (*Leucocytozoon* spp.). The shift in roosting behavior was consistent with measurements of parasite exposure at different habitat positions. Black fly activity was highest at mid-canopy level, and almost no black flies were active on open ground. Ground-roosting was not caused by poorly developed flying capability of juveniles, because solitarily-roosting adult owls showed the same behavioral shift in a second year of study. Black flies and avian malaria are widely distributed, and the effect of the vertical distribution of these parasites in forests on roosting, nesting, and foraging of sylvatic birds deserves further study.

Key words: *black flies, Bubo virginianus, forest*

owls, Great Horned Owls, Leucocytozoon, parasitism, roosting behavior.

Ornithophilic species of black flies (Simuliidae) can reduce the fitness of a host in a variety of ways (Møller 1990, Bennett et al. 1993). For example, black flies are a vector of *Leucocytozoon*, a protozoon causing avian malaria (Desser and Bennett 1993). As an example of possible consequences of disease, higher loads of *Leucocytozoon ziemanni* were associated with lower clutch sizes in female Tengmalm's Owls *Aegolius funereus* (Korpimäki et al. 1993). Detrimental effects may be directly caused by anemia. Blood extraction by the ectoparasite alone (or in concert with the blood parasite) may significantly contribute to anemia (Fitch et al. 1946, Richner et al. 1993, Hunter et al. 1997). In addition, there may be a cost of increased investment in immunological defense (Toft 1991, Richner et al. 1995).

We studied the response of Great Horned Owls (*Bubo virginianus*) to the 10-year population cycle of snowshoe hares *Lepus americanus* in the boreal forest from 1989–1992 (Krebs et al. 1995, Rohner 1996). Great Horned Owls are large and long-lived predators feeding mainly on lagomorphs, they defend long-term territories, and are widely distributed in North and South America (Voous 1988, Donazar et al. 1989, Rohner 1995, 1997). Several demographic parameters in Great Horned Owls were strongly affected by the population cycle of snowshoe hares (Rohner 1996).

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For example, juvenile survival was very high during the peak of the hare cycle but dropped in the first year of prey decline in 1991. Anemia, caused by *Leucocytozoon ziemanni* and feeding by black flies, was identified as a major cause of mortality of juvenile Great Horned Owls in our study area (Rohner and Hunter 1996, Hunter et al. 1997).

In this paper, we report on the roost site selection of juvenile and adult Great Horned Owls in response to varying densities of black flies. Initially, we were puzzled to observe that Great Horned Owls roosted on the ground during the post-fledging stage, often exposed at sites in the sun. Forest owls are known to roost concealed in trees, and adult Great Horned Owls always roosted well-hidden and on perches above 4–5 m in winter and early spring (Rohner and Doyle 1992b). After learning about black flies and avian malaria as agents of juvenile mortality in our study system (Rohner and Hunter 1996, Hunter et al. 1997), we investigated the hypothesis of whether Great Horned Owls modify their roosting behavior to escape these parasites. We predicted that exposed roost sites on the ground would be host refugia, because some studies indicate that ornithophilic black flies feeding on forest birds prefer dense vegetation at mid-canopy level where they are most likely to encounter their hosts (Bennett 1960, Hunter 1990).

Black flies emerge in spring when minimum daily temperatures rise above freezing. Subsequently, they swarm and mate over open water, then switch to nectar-feeding to gain resources for dispersal, undertake dispersal or migratory flights to specific habitats for blood-feeding, and then return to streams and rivers for egg-laying, with one to several generations per year (Bennett 1960, Sutcliffe 1986, Currie 1997). In early May, our study area was still covered by snow, and lake ice did not break up before the end of May. Based on more southerly reports on black fly phenology, maximum black fly activity in the study area was expected in late July and early August (Bennett 1960, Hunter 1990).

In order to test the hypothesis that Great Horned Owls selected roost sites with lower activity of black flies than elsewhere, we conducted a mensurative experiment (Hurlbert 1984) on the distribution and activity of black flies, and we collected information on roost sites of Great Horned Owls. We predicted that (1) black fly activity in summer will be highest in vegetation at mid-canopy level and much lower at exposed sites on the ground, (2) as black flies emerge and peak towards summer, Great Horned Owls will shift in their use of roost sites from higher to lower perches and from more concealed to more exposed sites. An alternative hypothesis may explain ground-roosting of owls by specific microhabitat requirements of juveniles at the post-fledging stage, possibly as a result of energetic or physiological constraints. This alternative hypothesis predicts that in contrast to owl families, nonbreeding adult owls will not select roost sites in summer that are different from any other season.

METHODS

We worked at Kluane Lake (60°57'N, 138°12'W) in the southwestern Yukon, Canada. The data for this

study were collected in 1991 and 1992. The study area comprised 350 km² of the Shakwak Trench, a broad glacial valley bounded by alpine areas to the northwest and the southeast. The valley bottom averages about 900 m above sea level and is covered mostly with spruce forest *Picea glauca*, shrub thickets *Salix* spp., some aspen forest *Populus tremuloides*, grassy meadows with low shrub *Betula glandulosa*, old burns, eskers, marshes, small lakes, and ponds.

During 1988–1992, we equipped a total of 21 adult owls and 55 owlets with radio-transmitters, which were attached with a shoulder harness (details in Rohner 1996, 1997). Radios on the backs of owls were hidden in feathers and weighed 50 g (< 5% of body mass, Kenward 1985). Because a position-specific mercury switch was installed, an observer was able to identify whether an owl was perched or flying.

Obtaining data on owl roost sites was extremely difficult, because visibility was limited in the coniferous boreal forest and because owls were elusive and did not use traditional roost sites (Rohner 1996). We located roost sites by carefully approaching radio-marked owls during daytime with hand-held antenna, receiver, and binoculars. Once a roosting owl was spotted, perch heights were estimated in meters, and a site was scored as exposed or in cover depending upon whether dense vegetation was present or absent within a radius of 1 m of the roosting owl. In order to avoid disturbance, most roost sites were examined later in detail. Observations only were used when an owl had not changed position (according to the motion-sensitive switch of the radio-transmitter) when it was approached. Usually, independent evidence such as feathers, feces, pellets, or claw marks confirmed the locations as roost sites that had been used for at least several hours. During 1991–1992, a total of 68 roost sites were located. All data from individual family members were pooled and used as one data point for each territory to avoid pseudo-replication (Hurlbert 1984).

Ornithophilic black flies were captured using the method of Bennett (1960). Live Bantam chickens *Gallus gallus*, which are commonly used as bait for attracting black flies, were exposed in cages after their heads were covered with a hood to prevent the chicken from pecking off any black flies. Exposure cages were placed on a white board of 60 × 60 cm, and then hoisted up to different heights in trees with the help of a pulley system. During each trial, we exposed the cages for 20 min, and then sealed them with a collecting cage of fine mesh. Within 30 min after a blood meal, engorged flies had left the chicken and settled on the sides of the cage. They were collected with an aspirator and finally preserved in 70% ethanol.

Black fly activity was sampled at four microhabitats or locations, representing a gradient of typical roost sites that were available in the boreal forest of our area (Fig. 1A): trap 1 in the upper canopy level at 9 m and 9.5 m above ground (canopy heights reached 12–14 m), trap 2 in mid-lower canopy level at 3 m and 3.5 m above ground, trap 3 on the ground at the base of a tree in cover, and trap 4 on open ground between trees (> 4 m from willow bushes). We sampled at two sites with an identical layout of traps on 7 days from

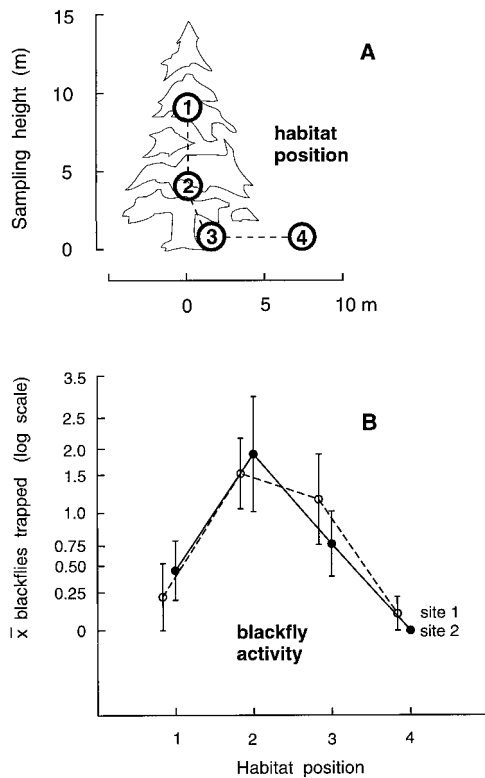


FIGURE 1. Blackfly activity at different habitat positions. A: Gradient of available roost sites chosen for sampling the activity of ornithophilic blackflies. B: Blackfly activity, mean \pm SE of flies collected from exposed Bantam chickens across a gradient of microhabitats according to Figure 1A (seven samples for each location at two sites).

21 July to 5 August 1992. Both sites were near previously-used Great Horned Owl nests, about 5 km apart in open spruce forest, which is the predominant habitat type of the area.

Identification of black flies was hindered by a lack of recent keys. The only taxonomic treatments for northwestern North America are long out of date (Stone 1952, Sommerman 1953) and include fewer than half of the 76 species now known from Alaska and the Yukon Territory (Currie 1997). Furthermore, many northwestern species have not been formally described, or belong to unresolved sibling complexes; these latter require examination of the polytene chromosomes of the larvae for species-level identification. Preserved black flies were examined under a stereomicroscope (magnification up to 130 \times) after genitalia had been cleared with lactic acid. Adults were identified to the lowest taxonomic level possible through comparisons with confirmed material in the Royal Ontario Museum (Toronto, Ontario, Canada) and the Canadian National Collection of Insects (Ottawa, Ontario, Canada). Voucher specimens were deposited in the entomological collection of the Royal Ontario Museum.

DATA ANALYSIS

For statistical testing, we generally used one-tailed probabilities because we had predicted the direction of differences prior to sampling. For calculating ANOVAs, we used log-transformed data, and probabilities for differences in the overall distribution of black flies across habitat positions and sampling sites are two-tailed.

RESULTS

BLACK FLY ACTIVITY

In all eight traps combined, we captured a total of 60 black flies. They included 48 specimens of the *Simulium* (*Eusimulium*) *aureum* complex, four *Helodon* (*Distosimulium*) *pleuralis*, one *Helodon* (*Parahelodon*) *decemarticulatus*, one specimen of the *Simulium* (*Eusimulium*) *annulum* group, one *Simulium* (*Eusimulium*) cf. *pugetense* complex, and one mutant *Simulium* (*Eusimulium*) sp. without signs of blood feeding.

The distribution of black fly activity across the sampled gradient is presented in Figure 1B. We used log-transformed values because the data points were not normally distributed. Most black flies were trapped at intermediate canopy height, fewer at the ground in cover, and almost none in the upper canopy and at exposed sites on the ground. The maximum numbers of black flies captured in a single sampling session were 11 for trap 2, 6 for trap 3, 3 for trap 1, and 1 for trap 4. Only one engorged black fly was encountered on the ground in the open during 14 trapping sessions, whereas trap 2 at mid-canopy level yielded engorged black flies in 11 of 14 sessions. In agreement with prediction (1), the habitat position at mid-canopy level (trap 2) had much higher black fly activity than on the open ground at trap 4 (Fig. 1B, Mann Whitney $U = 172.0$, $P < 0.001$). Overall, there was a significant effect of habitat position ($F_{3,55} = 7.8$, $P < 0.001$), but the two sampling sites 5 km apart were not different from each other ($F_{1,55} = 0.0$, $P > 0.5$), and there was no interaction between trap position and sampling site ($F_{3,55} = 0.4$, $P > 0.5$). Even when pooling all sampling days for each trap, there was a significant effect of habitat position ($F_{3,7} = 23.3$, $P = 0.005$) but not of sampling site ($F_{3,7} = 0.0$, $P > 0.5$).

ROOST SITE SELECTION BY GREAT HORNED OWLS

Adult owls in winter and early spring always roosted well-hidden and on perches above 4–5 m (Rohner and Doyle 1992b). As with prediction (2), roost heights were lower in summer (Fig. 2). During mid June to August, only 38% of the roosting owls were higher than 2 m above ground (mean perch height 1.82 ± 0.27 m, $n = 34$). Sixty-one percent were on stumps, logs, or on the ground, and only 39% were in the branches of trees. This decline in perch heights from winter conditions to summer in Figure 2 was significant (Kruskal–Wallis test, $H = 8.6$, $n = 37$, $P < 0.05$). Although the cover of roost sites differed during these seasonal stages, much variation but no clear decline was apparent in Figure 2.

In 1992 no owls bred, and all adults were roosting solitarily when approached. This situation provided an opportunity to test the alternative hypothesis that roost sites on or near the ground are explained by poorly

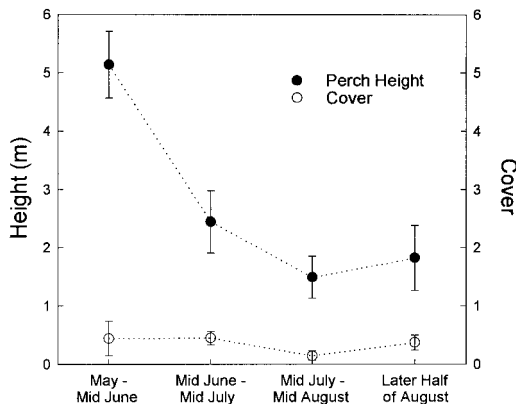


FIGURE 2. Seasonal trends in roost site characteristics of Great Horned Owls (mean \pm SE) from early spring (snow on ground) to late summer.

developed flight capability of fledglings. In contrast to the prediction of this hypothesis, adult owls without their young did not remain at high perches but showed the same seasonal decline in roost height as before (Kruskal-Wallis test, $H = 7.4$, $n = 18$, $P < 0.05$).

DISCUSSION

RESPONSES TO BLACK FLY ACTIVITY

Forest owls are known to roost concealed in trees, and exposed roost sites on or near the ground are highly unusual (Forsman et al. 1984, Hayward and Garton 1984, Belthoff and Ritchison 1990). Habitat selection by free-roosting birds is usually seen in the context of finding shelter from mobbing, predation, and thermal stress (Janes 1985). The seasonal decline in roosting height from winter and late spring to summer as black flies peak in activity is consistent with the hypothesis that Great Horned Owls are attempting to avoid parasitism by black flies. At the same time, we were able to show with direct measurements of black fly activity, that this shift in roosting behavior corresponded with drastically reduced exposure to these parasites.

Potential fitness gains of this behavior are more difficult to demonstrate. Black flies are a common vector of *Leucocytozoon*, a protozoon causing malaria in many species of all avian orders (Desser and Bennett 1993). About 50% of the examined individuals and species of Strigidae were infected with *Leucocytozoon* (Greiner et al. 1975, Bennett et al. 1982, Bishop and Bennett 1992). For some species, infection rates are even higher. In our study area, we conducted histological analysis of 23 Great Horned Owl mortalities, and found that at least 57% of individuals were severely infected by *Leucocytozoon*. This is likely an underestimate because the carcasses were partially decomposed (Hunter et al. 1997). In California and New Mexico, 91% of the investigated Spotted Owls *Strix occidentalis* were infected by *Leucocytozoon* (Gutierrez 1989). Korpimäki et al. (1993) found an infection rate of 95% for Tengmalm's Owls breeding in boreal Finland. Once individuals are infected, they do not appear to lose these blood parasites (Appleby et al.

1999). As an example of possible fitness consequences, higher loads of *Leucocytozoon ziemanni* were associated with smaller clutch sizes in female Tengmalm's Owls (Møller 1990, Bennett et al. 1993, Korpimäki et al. 1993). In addition to the transmission of blood parasites, black flies or other ectoparasites may also have direct detrimental effects (Fitch et al. 1946, Richner et al. 1993, Smith et al. 1998). In Great Horned Owls, exposure to a high number of sucking black flies leads to external lacerations, and the blood loss may contribute to reduced hematocrit levels and other symptoms of anemia, and finally lead to reduced survival (Rohner and Hunter 1996, Hunter et al. 1997).

As an alternative hypothesis, we considered whether roosting on or near the ground may have been the result of specific habitat requirements of juveniles. However, the results for solitary roosting adult owls were not different from owl families with young, and this alternative hypothesis can therefore be rejected. Also, we never observed any signs of walking or hunting at these sites, which would have indicated that the owls were looking for ground-dwelling insects, and often the presence of feathers, feces, or pellets indicated that the owls had spent much time at exactly the same spot. Not so clear were the results on cover at roost sites, which showed no consistent trend as predicted. However, our visual assessment of cover was very crude and was only rated as 0 (missing) or 1 (present), and with the variation of our sampling technique and the low statistical power of our sample size we cannot reject the possibility that a more subtle trend may actually exist. Further study is necessary to elaborate this point.

Great Horned Owls did not select the top of trees for roosting, yet this habitat position also had a lower activity of black flies. When we checked nests of Great Horned Owls during daytime and the parents perched on the top of trees, they were regularly harassed by gulls and shorebirds from nearby ponds, and we observed several attacks by Northern Harriers *Circus cyaneus*, Ravens *Corvus corax*, and Northern Goshawks *Accipiter gentilis* (Rohner and Doyle 1992a). In one instance, a Red-tailed Hawk *Buteo jamaicensis* physically hit a Great Horned Owl while dive-bombing from behind. Spruce trees in the study area were spindly, and roosting in the upper quarter of a tree would not have concealed a bird of the size of a Great Horned Owl.

Other alternative explanations may account for the observed seasonal shift in roost site selection. Owls have been assumed to avoid thermal stress in summer (Dunstan 1970, Janes 1985). It appeared unlikely to us that the often sun-exposed summer roost sites that we observed had in fact reduced heat stress, but more detailed studies on microclimate in relation to roost sites are necessary to test this hypothesis. Microclimate may also have indirect effects, for example the activity of black flies is partially influenced by temperature and humidity (Hunter 1990). A change in roost sites may also be associated with the energetic and physiological demands of molt, and further studies on the effect of molt on microhabitat selection of roosting birds could be fruitful. We found a strong association of roost-site shifts and black fly distribution, but as our study is of

correlative nature, this is not proof of a causal relationship and our main objective is to stimulate further research on this topic.

BROADER IMPLICATIONS

All species of the avian blood parasite *Leucocytozoon* are transmitted by an ornithophilic group of black fly species (Simuliidae), which have modified tarsal claws that enable them to crawl into the plumage of birds (Bennett and Fallis 1960, Sutcliffe 1986, Desser and Bennett 1993). To our knowledge, our sample is the first identification of blood-fed ornithophilic black flies for northwestern Canada (the species composition is similar to that found in other regions in the northwestern part of the continent; Corkum and Currie 1987, Currie 1997). Despite regional differences in species composition, ornithophilic black flies have a wide global distribution and may affect a broad range of bird species. To date, little is known about such effects.

Are negative effects of black fly feeding and behavioral avoidance by birds more common than previously recognized? Other investigations also have found that the sylvatic species of Simuliidae have a vertically stratified distribution, and many are most abundant at mid-canopy level where the abundance of forest birds may be highest (Bennett 1960, Bennett and Coombs 1975, Greiner et al. 1975). Greiner et al. (1975) compared this vertical distribution with the distribution of infection rates by blood parasites across bird species nesting in different strata. In a continent-wide comparison, there was too much variation for a clear pattern, but at three specific sites in eastern Canada the infection rates were highest in birds nesting at mid-canopy level. The potential effect of black flies on timing and location of nesting efforts deserves more study.

Do ectoparasites affect their hosts only at nest sites? We found it interesting that black flies affected Great Horned Owls beyond the stage of close affinity to a nest site. Previous studies found effects of ectoparasites at nest sites or at nesting cavities that were used as roosts during the nonbreeding season (De Feu 1992, Christe et al. 1994, Merilä and Allander 1995). The notion that birds may avoid ectoparasites at other places than a nest may lead to some re-assessment of current concepts.

As an example, we found an interesting trade-off in the system we studied. Open roost sites on the ground may reduce exposure to blood-sucking flies and the transmission of blood parasites, but they also increase the vulnerability to mammalian predators. With a decline of the density of cyclic snowshoe hare populations, the main prey biomass of most predators in the boreal forest, the mortality rates of juvenile Great Horned Owls increased drastically in 1991 due to predation (Boutin et al. 1995, Rohner and Hunter 1996). Most of this mortality was caused by lynx *Lynx canadensis* and coyotes *Canis latrans*, and it is unlikely that these predators would ever be able to kill an owl perched in a tree (Rohner and Hunter 1996). Such a trade-off between exposure to parasites and exposure to predators has received little study. Animals have to balance conflicting demands in order to enhance body condition, reproduction, and survival. There has been intense interest in trade-offs involving foraging and ex-

posure to predation risk (Lima and Dill 1990, McNamara and Houston 1990). If sylvatic birds are attempting to avoid black flies while foraging, trade-offs involving the exposure to these parasites may also have to be considered.

This study is dedicated to Gordon F. Bennett, founder of the International Reference Centre for Avian Haematozoa, Memorial University of Newfoundland, St John's, Newfoundland, Canada. Without his advice and guidance this study could not have been conducted, and we were sad to learn that he did not live to see its completion. We thank Samuel Wagnière for help in the field, and Irene Wingate for caring for our Bantam chickens. We also thank Baba Zimmermann and Cilla Kullberg for additional locations of owl roosts. Jamie Smith, Dolph Schluter, Dave Mossop, Ron Ydenberg, N. R. Liley, and Steve Petty helped through discussions and comments on earlier drafts of the manuscript. Funding was provided by the Natural Sciences and Engineering Council of Canada (grant to C. J. Krebs), a J. R. Thompson Wildlife Fellowship, a Graduate Fellowship by the University of British Columbia, and a MacLean-Fraser Summer Research Fellowship. This is publication 108 of the Kluane Boreal Forest Ecosystem Project.

LITERATURE CITED

- APPLEBY, B. M., M. A. ANWAR, AND S. J. PETTY. 1999. Short-term and long-term effects of food supply on parasite burdens in Tawny Owls, *Strix aluco*. *Funct. Ecol.* 13:315–321.
- BELTHOFF, J. R., AND G. RITCHISON. 1990. Roosting behavior of postfledging Eastern Screech-Owls. *Auk* 107:567–579.
- BENNETT, G. F. 1960. On some ornithophilic blood-sucking Diptera in Algonquin Park, Ontario, Canada. *Can. J. Zool.* 38:377–389.
- BENNETT, G. F., AND R. F. COOMBS. 1975. Ornithophilic vectors of avian haematozoa in insular Newfoundland. *Can. J. Zool.* 53:1241–1246.
- BENNETT, G. F., AND A. M. FALLIS. 1960. Blood parasites of birds in Algonquin Park, Canada, and a discussion of their transmission. *Can. J. Zool.* 38:261–272.
- BENNETT, G. F., M. A. PEIRCE, AND R. W. ASHFORD. 1993. Avian haematozoa: mortality and pathogenicity. *J. Nat. Hist.* 27:993–1001.
- BENNETT, G. F., M. WHITEAWAY, AND C. WOODWORTH-LYNAS. 1982. A host-parasite catalogue of the avian haematozoa. Memorial Univ. Newfoundland Occ. Pap. Biol. 5:1–243.
- BISHOP, M., AND G. F. BENNETT. 1992. Host-parasite catalogue of the avian haematozoa. Memorial Univ. Newfoundland Occ. Pap. Biol. 15:1–244.
- BOUTIN, S., C. J. KREBS, R. BOONSTRA, M. R. T. DALE, S. J. HANNON, K. MARTIN, A. R. E. SINCLAIR, J. N. M. SMITH, R. TURKINGTON, M. BLOWER, A. BYROM, F. I. DOYLE, C. DOYLE, D. HIK, L. HOFER, A. HUBBS, T. KARELS, D. L. MURRAY, V. NAMS, M. O'DONOGHUE, C. ROHNER, AND S. SCHWEIGER. 1995. Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. *Oikos* 74:69–80.

- CHRISTE, P., A. OPPLIGER, AND H. RICHNER. 1994. Ectoparasite affects choice and use of roost sites in the Great Tit. *Anim. Behav.* 47:895–898.
- CORKUM, L. D., AND D. C. CURRIE. 1987. Distributional patterns of immature Simuliidae (Diptera) in northwestern North America. *Freshwater Biol.* 17: 201–211.
- CURRIE, D. C. 1997. Black flies (Diptera) of the Yukon, with reference to the black fly fauna of northwestern North America, p. 563–614. *In* J. A. Downes and H. V. Danks [EDS.], *Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods)*, Ottawa, Canada.
- DE FEU, C. R. 1992. How tits avoid flea infestation at nest sites. *Ring and Migration* 13:120–121.
- DESSER, S. S., AND G. F. BENNETT. 1993. The genera *Leucocytozoon*, *Haemoproteus* and *Hepatozoon*, p. 273–305. *In* J. P. Kreier [ED.], *Parasitic protozoa*. 2nd ed. Vol. 4. Academic Press, London.
- DONAZAR, J. A., F. HIRALDO, M. DELIBES, AND R. R. ESTRELLA. 1989. Comparative food habits of the Eagle Owl *Bubo bubo* and the Great Horned Owl *Bubo virginianus* in six palearctic and nearctic biomes. *Ornis Scand.* 20:298–306.
- DUNSTAN, T. C. 1970. Post-fledging activities of juvenile Great Horned Owls as determined by radio-telemetry. Ph.D. diss., Univ. South Dakota, Vermillion, SD.
- FITCH, H. S., F. SWENSON, AND D. F. TILLOTSON. 1946. Behavior and food habits of the Red-tailed Hawk. *Condor* 48:205–237.
- FORSMAN, E. D., E. C. MESLOW, AND H. M. WIGHT. 1984. Distribution and biology of the Spotted Owl in Oregon. *Wildl. Monogr.* 87:1–64.
- GREINER, E. C., G. F. BENNETT, E. M. WHITE, AND R. F. COOMBS. 1975. Distribution of the avian hematophaga of North America. *Can. J. Zool.* 53: 1762–1787.
- GUTIERREZ, R. J. 1989. Hematozoa from the Spotted Owl. *J. Wildl. Dis.* 25:614–618.
- HAYWARD, G. D., AND E. O. GARTON. 1984. Roost habitat selection by three small forest owls. *Wilson Bull.* 96:690–692.
- HUNTER, D. B., C. ROHNER, AND D. C. CURRIE. 1997. Mortality in fledgling Great Horned Owls from black fly hematophaga and leucocytozoonosis. *J. Wildl. Dis.* 33:486–491.
- HUNTER, F. F. 1990. Ecological, morphological, and behavioural correlates to cytospecies in the *Simulium venustum/verecundum* complex (Diptera: Simuliidae). Ph.D. diss., Queen's Univ., Kingston, Ontario, Canada.
- HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54:187–211.
- JANES, S. W. 1985. Habitat selection in raptorial birds, p. 159–188. *In* M. L. Cody [ED.], *Habitat selection in birds*. Academic Press, London.
- KENWARD, R. E. 1985. Raptor radio-tracking and telemetry. *ICBP Tech. Publ.* 5:409–420.
- KORPIMÄKI, E., H. HAKKARAINEN, AND G. F. BENNETT. 1993. Blood parasites and reproductive success of Tengmalm's Owls: detrimental effects on females but not on males. *Funct. Ecol.* 7:420–426.
- KREBS, C. J., S. BOUTIN, R. BOONSTRA, A. R. E. SINCLAIR, J. N. M. SMITH, R. T. DALE, K. MARTIN, AND R. TURKINGTON. 1995. Impact of food and predation on the snowshoe hare cycle. *Science* 269:1112–1115.
- LIMA, S. L., AND L. M. DILL. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68:619–640.
- MENAMARA, J. M., AND A. I. HOUSTON. 1990. State-dependent ideal free distributions. *Evol. Ecol.* 4: 298–311.
- MERILÄ, J., AND K. ALLANDER. 1995. Do Great Tits *Parus major* prefer ectoparasite-free roost sites? An experiment. *Ethology* 99:53–60.
- MØLLER, A. P. 1990. Parasites and sexual selection: current status of the Hamilton-Zuk hypothesis. *J. Evol. Biol.* 3:319–328.
- RICHNER, H., P. CHRISTE, AND A. OPPLIGER. 1995. Paternal investment affects prevalence of malaria. *Proc. Natl. Acad. Sci.* 92:1192–1194.
- RICHNER, H., A. OPPLIGER, AND P. CHRISTE. 1993. Effect of an ectoparasite on reproduction in Great Tits. *J. Anim. Ecol.* 62:703–710.
- ROHNER, C. 1995. Great Horned Owls and snowshoe hares: what causes the time lag in the numerical response of predators to cyclic prey? *Oikos* 74: 61–68.
- ROHNER, C. 1996. The numerical response of Great Horned Owls to the snowshoe hare cycle: consequences of non-territorial 'floaters' on demography. *J. Anim. Ecol.* 65:359–370.
- ROHNER, C. 1997. Non-territorial 'floaters' in Great Horned Owls: space use during a cyclic peak of snowshoe hares. *Anim. Behav.* 53:901–912.
- ROHNER, C., AND F. I. DOYLE. 1992a. Food-stressed Great Horned Owl kills adult Goshawk: exceptional observation or community process? *J. Raptor Res.* 26:261–263.
- ROHNER, C., AND F. I. DOYLE. 1992b. Methods of locating Great Horned Owl nests in the boreal forest. *J. Raptor Res.* 26:33–35.
- SMITH, R. N., S. L. CAIN, S. H. ANDERSON, J. R. DUNK, AND E. S. WILLIAMS. 1998. Blackfly-induced mortality of nestling Red-tailed Hawks. *Auk* 115:368–375.
- SOMMERMAN, K. M. 1953. Identification of Alaskan black fly larvae (Diptera, Simuliidae). *Proc. Entomol. Soc. Washington* 55:258–273.
- STONE, A. 1952. The Simuliidae of Alaska (Diptera). *Proc. Entomol. Soc. Washington* 54:69–96.
- SUTCLIFFE, J. F. 1986. Black fly host location: a review. *Can. J. Zool.* 64:1041–1053.
- TOFT, C. A. 1991. Current theory of host-parasite interactions, p. 3–15. *In* J. E. Loye and M. Zuk [EDS.], *Bird-parasite interactions*. Oxford Univ. Press, Oxford.
- VOOUS, K. H. 1988. *Owls of the Northern Hemisphere*. Collins Sons, London.