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BLACKFLY-INDUCED MORTALITY OF NESTLING RED-TAILED HAWKS

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ABSTRACT.—We documented blackfly infestations (*Simulium canonicolum*) at 42 Red-tailed Hawk (*Buteo jamaicensis*) nests in Wyoming. Blackflies caused mortality at 6 of 42 (14%) nests where young hatched (13 of 87 nestlings) and were the only known cause of nestling mortality. The onset of infestations occurred when nestlings were 3 to 20 days old and usually lasted until nestlings died or fledged. Age of nestlings at mortality ranged from 9 to 43 days. Levels of blackfly infestation were highly variable among nests and were affected by weather. The cumulative effects of infestations on nestlings, including physical harassment, *Leucocytozoon* (a blood protozoan transmitted by blackflies) infection, and direct loss of blood and body fluids from biting flies, apparently resulted in mortalities through sustained physiological damage, trauma associated with early nest departure, or both. Because blackfly infestations can be detected only at close range, are ephemeral at nests, and can cause mortality of nestlings over a wide range of ages, the presence of blackflies and their influence on reproduction probably are undetected during most raptor productivity surveys. *Received 23 January 1997, accepted 26 August 1997.*

A VARIETY OF PARASITES has been found in raptors (Trainer 1969, Keymer 1972, Greenwood 1977, Gutiérrez 1989, Philips 1990, Forrester et al. 1994). Although the literature describing parasites in raptors is fairly extensive, few researchers have described the effects of these parasites on their raptor hosts. Blackflies (*Simulium* spp.) and the parasites they transmit have been associated with at least four species of raptors (Greiner and Kocan 1977, Jolly 1982, Hunter et al. 1997), but their effect on the health of these species is largely unknown.

Fitch et al. (1946) reported that 7 of 11 mortalities of nestling Red-tailed Hawk (*Buteo jamaicensis*) were due to blackflies (*Eusimulium clarum*). Similarly, Brown and Amadon (1968) reported that during wet years, biting flies (*Prosimulium* spp.) were a principal cause of mortality of nestling Red-tailed Hawks in California. However, they did not suggest possible mechanisms of mortality and gave no source for the information. Stabler and Holt (1965) reported a prevalence of blood protozoa in a number of different hawks, and Forrester et al. (1994) documented the relative occurrence of blood parasites in raptors in Florida but made no mention of the potential effects of these parasites on raptor productivity. Hunter et al. (1997) attributed mortality of Great Horned Owls (*Bubo virginianus*) to feeding blackflies (Simulidae), anemia, and blood parasite (*Leucocytozoon* spp.) infection. However, all of the mortality they observed occurred in owls tethered to platforms for experimental purposes.

In a portion of our study area in Grand Teton National Park (GTNP), northwestern Wyoming, the number of young Red-tailed Hawks fledged per nest declined from 1.4 to 0.7 between 1947 and 1975 (Craighead and Mindell 1981). More recent monitoring of productivity (1990 to 1991) indicated a high proportion of nesting failures, and dead young were found in and beneath some nests (S. Cain unpubl. data). In all cases where dead nestlings were found, prey items were in the nests, and adults were

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present and defended the nests, suggesting that parasitism or disease caused the mortalities (versus parental abandonment or starvation). These findings provided the impetus for a broad-based ecological study of Red-tailed Hawks. Here, we describe the effects of blackfly infestations, and associated transmission of the blood protozoan *Leucocytozoon*, on Red-tailed Hawk nestlings. Our primary objectives were to: (1) categorize both the levels and duration of blackfly infestation at individual nests, and (2) investigate the effects of blackfly infestations on the survival of Red-tailed Hawk nestlings.

Study Area and Methods

We studied Red-tailed Hawks in northwestern Wyoming within GTNP (43°67′N, 110°72′W). GTNP encompasses a high mountain valley surrounded by the Teton Mountains to the west, the Gros Ventre Mountains to the east, and the Yellowstone plateau to the north. All study nests were on the valley floor within a 226-km² core area in southern GTNP. The study area extended approximately 29 km north from the park's southern boundary and was approximately 10 km wide. The valley floor is dominated by numerous river terraces with minor elevational relief, glacial moraines, and several timbered buttes rising from 150 to 300 m above the valley floor. The study area contained large areas of previously or currently irrigated and grazed hay lands. Elevations range from 1,890 m in the valley floor to 4,197 m atop the surrounding mountain peaks. The climate is characterized by long, cold winters and short, cool summers. The 30-year mean maximum and minimum monthly temperatures during the breeding season (March to July) were 9.5°C (range 1.5 to 16.1°C) and −4.7°C (range −12.4 to 0.5°C), respectively (National Climatic Data Center 1992–1994). Approximately 67% of the annual precipitation occurs in the form of snow. Human developments included campgrounds, houses and guest ranches, and roads.

We estimated blackfly abundance 414 times at 42 nests from 1992 to 1994. The number of estimates at nests varied from 2 to 22. Of the 42 nests, 35 were monitored from incubation to fledging, and 7 were monitored from the early nestling period to either nest failure or fledging. Nest contents and blackfly abundance were monitored using a modified mirror-and-pole device (Parker 1972) or by climbing nest trees. Blackfly infestation levels were placed into four categories based on estimated numbers of blackflies found around the nestlings or nest: (1) low (<50 flies), (2) moderate (50 to 200), (3) high (200 to 500), and (4) severe (>500). To minimize observer variability, the same individual (RNS) made all estimates of blackflies. Blackflies were collected by passing a small hand-held net over the nest and by picking flies off of the nestlings by hand. *Protocalliphora* larvae (blowfly maggots) were removed from the ear cavity of several nestlings. Both blackflies and blowflies were preserved in 10% formalin.

We used nonparametric analyses because our data were categorical. Comparisons of levels of ectoparasitism were by Kruskall-Wallis one-way ANOVA. Statistical treatment of nestling mortality with G-tests followed Sokal and Rohlf (1995).

To assess blood parasitemia, a 0.5-cc blood sample was collected from one nestling in each nest (1993 and 1994 only) when young were approximately 30 to 35 days old. Samples also were collected from two adults. Fresh blood smears were air-dried, fixed, and stained with Hema 3 modified Wright's stain. Smears were scanned using dry and oil magnification. *Leucocytozoon* infection was diagnosed by the presence of elongate gametocytes. Smears were considered negative if no *Leucocytozoon* were detected after scanning the entire smear.

Laboratory analyses were performed at the Wyoming State Veterinary Laboratory. Nestling carcasses were examined grossly and selected tissues were collected, fixed in 10% buffered formalin, and processed for embedding in paraffin. Sections for light microscopy were sectioned at 5 to 6 μ and stained with hematoxylin and eosin (Luna 1992). Some sections of skin were stained by the periodic-acid Schiff method. Cloacal swabs and portions of liver, lung, and small intestine were collected from most carcasses for bacterial culture by routine methods (Carter and Cole 1990). Sections of skin from the neck of affected birds were cultured for fungi and examined by low-power microscopy for ectoparasites. Flotations were conducted on feces collected from the colon or cloaca. Neck skin from two nestlings was examined by negative-stain electron microscopy for viruses (Nunamaker and Williams 1986). The livers from four birds were examined for lead, cadmium, phosphorus, barium, manganese, magnesium, calcium, copper, molybdenum, zinc, iron, cobalt, chromium, vanadium, tin, nickel, arsenic, selenium, and mercury by inductively coupled plasma atomic emission spectroscopy. Brain tissues from two nestlings were analyzed for cholinesterase activity by a modification of the Ellman method (Ellman 1961). Liver tissues of two nestlings were tested for the presence of barbiturates by a commercial spot test (Toxi-lab, Inc., Irvine, California).

Minimum and maximum daily temperatures during the nestling stage were recorded at nearby Moose, Wyoming. Temperatures were examined with respect to their potential influence on blackfly activity at all nests monitored. Comparisons of maximum daily temperatures among years were by one-way ANOVA followed by Tukey's multiple compar-

TABLE 1. Overall mortality of Red-tailed Hawks and mortality attributed to blackflies in northwestern Wyoming, 1992 to 1994.

			Overall mortality		Mortality from blackflies	
Year	No. nests	Nestlings[a]	Nestlings (%)	Nests (%)	Nestlings (%)	Nests (%)
1992	14	37	19 (51.3)	8 (57.1)	10 (27.0)	5 (35.7)
1993	14	29	3 (10.3)	2 (14.2)	1 (14.2)	1 (7.1)
1994	14	28	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Total	42	94	22 (23.4)	10 (23.8)	11 (11.7)	6 (14.3)

[a] No. nestlings that hatched.

ison tests. Differences were considered significant at $P < 0.05$. All statistical procedures were done using SYSTAT for Windows (SYSTAT Inc. 1992).

RESULTS

Eleven of 94 (12%) nestlings monitored died of the effects of blackfly infestations (Table 1). Mortalities occurred in birds that were 9 to 43 days of age, and ranged from 0 to 10 nestlings annually. The onset of infestations occurred when nestlings were 3 to 20 days old and lasted until nestlings died or fledged. The duration of infestation prior to nestling mortality ranged from 7 to 30 days. The level of nestling mortality and the number of nests with mortality varied during the three years of study (Table 1). Levels of ectoparasitism (Kruskall-Wallis test, $H = 14.36$, $P < 0.0001$) and nestling mortality due to blackflies ($G = 17.37$, $P < 0.0001$) were higher in 1992 than in other years (Fig. 1). Mortalities attributed to blackflies included nine nestlings found on the ground and two found in nests. In addition, nine nestlings disappeared and died of unknown causes. Of these nine nestlings, two were siblings of birds found dead, three disappeared from a nest with unknown infestation during a 10-day period between nest visits, and four disappeared from a nest with a low blackfly infestation over a 4-day period when young were 14 to 17 days old. The timing and pattern of these disappearances suggested that blackflies caused the mortalities. However, we cannot rule out other possible causes of mortality, such as predation.

All blackflies collected at nests were identified as *Simulium canonicolum*, although another species of *Simulium* also may have been present (P. Adler pers. comm.). For the three years of study, mean Julian hatching date was 145 ± SD of 6.25 days (range 137 to 161 days), and mean fledging age was 45.5 ± 3.49 days (range 36 to 50 days).

Dermatitis, characterized by loss of feathers, thick crusting, and folding of skin, occurred with varying degrees of severity on the head, and from the intermandibular skin to the skin over the upper thorax of eight nestlings (three males, five females) examined postmortem. Multiple fractures of bones (skull, long bones, ribs) with associated hemorrhaging occurred in six nestlings. Splenomegaly was prominent in six nestlings. Tissues were pale, and the

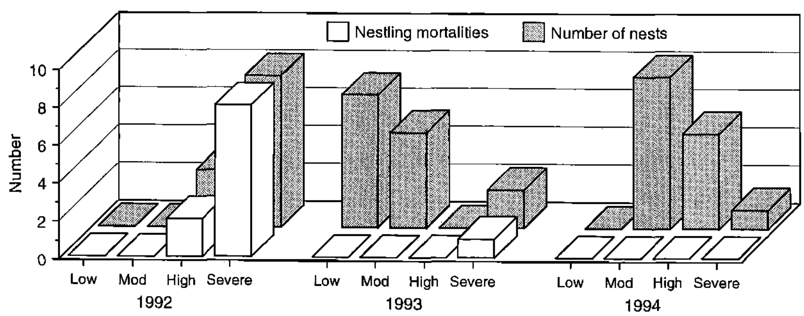

FIG. 1. Maximum level of blackfly infestation and associated nestling mortality documented at 42 Red-tailed Hawk nests from 1992 to 1994 in northwestern Wyoming. Low = 1 to 50 flies, moderate = 50 to 200, high = 200 to 500, severe = >500.

FIG. 2. Photomicrograph depicting inflammation of skin from the neck of a Red-tailed Hawk nestling. Note the large focus of necrotic dermis (margins delineated by arrowheads) and hyperkeratosis (arrow).

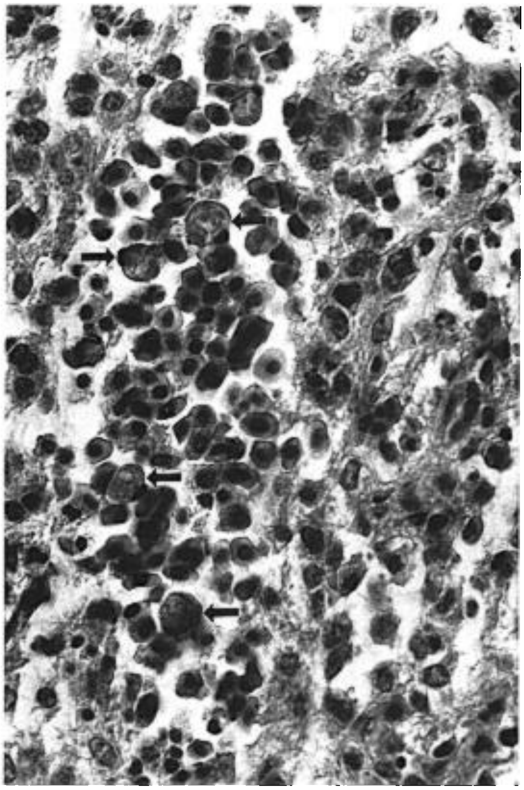

FIG. 3. Photomicrograph depicting round microgamonts or microgametes of *Leucocytozoon* (arrows) with dilated capillaries of the skin of the neck of an affected Red-tailed Hawk nestling.

blood appeared watery in seven of eight birds. Microscopically, the dermatitis was characterized by dermal edema, vascular congestion, multiple areas of necrosis, dense superficial infiltration of macrophages and heterophils, and marked hyperkeratosis (Fig. 2). Round microgamonts or macrogametes of *Leucocytozoon* sp. were found in dilated dermal capillaries of affected neck skin (Fig. 3). Megaloschizonts were present in the spleen and kidney of four birds. Multiple areas of acute hepatic necrosis without inflammatory reaction were found in one bird. Several birds had small aggregates of mononuclear cells in the renal interstitium. There was no microscopic evidence of significant bacterial or viral infection, or of toxicological disease.

Bacteria isolated from tissues and intestines of nestlings included *Escherichia coli*, *Streptococcus*, and coagulase negative *Staphylococcus* sp.; these isolates were not considered significant. No viruses were identified in skin by electron microscopy, and no pathogenic fungi were cultured. One fecal sample contained low numbers of *Eimeria* sp. oocysts, and sporulated oocysts of *Sarcocystis* sp. were found in the subepithelium of the villi in the small intestines of two birds. Cholinesterase levels were normal for raptors. No abnormalities were detected in the livers. Twenty-one of 28 (75%) blood smears taken from live nestlings and blood samples from six additional dead nestlings that were necropsied tested positive for the blood protozoan *Leucocytozoon*. The spleens and kidneys were greatly enlarged in five of the seven (71%) nestlings necropsied, and megaloschizonts were found in four of these individuals.

Blood-sucking blowfly larvae (*Protocalliphora avium*) were observed in the auricular openings of 32 of 33 nestlings between 4 and 11 June 1992 and were present in some nestlings until at least 22 June ($\bar{x}$ = 6.7 days). In 1993 and 1994, larval blowflies were detected in auricular openings of 21 of 21 and 29 of 29 nestlings, respectively. In all, larval blowflies were observed in 82 of 83 nestlings examined. In most cases, larvae completely filled the auricular openings. Nine larvae occurred in the auricular openings of one live nestling found on the ground beneath a nest. This nestling, estimated to be 14 days old, also had larvae on open and penetrating wounds on the neck region and beneath both wings.

Blackflies burrowed through the nestlings' downy plumage to bite the skin on the neck, underwings, or around the auricular openings, and alighted to bite the head, eye margins, and cere. Small dots and flakes of dried blood often occurred where the blackflies had fed. Nestlings frequently, if not incessantly, exhibited annoyance behavior during infestations, continuously flapping their wings, vigorously shaking their heads, moving around in the nest, and pecking at exposed areas of their bodies. Based on our field observations, these nestling behaviors did not occur when blackflies were absent.

Maximum daily temperatures during the nestling period varied significantly ($F = 19.28$, df = 2 and 213, $P < 0.0001$) among the three years of study. Blackfly abundance at nests decreased substantially or ceased when ambient temperatures were below 14°C. Ambient temperatures were below 14°C for 21 days during the nestling period for all years combined, with annual totals ranging from 2 to 15 days (Fig. 4). Blackfly abundance at nests decreased as wind velocity increased, but we collected no systematic data on wind velocity.

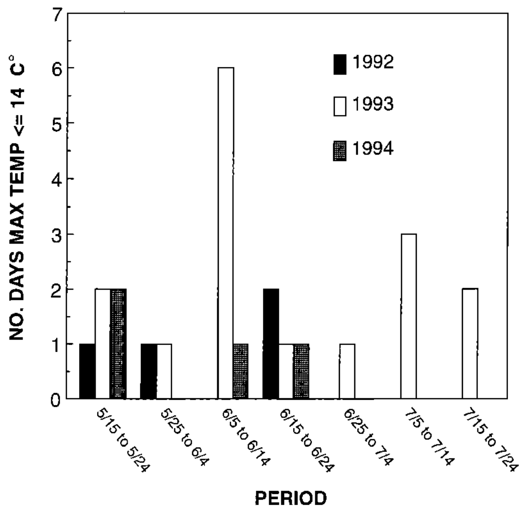

FIG. 4. Number of days during the nestling stage when maximum daily temperature was <14°C and blackfly infestations were interrupted.

DISCUSSION

Blackflies in the genus *Simulium* are nearly cosmopolitan (Crosskey 1990). To complete their life cycle, they require moving water with trailing vegetation and a blood meal for the females (James and Harwood 1979, Crosskey 1990). Blackflies are vectors for a variety of parasites, including nematodes and several species of blood protozoans (e.g. *Leucocytozoon*; Stabler and Holt 1965, Bennett 1987). *Leucocytozoon* spp. have been documented in more than 1,000 species of birds in 98 families (Bennett 1987) and have been found in Canada, California, and throughout the Rocky Mountains (Greiner et al. 1975, P. Adler pers. comm.). During the blackfly life cycle, *Leucocytozoon* may be transmitted among individual birds by feeding blackflies. The cycle starts when blackflies emerge in the spring and are infected while obtaining blood meals from adult birds that are chronically infected with *Leucocytozoon*. Sporozoites are then formed, which migrate to the salivary glands of infected blackflies and are injected into other birds, particularly nestlings, during subsequent feeding (Wobeser 1981, Atkinson and van Riper 1991, Cupp et al. 1993). Under most natural conditions, up to 60% of adult birds retain their infection from one year to the next (Bennet 1987). A relapse of parasitemia in chronically infected adult raptors during spring (P. Redig pers. comm.) may coincide with the emergence of blackflies. Spring relapses of parasitemia in breeding ducks and geese are well documented (Desser et al. 1968, 1978, Herman et al. 1975). During spring relapses, *Leucocytozoon* may be found in sub-epidermal capillaries of the skin where they are accessible to biting flies.

Differences among years in blackfly abundance at hawk nests were at least partially related to differences in ambient temperatures (Fig. 4). All fly activity ceased during a 4-day period in June 1992 when the mean daily temperature dropped from 22.5 to 12.8°C. During 1993, temperatures dropped below 14°C during six separate periods lasting approximately two days each. We estimated that nestlings received a break from fly harassment for 15 days (roughly 35% of the nestling stage) during the 1993 nestling period. This temperature pattern may help explain why infestations did not progress to more severe levels in 1993. In 1994, temperatures dropped below 14°C for only four days. However, the 1994 breeding season was unusually windy, which may have resulted in a lower effective infestation level and the subsequent absence of nestling mortality that we observed (Table 1). Crosskey (1990) reported that blackflies ceased all flight activity when temperatures dropped to 8 to 10°C and that flight resumed when temperatures rose above 13 to 15°C.

Thus, it would appear that breaks in infestation would have the highest potential to prevent nesting failure from blackflies by removing the associated harassment, excessive energy expenditure, dehydration, and anemia when nestlings are young. At early stages of nestling development, the effect of a reprieve from infestation may be similar to the effect of greater nestling age at the onset of infestation. Moreover, feather development and maturation of the immune system that normally occur during an infestation reprieve also may contribute to a lower "effective" infestation level when it resumes (Davidar and Morton 1993).

Blackflies have been documented on raptors elsewhere in Wyoming. R. Oakleaf and W. Heinrich (pers. comm.) indicated that blackflies caused considerable stress to Peregrine Falcons (*Falco peregrinus*) in the Greater Yellowstone Area (GYA). Harmata and Oakleaf (1993) found a dead Bald Eagle (*Haliaeetus leucocephalus*) nestling beneath a nest in the GYA with severe dermatitis on its neck and breast. A live sibling tested positive for *Leucocytozoon*, indicating exposure to blackflies, as did 7.3% of 96 nestling Bald Eagles in the GYA (Harmata and Oakleaf 1993). Blackflies also have been observed in nests of Bald Eagles and Ospreys (*Pandion haliaetus*) in the GYA (G. Montopoli pers. comm.).

Parasitism of nestling raptors by blowflies is well known (Burtch 1922, Sargent 1938, Hill and Work 1947, Hamerstrom and Hamerstrom 1954, Tirrell 1978, Crocall and Parker 1981, Bortolotti 1985). Although none of these studies attributed severe injury of nestlings to larval infestations, most suggested that blowflies contributed to an overall weakened condition. Mortality due to *Protocalliphora* larvae is rare (Sabrosky et al. 1989). They can, however, disfigure the outer ear, destroy the ear drums, and contribute to anemia in nesting birds (Bortolotti 1985, Sabrosky et al. 1989). Although the life history of *Protocalliphora* in North America is not well known, Sabrosky et al. (1989) reported that they overwinter as adult flies, and that only dead, empty, or parasitized puparia were found in nests during the fall and winter. It is not known whether female flies lay eggs in nests where larvae crawl onto the birds, or whether eggs are laid directly on the birds. However, Tirrell (1978) reported fairly conclusive evidence that the latter occurred on Red-tailed Hawks in North Dakota.

The cause of death of six of the nestlings in our study was severe trauma accompanied by fractured bones and hemorrhaging. We believe that birds found dead beneath nests probably fell or jumped due to harassment by blackflies. Blackfly bites caused severe dermatitis on the head, neck, and thoracic skin of nestlings. This severe inflammation in the neck would have caused considerable irritation to the birds. We found no evidence of other significant bacterial, viral, mycotic, or toxicologic diseases to account for the deaths of these birds.

Young hawks appeared to be particularly susceptible to blackfly bites, and therefore to the transmission of *Leucocytozoon* spp., when they were in the natal down stage (<25 days). After young were about 30 to 35 days old, their bodies were approximately 90% feathered. This may have provided some protection from flies, although agitated behavior due to feeding by flies was observed in nestlings until they fledged or died. Chronic infection by blood protozoans may have little effect on adult birds that survive the initial infection (Herman et al. 1975, Davidar and Morton 1993). In 1993 and 1994, more than 75% of the nestlings we sampled tested positive for *Leucocytozoon* infection, yet only one mortality was attributed to blackfly infestation.

Although we found no evidence that *Leucocytozoon* infection led directly to disease, the cumulative effects associated with blackfly infestation could cause illness and mortality in nestlings in the following scenario: (1) harassment by flies leads to energy expenditure and premature nest departure; (2) infection by *Leu-*

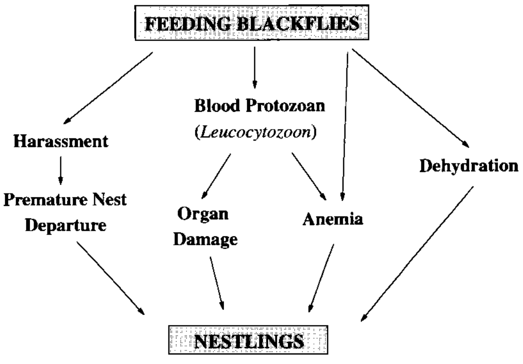

FIG. 5. Proposed cumulative effects of blackflies on nestling Red-tailed Hawks.

cocytozoon leads to anemia and organ damage; and (3) loss of blood from infestations of blood-sucking flies leads to anemia and dehydration (Fig. 5).

Herman et al. (1975) discussed the importance of looking at several cumulative factors related to waterfowl reproductive success and blackfly (*S. innocens*) infestation. Hunter et al. (1997) speculated that owl nestlings can recover from the effects of *Leucocytozoon* infection during years of high food supply. However, they did not mention the potential effects of weather on blackfly infestation and associated owlet survivorship. We found no evidence that food supplies were limited, and we propose that the age of nestlings at the time of the infestation, the level of infestation, and the timing of infestation reprieves due to cold or inclement weather act synergistically to affect nestling survivorship.

The influence of parasites on host populations is poorly known (Toft 1991). During one year of our study, blackflies reduced the reproductive success of Red-tailed Hawks by 27%. Preston and Beane (1993) reported that Red-tailed Hawk populations are regulated primarily by nest-site availability, food supply, and predation. Our data demonstrate that parasites can have a significant influence on the reproductive success of Red-tailed Hawks and suggest that they contribute to the regulation of populations. Moreover, because the cumulative effects of blackfly infestations can be important sources of nestling mortality, and because blackfly infestations and associated nestling mortality may go undetected in standard raptor surveys (i.e. two to three nest visits per season), researchers should design their studies so that the presence and effects of blackflies can be documented properly.

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