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Authors: Streby, Henry M., Peterson, Sean M., and Kapfer, Paul M.

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FLEDGING SUCCESS IS A POOR INDICATOR OF THE EFFECTS OF BIRD BLOW FLIES ON OVENBIRD SURVIVAL

HENRY M. STREBY^{1,2,4}, SEAN M. PETERSON¹, AND PAUL M. KAPFER³

¹Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, 200 Hodson Hall, St. Paul, MN 55108

²U.S. Geological Survey, Minnesota Cooperative Fish and Wildlife Research Unit, 200 Hodson Hall, St. Paul, MN 55108

³Conservation Biology Program, University of Minnesota, 200 Hodson Hall, St. Paul, MN 55108

Abstract. Infestations of bird blow flies (*Protocalliphora* spp. and *Trypocalliphora braueri*) have various negative effects on the condition of nestling birds. In the absence of other stressors such as inclement weather, however, infestation alone rarely reduces fledging success. Previous studies have documented effects of blow flies on nestling condition and fledging success. Without information regarding fledgling survival, the full effect of blow-fly infestation remains unclear. To fully investigate the effect of blow-fly infestation on reproductive success of the Ovenbird (*Seiurus aurocapilla*), we monitored infested and non-infested nests and monitored fledglings from each by using radio telemetry. Blow flies did not affect birds during the nestling period, as brood size, mean nestling mass, fledging success, and time to fledging in infested and non-infested nests were no different. Fledgling survival and minimum distance traveled the first day after fledging, however, were significantly lower for infected fledglings than for those that were not infected. We conclude that the stress of the early fledgling period combined with recent or concurrent blow-fly infection increases mortality in young Ovenbirds. Our results demonstrate the importance of including the post-fledging period in investigations of the effects of ectoparasitic infestations on birds.

Key words: blow fly, *Trypocalliphora braueri*, Ovenbird, *Seiurus aurocapilla*.

El Éxito de Emplumamiento es un Mal Indicador de los Efectos de las Moscas Parásitas de Aves sobre la Supervivencia en *Seiurus aurocapilla*

Resumen. Las infestaciones con las moscas parásitas *Protocalliphora* spp. y *Trypocalliphora braueri* tienen varios efectos negativos sobre la condición de los pichones de las aves. Sin embargo, la infestación por sí sola rara vez reduce el éxito de emplumamiento en ausencia de otros agentes de estrés, como el clima inclemente. Estudios previos han documentado los efectos de estas moscas sobre la condición de los pichones y el éxito de emplumamiento, pero sin información acerca de la supervivencia de los volantones, por lo que el efecto completo de la infestación no resulta claro aún. Para investigar de forma completa el efecto

de la infestación con estas moscas sobre el éxito reproductivo de *Seiurus aurocapilla*, monitoreamos nidos infestados y no infestados, y seguimos a los volantones salidos de éstos mediante telemetría con transmisores de radio. Las moscas no afectaron a los pichones durante su permanencia en el nido, pues no existieron diferencias entre nidos infestados y no infestados en el tamaño de la parvada, la masa promedio de los pichones, el éxito de emplumamiento o el tiempo transcurrido hasta el emplumamiento. Sin embargo, la supervivencia de los volantones y la distancia mínima de desplazamiento en el primer día posterior al abandono del nido fueron significativamente menores en los volantones salidos de nidos infestados. Concluimos que el estrés de la primera etapa de vida fuera del nido, en combinación con la infestación previa o concurrente por parte de las moscas, incrementa la mortalidad de los individuos jóvenes de *S. aurocapilla*. Nuestros resultados demuestran la importancia de considerar el período posterior al abandono del nido en las investigaciones acerca de los efectos de los ectoparásitos sobre las aves.

Identification of factors that influence avian reproductive success is an important goal of ornithological research. The effects of infestations of hematophagous ectoparasites such as bird blow flies (*Protocalliphora* spp. and *Trypocalliphora braueri*) on survival of young birds remain largely unclear. Although these parasites often negatively affect the condition of nestling hosts (Hurtrez-Boussès et al. 1997a, O'Brien et al. 2001), fledging success is rarely altered (Whitworth and Bennett 1992, Sabroski et al. 1989). Therefore, one might conclude that bird blow flies have little, if any, effect on host survival. Many authors, however, suggest that the effects of blow flies on the survival of young birds may be more apparent after fledglings leave the nest (Roby et al. 1992, Hurtrez-Boussès et al. 1997b, Merino and Potti 1998, Akesson et al. 2002).

Although parasitic blow-fly larvae can remove up to 55% of a nestling's blood volume (Gold and Dahlsten 1983), even such extreme infestations of *Protocalliphora parorum* have "surprising little direct effect" on hematocrit counts and survival of House Wren (*Troglodytes aedon*) nestlings (Johnson and Albrecht 1993:255). O'Brien et al. (2001) demonstrated that although hematocrit levels in nestling wrens are not affected by *P. parorum*, hemoglobin concentrations decline more than 25% in heavily infected nestlings. However, those authors did not observe increased mortality associated with the decline in condition. Additional

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⁴E-mail: streb006@umn.edu

observational (Akeson et al. 2002) and experimental (Roby et al. 1992, Hurtrez-Boussès et al. 1997b) studies of blow-fly infestations have found a range of effects on nestling condition but no effect on fledging success. It has been suggested that increased feeding by adults could compensate for negative effects of parasitic blow flies (Hurtrez-Boussès et al. 1997b). Indeed, Merino and Potti (1998) demonstrated that food supplementation can compensate for decreased hematocrit values in nestling Pied Flycatchers (*Ficedula hypoleuca*) with a low number of parasites.

Sabroski et al. (1989) concluded that bird blow flies are likely rarely a direct cause of mortality but may weaken nestlings, increasing their vulnerability to other causes of mortality. For example, in Alaska Matsuoka et al. (1997) found 50% of Townsend's Warbler (*Dendroica townsendi*) nests infested with *T. braueri* and mortality in 4 of 24 infested nests, but inclement weather confounded the implication of *T. braueri* as the cause of the mortality. Meadow Pipits (*Anthus pratensis*) and Bluethroats (*Luscinia svecica*) also experience increased nestling mortality with the combination of *T. braueri* infestation and heavy rainfall (Pavel et al. 2008). Similarly, in one year in Idaho Howe (1992) found that *T. braueri* infestation combined with inclement weather increased mortality of nestling Sage Thrashers (*Oreoscoptes montanus*). *Trypocalliphora braueri* infestation alone, however, did not affect survival or growth rate of Sage Thrasher nestlings in that population the following year.

Despite fledging success being generally unaffected, Merino and Potti (1998) posited that if nestling condition does not improve rapidly following infestation, a negative effect on fledgling survival is probable. Consequently an investigation of nestling and fledgling survival could clarify the effects of parasitism on bird fitness (Sabroski et al. 1989, Whitworth and Bennett 1992, Hurtrez-Boussès et al. 1997a, O'Brien et al. 2001). For many species the early post-fledging period is a time of high mortality from predation and inclement weather (Ricklefs 1968, King et al. 2006, Berkeley et al. 2007). To our knowledge, the effect of blow-fly infestation on the survival of fledglings has not been documented. We sought to quantify the effects of *T. braueri* infestation on fledging success and early fledgling survival in a population of Ovenbirds (*Seiurus aurocapilla*) in a mixed hardwood-coniferous forest in north-central Minnesota. We predicted that the combination of recent or current blow-fly infection with the stress of the early post-fledging period may significantly increase mortality in Ovenbirds.

METHODS

HOST AND PARASITE SPECIES

The Ovenbird is a neotropical migrant songbird that nests exclusively on the ground in mature forests of eastern and central North America. In our study population Ovenbirds have a 24-day nesting cycle with the nestling period averaging 8 days (Streby, unpubl. data). Ovenbirds may renest up to four times after failed attempts, but they do not renest after successfully fledging a brood (Podolski 2002).

Bird blow flies are parasitic dipterans that deposit eggs in nests containing nestlings (Gold and Dahlsten 1983). The larvae hatch, live in the nesting material, and feed on the host nestlings intermittently. In this group of parasites, *T. braueri* is unique in that its larvae burrow into the flesh of nestlings, where they spend the entirety of the larval stage. Infestations of *T. braueri* are most commonly reported in birds that nest on or near the ground or in cavities (Bennett and Whitworth 1991).

We located nests of breeding Ovenbirds in the spring and summer of 2008 by systematically searching and following adults within territories in mature mixed coniferous and northern hardwood forest in the Chippewa National Forest, Itasca County, Minnesota (47° 29' N, 93° 59' W). Nests were located in stands dominated by red pine (*Pinus resinosa*), quaking aspen (*Populus tremuloides*), big-tooth aspen (*P. grandidentata*), and northern white cedar (*Thuja occidentalis*). The understory in nesting territories consisted of patchy and often dense areas of sugar maple (*Acer saccharum*) and hazelnut (*Corylus* spp.).

We visited nests and recorded contents at approximately 4-day intervals following standard nest-monitoring procedures described by Martin and Geupel (1993). We visited nests more often when an event such as hatching or fledging was expected. We recorded brood size, defined here as the number of nestlings present at the first visit after hatching (usually within 1 day). To reduce disturbance of nests, we briefly checked nestlings for conspicuous blow-fly infection during regular nest checks.

One day before expected fledging we weighed each nestling to the nearest 0.25 g, using a Pesola (use of trade names does not imply endorsement by the U.S. Geological Survey or the University of Minnesota) 30-g spring scale, banded all nestlings with standard aluminum U.S. Geological Survey leg bands, and attached a radio transmitter to at least one nestling per nest. During banding, we recorded presence or absence of *T. braueri* infection, ranking infection rates as low (1–10 visible larvae per nestling) or high (>10 visible larvae per nestling). Transmitters were attached by means of a figure-eight harness design described by Rappole and Tipton (1991). We subsequently relocated fledglings daily via ground-based telemetry. We used triangulation to estimate the location of individuals and confirmed the result visually to determine survival and improve accuracy of recorded locations.

STATISTICAL ANALYSIS

Brood size, mean nestling mass, time to fledging, and minimum first-day distance (i.e., straight-line distance from the nest to the fledgling's location 1 day after fledging) were compared with Student's *t*-tests. Because we observed no partial losses of broods (i.e., nests either fledged all hatched young or lost all hatched young) fledging success was compared with a χ^2 test of independence with nest as the sample unit. Early fledgling survival (i.e., whether or not the fledgling survived the first 3 days after fledging) was also compared with a χ^2 test of independence. Tests were considered significant when $P \leq 0.05$.

RESULTS

We monitored a total of 42 active Ovenbird nests, 39 of which hatched nestlings. We observed *T. braueri* infestations in eight (21%) nests. Four nests had high levels of infestation, with each nestling hosting >10 visible larvae. Three nests had low levels of infestation, with each nestling hosting 1–10 visible larvae. One additional nest had a low-level infestation, with one of four nestlings hosting one visible larva. The majority of parasite larvae were embedded in the face and wings of nestlings (Figure 1), but some were also found in the feet, head, and back. One infested nest and seven non-infested nests failed, all from predation. We monitored the survival and daily movements of 9 fledglings from seven infested nests and 25 fledglings from 24 non-infested nests.

Brood size, mean nestling mass, fledging success, and time to fledging in infested and non-infested nests were not significantly different (Table 1). Survival and minimum first-day distance were both significantly lower for fledglings from infested



FIGURE 1. Deformation caused by blow fly (*Trypocalliphora braueri*) infection of (a) the face and (b) wing of an Ovenbird nestling in 2008 in the Chippewa National Forest, Minnesota. Photos by H. Streby.

nesses than for those from non-infested nests. Of the nine infected fledglings, eight died within 3 days of leaving the nest: seven were found dead with no sign of predation, and the eighth was apparently depredated by a small mammal. Significantly more (74%) non-infected fledglings survived the same period. Of the six mortalities of non-infected fledglings in the first 3 days after fledging, five were from predation and one was from apparent starvation. The ninth infected fledgling was depredated by a small mammal 12 days after leaving the nest.

DISCUSSION

Although blow-fly infestation did not affect survival or physical condition of nestling Ovenbirds, it did significantly decrease daily movements and increase mortality of fledglings during the early post-fledging period. These results suggest that the stress associated with the early post-fledging period and infection by *T. braueri* combine to increase mortality of recently fledged Ovenbirds significantly. In studies focusing solely on the nesting period, ectoparasites are often reported to have no significant effects on the fitness of host birds (e.g., Young 1993). Our results, however, clearly indicate that fledgling survival is affected by infestation by *T. braueri*. Future studies that aim to address the effects of nestling parasites on bird fitness should assess both the nestling and fledgling periods.

We recognize the potential issue of pseudoreplication in our analysis of fledgling survival. The probabilities of survival of fledglings from a single nest are likely not independent. Therefore, treating each fledgling as an independent sample tends to increase the probability of making a type-1 error. We attempted to minimize the effect of pseudoreplication by monitoring only one fledgling from each nest in most cases. We monitored survival of more than one fledgling from a single nest in three cases. Including only one fledgling from each of those nests in later analyses did not change the results.

Increased nestling activity due to irritation from parasites and increased feeding activity by adults may be expected to increase predation on blow-fly-infested broods. On the basis of limited video surveillance during our study, adults did not seem to visit infested nests at higher rates. However, infested broods were noticeably more active, with nearly constant scratching and twitching. In contrast, non-infested broods remained largely motionless between visits by adults. Hurtrez-Boussès et al. (1997b) also observed infested broods to be more active than experimentally deparasitized broods. Neither that study, nor the observations from our study, however, suggest an association between nestling activity and probability of predation. During video monitoring of nests, we made several observations of nestlings rolling or hopping out of the nest and subsequently climbing back in. We did not observe this activity in non-infested nests. If this activity

TABLE 1. Characteristics of Ovenbird nests and fledglings infested and not infested by *Trypocalliphora braueri* in 2008 in the Chippewa National Forest, Minnesota.

Variable	Mean infested	Mean non-infested	Test statistic	df	P
Brood size (no. nestlings)	4.50 (± 0.19)	4.35 (± 0.14)	$t = 0.6$	37	0.54
Nestling mass (g)	14.1 (± 0.4)	3.8 (± 0.2)	$t = 0.8$	27	0.43
Time to fledge (days)	8.0 (± 0.3)	7.7 (± 0.2)	$t = 0.9$	30	0.38
Fledgling success	0.88 (± 0.05)	0.81 (± 0.03)	$\chi^2 = 0.3$	1	0.61
Fledgling survival	0.11 (± 0.11)	0.74 (± 0.09)	$\chi^2 = 11.5$	1	<0.001
First-day distance (m)	23.6 (± 6.2)	41.6 (± 5.0)	$t = 2.2$	32	0.035

is common, it could have a large effect on survival for infested nests of species nesting above the ground.

We detected no difference in mass between nestlings in infested and non-infested nests. We caution that mass may be an unreliable indicator if larvae are in the flesh of nestlings at the time of weighing. Because *T. braueri* larvae weigh ~0.1 g each, they may contribute 7–20% of the mass of heavily infested (10–25 larvae) Ovenbird nestlings. We did not remove larvae before weighing because we intended to continue to monitor the effects of infection on fledglings. It is possible, however, that the additional mass of the larvae could have compensated for the lower masses of infected fledglings. Had we removed the larvae before weighing, infected nestlings may have weighed less than non-infested nestlings.

Larvae of *T. braueri* burrow into the flesh of nestlings and spend the entirety of their 10-day larval stage within the host. Infected Ovenbirds may be particularly vulnerable to early fledgling mortality because the relatively short 8-day nestling period increases the probability that Ovenbirds will retain larvae after fledging. Because birds generally regenerate blood quickly (Hoysak and Weatherhead 1991), the negative effects associated with blood loss may not be expected to persist long after blow-fly larvae exit nestlings. After exiting the skin, however, larvae left large open wounds that sometimes deformed wing development. These wounds could expose fledglings to other infections (Warren 1994) or continued blood loss. Of much interest would be continued study of fledgling survival in species with longer nestling periods in which *T. braueri* larvae are more likely to exit nestlings before the birds fledge. We recommend studies of fledgling survival in any bird species infested by *T. braueri* or other blow flies.

In our study we attached transmitters to birds because monitoring unmarked fledgling songbirds is extremely difficult. For the same reason, comparing marked and unmarked fledglings to assess the transmitters' effects is also difficult. Neudorf and Pitcher (1997) used transmitters weighing 8.5% of the body mass of breeding Hooded Warblers (*Wilsonia citrina*) and found no differences in nest-visitation rates. Nudds and Sjöberg (1989) concluded that transmitters weighing 4.1–5.6% of body mass had minimal effect on the foraging of Barn Swallows (*Hirundo rustica*). Transmitters weighing 5.1–5.9% of body mass cause significant reductions in activities like flying and flycatching in the Acorn Woodpecker (*Melanerpes formicivorus*), whereas smaller transmitters weighing 3.5–3.9% of body mass did not significantly affect monitored activities (Hooge 1991). Each of those studies investigated high-energy activities including flight. We used transmitters weighing 4.3–4.9% of body mass of early post-fledgling Ovenbirds, which do not fly during the period studied (H. Streby, unpubl. data). During limited observations, we saw no apparent differences in movements, preening, or parental care of nestlings and fledglings with and without transmitters. We attached transmitters to the heaviest bird(s) from each nest because nestling mass generally correlates positively with survival (e.g., Tinbergen and Boerlijst 1990). We assumed that a small transmitter-induced reduction in survival would, at most, cause those fledglings to be more representative of their broods. Bird blow fly larvae weighed an estimated 1–20% of body mass and parasitized their hosts by removing tissue and blood. Although it is possible that the addition of a transmitter is just enough to cause mortality in ailing fledglings, in light of the available information, it is unlikely.

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