

## Blowfly *Trypocalliphora braueri* (Diptera: Calliphoridae) larvae infestation in Willow Warblers *Phylloscopus trochilus* breeding in a hybrid zone

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### Abstract

We examined the occurrence of blowfly larvae *Trypocalliphora braueri* in Swedish willow warbler *Phylloscopus trochilus* nestlings at three nearby breeding sites in Central Sweden. The occurrence of parasites was examined in nestlings by visual inspection during ringing. Larvae were encapsulated in the wings, head, neck, or the sides of the body of the nestlings and caused large swellings. Some of the larvae had already left the site of burrowing by an opening in the skin that was visible as a dark crater surrounded by dry skin. Tissue near the encapsulated larvae was swollen and showed clear symptoms of inflammation, in some cases causing deformation of wings.

We observed parasites at two of the three sites in 5 out of a total of 36 nests (14%) in two years, corresponding to 20 (9.6%) out of 208 nestlings inspected. In nests with parasites 74.1% of the chicks were infested, each containing one to five parasites. No nestlings were found dead in the nests at the date of inspection.

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Wild caught passerines normally appear healthy. Although ticks and other external parasites might heavily infest some individuals, they seem only rarely to affect the general performance of the bird. Perhaps because of such observations, the prevailing view was for long that parasites and diseases were relatively unimportant in terms of regulating bird populations (Lack 1954). In recent years, however, it has become increasingly clear that parasites and diseases can have profound effects on wild birds, both at the level of individuals (Møller 1990) and populations (Warner 1968). Important groups of parasites on birds are those that live in the plumage and feed on blood or feathers (ectoparasites) and those living inside the body (endoparasites) including blood dwelling haematozoans and various gastrointestinal living nematodes and trematodes (Loye & Zuk 1991). Whereas almost all endoparasites are microscopic and thus require specific methods or equipment to be studied, many ectoparasites are arthropods that can be studied by simple inspections of the plumage and skin. In this paper we report on a blowfly *Trypocalliphora braueri* that lives embedded in subcutaneous cavities (Rognes 1991).

Such an embedded life style is exceptional among parasitic *Diptera*. Most species of avian parasitic blowflies live as larvae in the nests of birds and intermittently suck blood from the nestlings (Gold & Dahlsten 1983). *T. braueri* may negatively affect the nestlings by taking resources when drinking blood, causing large malformations of infested body parts (Gaponov & Truphanova 1995), or causing secondary bacterial subcutaneous infections (Matsuoka et al. 1997). Though *T. braueri* is uncommon in Scandinavia (Rognes 1991), we here report that it is a common parasite in some populations of Willow Warblers *Phylloscopus trochilus* and thus could have strong negative effect on reproductive success at both the individual and population level.

### Methods

#### *The parasite*

Parasite larvae of the genus *Trypocalliphora* Peus 1960, infest nestlings by burrowing under the skin, and one nestling may support between 1 and 57 larvae (Rognes 1991). The larvae of the blowfly *T.*

*braueri* develop inside encapsulations measuring up to 12 mm deep by 4.1 mm wide on various parts of the body, but usually at the wings of the nestling (Rognes 1991). Mature larvae leave the host at death or fledging stage, and pupate in or close to the nest on the ground (Gaponov & Truphanova 1995). In Fennoscandia only one species of blowfly, *T. braueri*, with this life cycle has been found. In this area more than ten passerine species of ground as well as hole nesters have been recorded as hosts for *T. braueri*, for instance Meadow Pipit *Anthus pratensis*, Pied Flycatcher *Ficedula hypoleuca*, Bluethroat *Luscinia svecica*, White Wagtail *Motacilla alba*, Great Tit *Parus major*, Wood Warbler *Phylloscopus sibilatrix* and Willow Warbler. *T. braueri* is widespread in Norway and Finland, but there are only a few records in Sweden and none in Denmark (Rognes 1991). The species has also been reported from Austria, the Czech Republic and Slovakia, East Germany, Hungary, Poland and Russia. In addition, other species of *Trypocalliphora* have been recorded in Japan and in North America from Alaska to Quebec in the north and from New Mexico to Georgia in the south (Rognes 1991).

#### Study species and location

We located nests of breeding Willow Warblers on territories in June of 2000 and 2001 at three sites within the expected hybrid zone of the two subspecies of Willow Warblers *Phylloscopus t. trochilus* and *P. t. acredula* breeding in Central Sweden (Hedenström & Pettersson 1987, Bensch *et al.* 1999). The hybrid zone has been located on the basis of morphological measurements, plumage colour scores, and ratios of stable isotopes in feathers (Bensch *et al.* 1999, Chamberlain *et al.* 2000). Sites were situated near Klångstavallen (61°40'N, 16°51'E), near Tanna (61°48'N, 16°54'E), and at Mörtsjön (61°43'N, 17°25'E).

All nestlings were visually inspected for encapsulated blowfly larvae at ringing. In two of the nests where we encountered parasites in the nestlings in 2001 we collected a number of the emerging larvae for species identification. We counted the number of infested nestlings per nest and the number of larvae in each nestling during ringing (at nestling age of 7–14 days). We observed the nests for dead nestlings and non-hatched eggs.

Table 1. Number of Willow Warbler nests infested by *Trypocalliphora braueri* larvae at six locations in Sweden (SWE) and one in Norway (NOR).

*Antal lövångarborn angripna med larver av Trypocalliphora braueri vid sex lokaler i Sverige (SWE) och en lokal i Norge (NOR).*

Site, Coordinates Lokal, Koordinater	Year År	Infested Angripna	Inspected Undersökta	% infested parasiterade	Source Källa
Klångstavallen, SWE 61°40'N, 16°51'E	2000–2001	4	10	40	This study
Tanna, SWE 61°48'N, 16°54'E	2000–2001	1	12	18	This study
Mörtsjön, SWE 61°43'N, 17°25'E	2000–2001	0	14	0	This study
Ammarnäs, SWE 65°58'N, 16°07'E	1963–1996	0	130 (835 observations#)	0	A. Enemar, <i>et al.</i> , pers. comm.
Tovetorp, SWE 58°56'N, 17°08'E	1980–1992	0	105* (589 nestlings ungar)	0	Sven Jacobsson, pers. comm.
Gunnebo, SWE 57°39'N, 12°04'E	1984–1986, 1988, 1994	0	84 (425 nestlings ungar)	0	Björn Arvidsson, pers. comm.
Øvre Heimdalen, NOR 61°25'N, 08°52'E	1993–1997, 2001	0	60	0	Jan Lifjeld, pers. comm.

\* Number of fledged clutches. *Antal flygga kullar*

# Number of observations with nestling in nest.

*Antal observationer med ungar i bo*

## Results

In total we recorded *T. braueri* larvae in one out of 17 nests in 2000 and in four of 19 nests in 2001 (Table 1). Parasites were recorded in 22 nestlings in two of the three sites, near Klångstavallen and Tanna, while we found no parasites in the 14 nests located at Mörtsjön. As many as 20 (9.6%) of 208 inspected nestlings carried parasite larvae (four out of 98 nestlings in year 2000; 15 out of 110 in 2001). In infested nests 74.1% of the nestlings were infested (range: 33.3%–100%). We observed between one and five larvae per infested nestling and the mean number of larvae per nestling was 2.6 (for four nests; Table 2). The majority of the infested nestlings carried parasites in the wings (Figure 1), but we observed burrowing blowfly larvae also in the head, neck, and on the sides of the body. Some of the larvae had already left the body of the nestlings at inspection, and in those cases the nestlings were close to fledging (ca 15 days old). The opening where the larvae had left the host was clearly visible as a dark crater surrounded by dry skin. All nestlings in which we observed larvae were alive at inspection, and we found no dead nestlings in these nests. However, in some of the nestlings the wings were deformed due to larvae located at the base of the primaries, and those nestlings most likely were never going to be able to fly.

We collected four *T. braueri* larvae that were almost ready to emerge from one clutch of the

nestlings in 2001. The mean mass of these larvae was 73.8 mg (Range: 61–101 mg, N=4).

## Discussion

There are only a few previous observations of the parasite *Trypocalliphora braueri* in Sweden. All of them have been observed as larvae in nestlings, and no adults have been captured in the wild (Rognes 1991). During a period of three years in the mid 1950s, a Swedish ornithologist and ringer, Lennart Magni, reported five cases of larvae infestation in passerine nestlings in South Sweden (Småland), but he never observed any larvae again during the subsequent 25 years of ringing in the same area (Rognes 1991). We have observed five infested Willow Warbler nests during two years of study in Central Sweden. Four of these cases occurred in the same study area in both years.

In light of our findings, it is interesting that *T. braueri* was not observed in four other studies of large numbers of Willow Warbler nests in Sweden and Norway. Sven Jacobsson (pers. comm.), studying breeding Willow Warblers approximately 300 km south of our study site in east Central Sweden (Sörmland), has never observed any infestation of blowfly *T. braueri* larvae in his study population of more than hundred observed nests (Table 1). The same observation of no *T. braueri* larvae was reported by Anders Enemar and Björn Arvidsson (pers.

Table 2. Number of Willow Warbler nestlings infested with *Trypocalliphora braueri* larvae at two sites in Hälsingland, Sweden during 2000 and 2001. Total number of eggs and young in the nest, mean number of larvae counted per infested nestling, and the sites on body where larvae were burrowing are also given  
*Antalet boungar av lövsångare som observerats vara angripna av tvåvingelarver av parasiten Trypocalliphora braueri vid två häckningslokaler i Hälsningland 2000 och 2001. Angivet är även totalt antal ägg och ungar i boet, medelantal larver per bounge och plats på kroppen där larver fanns inbäddade*

Location <i>Lokal</i>	Year <i>År</i>	Eggs <i>Ägg</i>	Nestlings <i>Boungar</i>	Infested <i>Angripna</i>	Larvae/nestling <i>Larver/unge</i>	Infestation site <i>Angreppsplats</i>
1. Klångstavallen	2000	2	4	4	3.2	Head, wings, body <i>Huvud, vingar, kropp</i>
2. Klångstavallen	2001	0	6	2	2.0	Head, wings, body <i>Huvud, vingar, kropp</i>
3. Klångstavallen	2001	0	6	3	2.0	Wings, body <i>Vingar, kropp</i>
4. Klångstavallen	2001	0	6	6	2.7	Head, throat, neck, wings <i>Huvud, strupe, nacke, vingar</i>
5. Tanna	2001	0	5	5	1–4	Neck, wings <i>Nacke, vingar</i>



Figure 1. Willow Warbler nestling (14 days old) infested in wing and neck with larvae of the blowfly *Trypocalliphora braueri*. Arrows denotes the openings in the skin where the parasites have left the wing and the neck. Parasites occurred in one or several of the following sites of the body: wings, head, neck, or sides of body. Photo by Susanne Åkesson.

*Boung* av lövsångare (14 dagar) med larver av *Trypocalliphora braueri* i vingarna och nacken. Larverna har lämnat vingen eller nacken genom en öppning i huden (pilarna). Alla ungar som vi observerade bära på larver hade dem inpackslade i vingarna, huvudet, nacken, strupen eller på sidorna av kroppen. Foto av Susanne Åkesson.

comm.) who have been ringing Willow Warblers in North Sweden (Ammarnäs) for several years and near Göteborg in southwestern Sweden, as well as from Jan Lifjeld (pers. comm.) working in Norway (Table 1). These sites were located southwest (Norway, Bohuslän), south (Södermanland) and north (Lapland) of our study sites. However, in Russia Gaponov & Truphanova (1995) reported 25% infestation rate of *T. braueri* in Willow Warblers (2 out of 8 nests), and with high numbers of larvae per nestling (76 larvae in 9 nestlings; 4 nestlings with 1–5 larvae and 5 nestlings with 10–15 larvae). These observations suggest that the occurrence of blowfly larvae infestation in Willow Warblers is restricted to local geographical areas, but it is also possible that outbreaks occur only for short periods of time.

The infestations that we observed appeared to have had potentially important effects on the development of the birds. The larvae created large open wounds, some of which caused deformations of the wings. Other studies have shown that the parasites can cause other problems as well. Gaponov and Truphanova (1995) reported that nestlings of passerine birds in Russia that were infested with *T. braueri* had a lower growth rate, poor plumage development, and delayed fledging. At high levels of

infestation (11–15 larvae per nestling) 62% of nestlings died before fledging. In a few cases, the larvae of *T. braueri* emerged into the body cavity of the host, leading to death of the host. In other cases, important organs such as eyes were damaged (Gaponov & Truphanova 1995). Matsuoka et al. (1999) found that about 50% of nests of Townsend's Warbler *Dendroica townsendi* in Alaska were parasitised by *T. braueri*. They suggested secondary infections to be a potential cost for parasitized birds in addition to loss of resources (for discussion of costs associated with parasites see also, Sheldon & Verhulst 1996). Howe (1992) reported 26.5% mortality in Sage Thrasher *Oreoscoptes montanus* nestlings infected by *T. braueri*, compared to only 3.7% mortality in nonparasitized nestlings, but the high mortality was presumably a combined effect of parasites and cold weather (Howe 1992). Infestations with *T. braueri* larvae have also been shown to be pathogenic to Marsh Wren *Cistothorus palustris* nestlings (Warren 1994). However, infestations of passerine nests by other species of blowflies (*Protocalliphora sialia* and *Protocalliphora azurea*, both blood sucking but not embedded in subcutaneous cavities) have resulted in no or only minor effects on fledging success of nestlings, despite very high

infestation rates of 72% (e.g. Gold & Dahlsten 1983, Rogers et al. 1991, Gaponov & Truphanova 1995, Matsuoka et al. 1997).

The present study in which we found 14% of nests parasitised by *T. braueri* is located in the hybrid zone between two subspecies of Willow Warblers (Bensch et al. 1999). South of our study site is the subspecies *P.t. trochilus*, and to the north *P.t. acredula*. The two subspecies differ slightly in size, coloration and migratory behaviours (Hedenström & Pettersson 1987). The occurrence of *T. braueri* in the hybrid zone could of course be a mere coincidence but one can speculate that hybrid populations might be more vulnerable to parasites than either of the parental taxa.

We believe that the possibility that hybrid populations are more vulnerable to attacks of parasites will be interesting to study further in the future. It would also be interesting to investigate if burrowing blowfly larvae occur in other host species breeding in the same area of Central Sweden, where our study population is located, compared to other geographical areas. We would be very interested to hear if other ringers have found blowfly larvae in passerine nestlings from different regions of Sweden.

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## Sammanfattning

*Infektion av larver av spyflugan Trypocalliphora braueri* (Diptera: Calliphoridae) hos lövsångare *Phylloscopus trochilus* som häckar i en hybridzon

Vi har undersökt förekomsten av tvåvingelarver (spyflugor) av släktet *Trypocalliphora* i boungar av lövsångare, som häckar i hybridzonen mellan den nordliga *Phylloscopus t. acredula* respektive sydliga rasen *P. t. trochilus* i centrala Sverige (Hedenström & Pettersson 1987, Bensch et al. 1999), under åren 2000 och 2001. Flugornas larver borrar in sig under huden och lever i boungar av ett antal olika fågelarter, däribland, ängspiplärka, svartvit flugsnappare, blåhake, sädesärta, talgoxe, grönsångare och lövsångare (Rognes 1991). Där utvecklas de till dess att boungarna dör eller flyger ur boet. Förpuppningen sker i eller i närheten av boet. Flugorna övervintrar som adulta. *Trypocalliphora braueri* har konstaterats i ett flertal länder i Europa, såsom Sverige, Norge och Finland, dock inte i Danmark. Dessutom finns observationer i Österrike, Tjeckoslovakien, Tyskland, Ungern, Polen och Ryssland. De förekommer också från Alaska till Quebeck i Kanada och söderut till New Mexiko och Georgia, samt i Japan. För en nordamerikansk sångare, Townsend's warbler *Dendroica townsendi*, har 50% av bona

rapporterats vara angripna av *T. braueri* (Matsuoka m.fl. 1997).

Vi lokaliserade lövsångarbron med ungar i Häl-singland under juni i tre områden nära Klångstaval-len (61°40'N, 16°51'E), Tanna (61°48'N, 16°54'E) och Mörtsjön (61°43'N, 17°25'E). Vi fann *T. braueri* larver i 5 bon av 37 undersökta, och i dessa bar 20 ungar av 208 (4 av 98 år 2000; 15 av 110 år 2001) parasiter (Tabell 1). Av de angripna kullarna bar 74.1% av ungarna på larver. Ungar som hade larver inkapslade bar på mellan 1 och 5 larver var (Tabell 2). De flesta återfanns i vingarna vid vingknogarna, men också i huvudet, nacken, strupen och på sidorna av kroppen. I de flesta fall var området i närheten av de inkapslade larverna kraftigt inflammerat. I några fall hade larverna redan lämnat värden genom håll i huden, och dessa ungar var nära att flyga ur boet (ca 15 dagar). Vi fann inga döda ungar i de bon där ungar var parasiterade, men i de fall då parasiter satt vid vingknogen hade handpenneutvecklingen hämmats och de missbildade ungarna skulle med största san-

nolikhhet aldrig bli flygförmögna. Medelvikten för fyra insamlade larver som stod i begrepp att lämna värden var 73.8 mg (Min: 61, Max:101 mg).

Enligt uppgift från Sven Jacobsson (pers. komm.), som studerat över hundra lövsångarbron i Sörmland, Anders Enemar och Björn Arvidsson (pers. komm.) som studerat samma art i Ammarnäs och i närheten av Göteborg, samt Jan Lifjeld som arbetat i Norge, har aldrig observerat angrepp av larver från *T. braueri* i boungar av lövsångare från dessa områden (Tabell 1). Lennart Magni som ringmärkte fåglar i Småland, observerade fem fall av *T. braueri* larver under 1955–1957 hos mindre tättingar, men inga under de efterföljande 25 årens ringmärkning i området (Rognes 1991). Detta tyder på att angreppen av flugorna kan vara begränsade i geografisk utsträckning såväl som i tid. Det vore intressant att höra om fler ringmärkare noterat angrepp av larver i boungar hos lövsångare eller andra arter, från samma geografiska område såväl som från andra delar av Sverige.