Parasitism of the Katydid Neoconocephalus triops (Orthoptera: Tettigoniidae) by the Tachinid Flies Ormia lineifrons and Neomintho sp. (Diptera: Tachinidae)

Author: Beckers, Oliver M.

Source: Florida Entomologist, 105(2) : 133-136

Published By: Florida Entomological Society

URL: https://doi.org/10.1653/024.105.0205

Parasitism of the katydid *Neoconocephalus triops* (Orthoptera: Tettigoniidae) by the tachinid flies *Ormia lineifrons* and *Neomintho* sp. (Diptera: Tachinidae)

Oliver M. Beckers[1,*]

Abstract

Conspicuous mating signals of insects can be exploited by unintended predators and parasites to locate the signaler. Since these interactions can bear a substantial cost for the signaler, selection may cause changes in their signals, possibly contributing to the evolution of the communication system. Understanding the life history of the interacting species, especially that of the eavesdropper, is essential to better quantify the selective pressures in these interactions. The katydid, *Neoconocephalus triops* L. (Orthoptera: Tettigoniidae), is parasitized by the lethal tachinid fly, *Ormia lineifrons* Sabrosky (Diptera: Tachinidae), in Florida. I collected *N. triops* in the field to characterize its parasitism by *O. lineifrons* and determine the efficiency of the fly's host use. The parasitism rate of *N. triops* was 48.2% and about half of the parasitized males (47.2%) were superparasitized. All parasitized katydids died and no larva that was the result of superparasitism survived the host's death. The average parasite load was 2.73 ± 1.20 larvae, and 49.5% of the fly pupae successfully developed into adult flies in 12.12 ± 0.60 d. *Neoconocephalus triops* also was parasitized by an undescribed species of *Neomintho* (Diptera: Tachinidae). The high superparasitism rate despite its low success suggests that *O. lineifrons* has not evolved traits to reliably distinguish between unparasitized and parasitized hosts. The high parasitism rate of *N. triops* suggests that *O. lineifrons* exerts substantial selective pressure on *N. triops*. However, the low developmental success of fly larvae may indicate that *N. triops* has evolved counter adaptations in its arms race with *O. lineifrons*, or *N. triops* might be a low-quality host.

Key Words: eavesdropping; parasitoid; superparasitism

Resumen

Depredadores y parasitoides no intencionados pueden aprovechar las conspicuas señales de apareamiento de los insectos para localizar al emisor. Dado que estas interacciones pueden asumir un costo sustancial para el emisor de señales, la selección puede provocar cambios en sus señales, lo que posiblemente contribuya a la evolución del sistema de comunicación. Comprender la historia de vida de las especies que interactúan, especialmente la del espía, es esencial para cuantificar mejor las presiones selectivas en estas interacciones. La esperanza, *Neoconocephalus triops* L. (Orthoptera: Tettigoniidae), es parasitado por la letal mosca taquínida, *Ormia lineifrons* Sabrosky (Diptera: Tachinidae) en la Florida. Recolecté *N. triops* en campo para caracterizar su parasitismo por *O. lineifrons* y determinar la eficiencia del uso de este como un hospedero de la mosca. La tasa de parasitismo de *N. triops* fue del 48,2% y aproximadamente la mitad de los machos parasitados (47,2%) estaban superparasitados. Todos las esperanzas parasitadas murieron y ninguna larva resultante del superparasitismo sobrevivió a la muerte del hospedero. El promedio de la razón de parasitismo fue de 2,73 ± 1,20 larvas y el 49,5 % de las pupas de mosca se convirtieron con éxito en moscas adultas en 12,12 ± 0,60 días. *Neoconocephalus triops* también fue parasitado por una especie no descrita del género *Neomintho* (Tachinidae). La alta tasa de superparasitismo a pesar de su bajo éxito sugiere que *O. lineifrons* no ha desarrollado rasgos para distinguir de manera confiable entre hopederos parasitados y no parasitados. La alta tasa de parasitismo de *N. triops* sugiere que *O. lineifrons* ejerce una presión selectiva sustancial sobre *N. triops*. Sin embargo, el bajo éxito en el desarrollo de las larvas de mosca puede sugerir que *N. triops* ha desarrollado adaptaciones defensivas en su carrera armamentista con *O. lineifrons*, o que *N. triops* podría ser un hospedero de baja calidad.

Palabras Claves: escuchas clandestinas; parasitoide; superparasitismo

Acoustic insects produce conspicuous signals primarily to attract the opposite sex for mating (Gerhardt & Huber 2002). Evolution of these signals is complex and is driven typically by sexual selection based on receiver preferences or biases, and natural selection based on the signaling environment, signaling costs, and properties of receiver perception, to mention a few of the main factors (Endler & Basolo 1998). These signals also can be intercepted by illegitimate receivers (Cade 1975; Endler 1980, 1983; Zuk & Kolluru 1998; Hedwig & Robert 2014), such as eavesdropping parasites or predators, adding further selective pressures on the communication system, ultimately leading to its diversification (Belwood & Morris 1987; Zuk et al. 2006; Beckers & Wagner 2018; Tinghitella et al. 2018, 2021). Tachinid flies of the genus *Ormia* use orthopterans as hosts for their larvae (Lehmann 2003) and have caused a range of changes in the communication system of their hosts (Zuk et al. 2006; Beckers & Wagner 2018; Tinghitella et al. 2018, 2021), offering valuable opportunities to study fundamental questions of evolutionary ecology (Lehmann 2008). The extent to which the parasitoid exerts selection on its host is related substantially to its effectiveness of utilizing the host, which is the focus of this study.

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[1] Murray State University, Department of Biological Sciences, Murray, Kentucky 42071, USA; E-mail: obeckers@murraystate.edu
*Corresponding author; E-mail: obeckers@murraystate.edu

Males of the conehead katydid, *Neoconocephalus triops* (Linnaeus) (Orthoptera: Tettigoniidae), call at night to attract females. These mating calls are intercepted by the eavesdropping parasitoid fly, *Ormia lineifrons* Sabrosky (Diptera: Tachinidae) (Sabrosky 1953), that uses these mating calls to locate and parasitize *N. triops* (Burk 1982). The deposited fly larvae develop inside the host and emerge after 7 to 9 d, pupate, and metamorphose into adult flies (Burk 1982). Parasitized *N. triops* males continue to call for up to 5 d (Burk 1982), allowing for multiple parasitism events (i.e., superparasitism) during subsequent nights. The emergence of the parasitoid larvae from the host is lethal to the katydid and can reduce drastically the reproductive lifetime of the katydid from 2 to 3 mo to 1 to 2 wk (Burk 1982). Besides *N. triops*, the fly also uses other *Neoconocephalus* species, such as *Neoconocephalus robustus* (Scudder), *Neoconocephalus velox* Rehn & Hebard, and *Neoconocephalus nebrascensis* Bruner (all Orthoptera: Tettigoniidae) as hosts in Kentucky (Rogers & Beckers 2022) as well as meadow katydids of the genus *Orchelimum* (Orthoptera: Tettigoniidae) (Feaver 1983; Shapiro 1995). Parasitism of silent females by this fly has not been observed.

In northern Florida, *N. triops* has 2 reproductive generations per yr, 1 in early spring and 1 in late summer (Whitesell 1974). Both generations are parasitized heavily by *O. lineifrons*, sometimes reaching parasitism rates of up to 100% (Burk 1982). However, besides the parasitism rate, not much else is known about the life history and host use efficiency of *O. lineifrons*. To further develop this understudied evolutionary arms race, data is presented here on the characteristics and efficiency of parasitism of *N. triops* by *O. lineifrons*. Additionally, a first-time report of parasitism of *N. triops* by an undescribed tachinid fly species is provided.

Material and Methods

ANIMAL HUSBANDRY

Neoconocephalus triops males (*n* = 86) were collected along roads and in fields within 15 Km (10 miles) west of Gainesville, Florida, USA, between 19 Jul and 21 Jul 2021. This time window corresponds to the population peak of the summer generation in this location (Burk 1982). The mating calls of male *N. triops* were used to find the katydids, which were collected by hand. The animals were transported to my lab at Murray State University, Murray, Kentucky, USA (USDA Permit #P526P-19-00002) for the study. Each male was placed in a separate cage (9 cm W × 16 cm L × 11 cm H) (Lee's Aquarium and Pet products, San Marcos, California, USA) with its lid lined with insect screen (small bug screen #14151, M-D Building Products, Inc., Oklahoma City, Oklahoma, USA) on the underside to prevent roaming fly larvae from escaping. The individual cages were sprayed daily with water and apple, and rolled oats were provided as food for the katydids ad libitum. The individual cages were placed inside an incubator (Model #PR505755L, Thermo Fisher Scientific, Marietta, Ohio, USA) with a light/dark cycle of 15:9 h (L:D) and high/low temperatures at 26.0 ± 1.0 °C and 22.0 ± 1.0 °C, respectively, which approximates a long summer d in northern Florida. The katydids were kept in their individual cages for at least 11 d after collection, which corresponded to 3 d after the last larva emerged, before they were used for breeding to maintain the laboratory stock. Note that *O. lineifrons* larvae emerge from *N. triops* within 9 d in Florida (Burk 1982), and the breeding enclosures were monitored for an additional 3 d after transferring the males and no dead male katydids were found in these enclosures.

The individual cages were checked daily for the presence of fly larvae or pupa and the date of their appearance was noted. On the day of emergence, pupae were placed on a piece of cotton (#3166, Dynarex Corporation, Orangeburg, New York, USA) inside a centrifuge tube (50 mL, Corning Science, Reynosa, Tamaulipas, Mexcio), and were sprayed with a saturated Methylparaben solution to restrict fungal growth and provide moisture. The lid of the tube had holes to allow for gas exchange. Larvae of the same host were placed in the same centrifuge tube and kept under the same conditions as the katydid hosts (see above). The tubes were checked daily for adult flies and the dates of appearance were noted. The hosts were kept inside their cages for 24 h after death to allow for additional larvae to emerge. After 24 h, the katydid was dissected under a dissecting scope (Stemi 1000, Carl Zeiss, Oberkochen, Germany) to search for larvae inside the host.

CALCULATIONS

The proportion of parasitized males was calculated by dividing the number of all males from which *O. lineifrons* larvae emerged and/or were found inside the host by the total number of collected males. In the closely related fly, *Ormia ochracea* (Bigot) (Diptera: Tachinidae) that uses field crickets as hosts, superparasitism after 24 h led to the death of the second clutch of larvae, whereas the first clutch emerged and killed the host (Adamo et al. 1995). Similarly, it was found that 24 h after the emergence-related death of *N. triops* hosts, all remaining larvae inside the hosts (*n* = 17 hosts) were dead at the time of dissection. The rate of superparasitism was estimated by determining the proportion of parasitized katydids that had both larvae emerged from their body and at least 1 dead larva inside their body relative to all parasitized katydids (*n* = 36). Five katydids that died before the larvae could emerge and had more than 1 larva inside were not included in this calculation since their superparasitism status could not be determined.

The developmental success rate from pupa to adult fly was determined by calculating for each host (*n* = 33) the proportion of larvae that pupated and developed into adult flies relative to all larvae that emerged from the host, i.e., each host contributed 1 data point ranging from 0 to 1. Eight pupae were damaged and were not used to calculate the success rate.

The pupal development time was calculated as the time span between emergence from the host and metamorphosis into the adult fly. Fly larvae pupate within a few h on the same d they emerge from the host (Adamo et al. 1995; personal observation). Note that the temperatures used to rear the pupae (see above) approximated summer conditions in northern Florida. However, data on habitat conditions used for pupation in the field (e.g., temperature, moisture) are not available and the reported development times are an approximation based on lab conditions. The average development time of all pupae that emerged from each host (*n* = 16) was calculated, i.e., each host contributed 1 data point. The developmental time of larvae from 3 hosts could not be determined because the indistinguishable pupae were stored in the same centrifuge tube but emerged and matured into adults on different d. Note that flies that pupated but did not develop into adult flies contributed data to the developmental success rate but not development time.

The sex of each adult fly was identified using the placement of the compound eyes, i.e., the eyes of *O. lineifrons* males almost touch on the dorsal side of the head, whereas the eyes of females clearly are separated (Sabrosky 1953), and the proportion of males and females was determined. One *N. triops* male was parasitized by a different fly species. The 2 flies were reared to adulthood as described above and were sent to James O'Hara at the Canadian National Collection of Insects, Arachnids, and Nematodes (Ottawa, Ontario, Canada) for identification. Data from this host were not used for any of the calculations outlined above.

Results

Out of 85 collected *N. triops* males, 41 were parasitized by *O. lineifrons*, which corresponds to a parasitism rate of 48.2%. None of the hosts that were parasitized survived the emergence of the larvae from their bodies. The values reported below are averages (± SD). The parasite load of *N. triops* males was 2.73 ± 1.21 larvae, of which 1.85 ± 1.35 larvae emerged from their hosts and pupated, and 0.88 ± 0.90 larvae were found inside their hosts. All larvae found inside a host were dead 24 h after the host's death. The development time from pupa to adult fly was 12.12 ± 0.60 d. The developmental success of *O. lineifrons* pupae to adult flies across all host individuals was 49.54 ± 44.65%. Of those pupae that successfully developed into adults, 21 were females (65.6%) and 11 were males (34.4%); however this ratio was not significantly different from a 1:1 sex ratio (Chi square test: $\chi^2 = 3.125$; $P = 0.077$). Of all parasitized males, 47.2% were superparasitized, which corresponded to 20.0% of all collected males.

One *N. triops* male was parasitized by an undescribed *Neomintho* sp. (Tachinidae), and this is the first report of parasitism by this fly. The host contained 3 larvae, 2 of which pupated and developed into 1 male and 1 female adult *Neomintho* fly after 18 d, whereas the third larvae was found dead inside the expired host, suggesting a case of superparasitism.

Discussion

The parasitism rate determined for Jul (48.2%) was similar to those of *N. triops* from the same location and mo in 1980 and 1981 (38–43%) (Burk 1982) and was comparable to the parasitism rate of another tachinid fly, *Therobia leonidei* (Mesnil) (Diptera:Tachinidae), that parasitizes the katydid *Poecilimon marianne* Willemse & Heller (Orthoptera: Tettigoniidae) at a rate of 50 to 57% (Lehmann 2008). In contrast, parasitism rates of *O. ochracea* that uses field crickets as hosts are lower and range between 3% in *Gryllus rubens* (Scudder) (Orthoptera: Gryllidae) (Walker & Wineriter 1991) to 28% in *Teleogryllus oceanicus* (Le Guillo) (Orthoptera: Gryllidae) (Zuk et al. 1993). The high parasitism rate of *N. triops* males by *O. lineifrons* indicates substantial selection pressure on male traits to reduce the adverse effects of parasitism, potentially leading to male satellite behavior (Cade 1975; Bertram et al. 2004), reduced calling (Zuk et al. 2006), change of call features (Tinghitella et al. 2021), calling activity (Cade et al. 1996), or calling in aggregations to reduce the risk of detection (Goodale et al. 2019; Lehmann & Lakes-Harlan 2019) to mention a few possible adaptations documented in other *Ormia* host species. Such changes related to the eavesdropping parasitoids can introduce changes in signals and signal preferences, ultimately having the potential for the communication or mating system to evolve.

About half of the parasitized *N. triops* males were superparasitized (47.2%) by *O. lineifrons.* For reference, *O. ochracea* superparasitism of parasitized crickets ranges between 4.7% (Kolluru & Zuk 2001) and 25% (Adamo et al. 1995), and that of *Therobia leonidei* using the katydid *Poecilimon thessalicus* Brunner & Wattenwyl (Orthoptera: Tettigoniidae) is 17.6% (Lehmann 2008). The high rate of superparasitism in *N. triops* was unexpected, considering that a substantial proportion (> 50%) of unparasitized *N. triops* males was available as hosts. Potential preferences of *O. lineifrons* for particular call features (Wagner 1996; Lehmann et al. 2001) may explain why some katydid males were parasitized more than once, i.e., superparasitized, while others were not parasitized. Superparasitism, despite its ineffectiveness (see below), suggests that *O. lineifrons*, like other tachinid parasitoids (Adamo et al. 1995; Lehmann 2008), may not to be able to discriminate between unparasitized and parasitized hosts. In contrast to parasitic Hymenoptera, tachinids do not have a piercing ovipositor and typically do not contact their hosts during larviposition (Lehmann 2008), providing little opportunity to directly determine the parasitism status of the host. Also, changes in the calls (Lehmann & Lehmann 2006) that could have indicated the host's parasitism status likely did not occur or were too small to be detected by *O. lineifrons*.

Dissections of the hosts 24 h after death indicate that larvae that did not synchronize their emergence with the larvae that emerged before them had a very low chance of survival. Evolutionary theory suggests that the direct benefits to the mother and indirect benefits to genetic siblings are expected to exert strong selection on synchronous emergence of related larvae. Along this line of reasoning, the stragglers would represent larvae placed on the host in separate infestation events, i.e., superparasitism. However, superparasitism may be beneficial to the fly if it occurs within the same night because this would allow for such synchronization with larvae of an earlier infestation to happen. Note that if superparasitism occurred during the same night, these instances could not be distinguished from regular parasitism, suggesting that the superparasitism rates of *N. triops* in Florida could be even higher than reported here. Overall, superparasitism of *N. triops* by *O. lineifrons* was mostly ineffective, which represents a pattern that was shared with the parasitoid flies *T. leonidei* (Lehmann 2008) and *O. ochracea* (Adamo et al. 1995).

The developmental success of emerged fly pupae, with about half of them not developing to adulthood, was surprisingly low. This suggests that *N. triops* might be a low-quality host (e.g., poor nutritional resource) (Mackauer et al. 1996) for *O. lineifrons* larvae. Note that *O. lineifrons* parasitizes other *Neoconocephalus* species in Kentucky (Rogers & Beckers 2022) and Florida (Theodore Burk, personal communication), as well as *Orchelimum* species (Feaver 1983; Shapiro 1995), and it may be better adapted to these, potentially higher-quality hosts. It also may be possible that in the arms race between the host and its parasitoid, *N. triops* is currently ahead and has evolved better defenses (e.g., a more efficient immune response) (Thomson et al. 2012; Wilson & Cotter 2013) that interfere with the development of the fly. However, further research is necessary to better understand the low developmental success rate of the flies in *N. triops*.

The collection of *N. triops* indicated that another previously unknown tachinid fly species of the genus *Neomintho* parasitizes this katydid in Florida. Currently, nothing is known about the ecology and life history of this fly. In contrast to *O. lineifrons* and other members of Ormiini, members of Euthelarini, to which *Neomintho* belongs, typically do not have specialized sterna with tympana (Wood & Zumbado 2010) indicating that this fly is not using *N. triops* mating calls to find its hosts. Further study on this species is necessary to understand how *Neomintho* finds its host(s) and what evolutionary impact it may have on *N. triops*.

Acknowledgments

I want to thank James O'Hara (Ottawa, Ontario, Canada) for his help with identifying the newly discovered fly. I thank the 2 anonymous reviewers for their helpful comments on the manuscript. I am indebted to Tom Walker, University of Florida, Gainesville, Florida, USA, for his advice on *N. triops*, identifying collection sites in Gainesville, and providing space for storage of the animals during my collection. I also want to thank Stephen Shey for supporting my collections on his property. This research was supported by an award of the National Science Foundation to OMB (NSF #1755118).

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