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Influence of Nematode Parasitism, Body Size, Temperature, and Diel Period on the Flight Capacity of *Sirex noctilio* F. (Hymenoptera: Siricidae)

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Abstract *Sirex noctilio* F. (Hymenoptera: Siricidae) is a woodwasp of pine trees that has recently invaded and established in North American forests. Although *S. noctilio* has had a limited impact in North America to date, there is some concern that it could have a significant impact on pine plantations, especially in the southeastern U.S.A. Moreover, there are few data on the flight capacity of male *S. noctilio*. We found no association between parasitism by *D. siricidicola* and whether or not *S. noctilio* initiated flight on the flight mill. Male wasps that were parasitized by nematodes were heavier than non-parasitized males, but there was no significant difference in mass between parasitized and non-parasitized females. We also examined the flight capacity of male and female *S. noctilio* in relation to nematode parasitism, body mass, temperature (for only males), and diel period. Body mass, temperature, and diel period affected flight in *S. noctilio* such that wasps were generally observed to fly faster, farther, and more frequently if they were heavier, flying at warmer temperatures, and flying during the photoperiod. The fact that nematode-parasitized male wasps were found to fly farther than the non-parasitized males is consistent with the hypothesis that nematode parasitism does not negatively affect the flight capacity of *S. noctilio*.

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Introduction

The European woodwasp, *Sirex noctilio* F. (Hymenoptera: Siricidae), is a wood-boring wasp, native to Eurasia and North Africa, that attacks *Pinus* L. (Pinales: Pinaceae). It has been accidentally introduced into parts of the Southern Hemisphere and, more recently, North America (Slippers et al. 2015). In the Southern Hemisphere, it is considered one of the most threatening and damaging pests of softwood plantation forests. Similar pine forests, often of the same species, are prevalent throughout North America. The establishment of *S. noctilio* in North America in 2004 (Hoebeke et al. 2005) raised concerns about the potential impact it would have on North American pine resources (Carnegie et al. 2006). Climate models predict that *S. noctilio* can readily colonize forests in Canada, the U.S.A., and Mexico, and some predict this will have significant ecological and economic impacts (Carnegie et al. 2006; Yemshanov et al. 2009).

Sirex noctilio is an important problem in parts of its introduced range, resulting in millions of tree deaths and causing extensive economic loss in pine plantations (Haugen and Underdown 1990; Tribe and Cillié 2004). However, in its native range, it is an infrequent and minor pest (Madden 1988; Hurley et al. 2007). Thus, it appears that some pine forests are more resistant than others to this invasive wasp (Dodds et al. 2007), and it has been hypothesized that this might be due to a more diverse and complex composition of natural enemies and competition among pine-inhabiting species in resistant than susceptible forests (Ryan et al. 2012a, b). Such natural mortality factors could be the key to reducing populations of *S. noctilio*, slowing its spread, and, ultimately, lowering pine mortality (Dodds and de Groot 2012).

The parasitic nematode, *Deladenus* (= *Beddingia*) *siricidicola* Bedding (Tylenchida: Neotylenchidae), is a major component of management plans for *S. noctilio* in the Southern Hemisphere. *Deladenus siricidicola* has a bicyclic life cycle, alternating between a free-living, mycetophagous stage and a parasitic stage. It can live independently of *S. noctilio* by feeding on *Amylostereum areolatum* (Chaillet ex Fr.) Boidin (Russulales: Amylostereaceae), a fungus that is vectored by the woodwasp and colonizes the pine's xylem, but it can also change into a parasitic form in the presence of *S. noctilio* larvae (Bedding 1967, 1972; Bedding and Akhurst 1974). In some cases, *D. siricidicola* can parasitize up to 100 % of *S. noctilio* after only a small number of host generations (Bedding 1993), making it an effective biological control agent, including in Australia, South Africa, and South America (Slippers et al. 2012).

Nematode parasitism can leave female wasps sterile and their eggs infested with nematodes (Bedding 1967, 1972). Males do not transfer nematodes to females during copulation because they become parasitized too late in their development and, at this time, sperm has already entered the seminal vesicles (Bedding 1972). Other physiological effects of nematode parasitism include reductions in fecundity (Kroll et al. 2013; Haavik et al. 2016) and varying effects on body size (Villacide and Corley 2008; Haavik et al. 2016). The occurrence of sterilization varies by strain and across the landscape. In some cases, this is likely due to a loss of virulence after many generations of culturing and the timing and location of releases (Villacide and Corley 2008). Non-sterilizing strains of *D. siricidicola*

have been observed in northeastern North America (Yu et al. 2009; Kroll et al. 2013) and New Zealand (Zondag 1975), where it and *S. noctilio* have been introduced conjointly, as well as in Europe and Japan, where *D. siricidicola* is native (Bedding and Akhurst 1974). It has been proposed that selection for non-sterilizing nematode strains may have occurred naturally in isolated populations of *S. noctilio* (Bedding 1972).

Parasitism by nematodes has been reported to both affect (e.g. Villacide and Corley 2008) and not affect (e.g. Bedding 1979) the flight capacity of *S. noctilio*. Male wasps fly to the top of the canopy after emergence in a lekking behavior (Madden 1988; Martínez et al. 2014), and it is possible that the effects of nematode parasitism on male flight behavior could negatively affect male fitness by reducing male mating success within leks or by reducing the ability of males to locate leks. Moreover, parasitized wasps have been observed to be both smaller (Eskiviski et al. 2004; Villacide and Corley 2008) and larger (Hurley et al. 2008; Haavik et al. 2016) than non-parasitized wasps, and increasing temperatures simulating climate change scenarios have been shown to reduce *S. noctilio* size (Yousuf et al. 2014). This variation among studies may be due to only testing a subset of the body sizes observed in *S. noctilio*, along with other factors including: 1) the direct effects of parasitism on body size, 2) the amount of body-fat reserves gained during the larval stages, and 3) genetics of *S. noctilio*.

The impact of abiotic and biotic factors on insect dispersal varies greatly across different insect taxa, and this necessitates a more detailed understanding of the flight capabilities of pest insects to better the chances of successfully implementing integrated pest management programs. Flight mills are a tool to quantitatively compare the flight capacity of insects, including invasive species, e.g. *Cydia pomonella* (Schumacher et al. 1997), *Cydia molesta* (Hughes and Dorn 2002), *Agrilus planipennis* (Taylor et al. 2010), and *Agrilus auroguttatus* (Lopez et al. 2014). Here, we used flight mills to examine two abiotic factors that influence dispersal of *S. noctilio*, temperature and diel period, as well as two biotic factors, nematode parasitism and body size. Our goal was to understand the flight capacity of male *S. noctilio* because little is known about male flight capacity. Sub-objectives were to: (1) determine if parasitism by *D. siricidicola* affects the size and flight capacity of male and female *S. noctilio*; (2) investigate the relationship between the flight capability and pre-flight body mass of male and female *S. noctilio*; (3) examine if temperature affects the flight capacity of male *S. noctilio*; and (4) document how diel period affects male and female *S. noctilio* flight activity.

We hypothesized that flight in *S. noctilio* is a function of body size, temperature, and diel period, but not nematode parasitism and we predicted that (1) parasitism by *D. siricidicola* would not affect body size and the flight capacity of male and female *S. noctilio*; (2) male and female wasps with greater pre-flight body mass would have greater flight capacities; (3) an increase in temperature would increase male *S. noctilio* flight capabilities; and (4) male and female wasps would fly farther during the photoperiod.

Materials and Methods

Wasp Collection

Sirex-infested trees (*P. sylvestris*, *P. resinosis*, and *P. banksiana*) were identified by resin beading on the main bole of trees at several sites in southern Ontario, Canada. These

trees were felled several weeks prior to adult emergence and cut into 1-m bolts during late-June 2014. Bolts were brought into the laboratory, put in cardboard rearing tubes, and reared using the protocol described by [Ryan et al. \(2013\)](#). Adult wasps were collected from rearing tubes five times per week from early-July until early-October and kept at 4 °C until flown using flight mills.

Flight Mill Construction and Data Processing

Flight mills were custom built as described by [Jones et al. \(2010\)](#); [Wiman et al. \(2014\)](#), and [Haavik et al. \(2016\)](#). Each flight mill was equipped with a Hall-effect sensor connected to a National Instruments USB-6501 Digital I/O device that was connected to a desktop computer. All raw, in-flight data were recorded by LabVIEW Full Development System software using modified block diagrams and imported into Scout 1.5.0.0 (Signal.X Technologies LLC, Commerce Township, MI). Scout was used to export the data to Microsoft Excel. Summary statistics, including flight bout speed, total distance flown, and number of flight bouts, were then calculated using an R software package, flightmillR, developed by CJK MacQuarrie. Flights were considered unsuccessful and excluded from the analyses of flight capacity if a wasp fell from the flight mill or did not fly for at least 30 consecutive seconds during the 24-h assay period. Thus, a flight bout is defined as 30 or more seconds of continuous flight.

Experimental Procedures

Wasps were flown 1–4 days following emergence. The body mass of each wasp was measured to the nearest 0.0001 g before each flight using a digital analytical balance (Mettler Toledo AG285) and used as a proxy for wasp size (e.g. [Bruzzone et al. 2009](#)). The head of an insect pin (# 1) was attached to the pronotum of each wasp using a quick-drying glue (Quick Grip Permanent Adhesive, Beacon Adhesives, Mt. Veron, NY). After flight, wasps were dissected and the presence or absence of nematodes was recorded. Male wasps were flown at 15, 20, and 25 °C and female wasps were flown at 20 °C. Not enough female wasps were collected to evaluate female flight capacity at all three temperatures. All wasps were flown for 24 h under controlled conditions [i.e. 16:8 (light:dark), 50–70 % RH].

Data Analyses

All analyses were conducted using the R statistical environment, version 3.2.0 (R Core Team 2015). We used generalized linear models (GLM) to test for the effect of parasitism on body mass and flight capacity, the effect of pre-flight mass on flight capacity, the effect of temperature on flight capacity, and the effect of diel period (i.e. time of day) on flight capacity. Flight capacity included the flight bout speed, total distance flown, and the number of flight bouts taken. Males and females were tested separately in all analyses, except for when we tested the effect of temperature on flight where only males were tested because not enough female wasps were available to test all temperatures. We also tested for an association between nematode parasitism and the occurrence of flight using Pearson's chi-squared test (males) and Fisher's exact test (females). For all GLMs, we first fit a simple linear model, which we diagnosed for constancy of variance and normality of residuals using graphical methods. We also assessed for over and underdispersion in models where the response data

were counts (e.g. number of flight bouts). These analyses found that GLMs testing for the effect of parasitism on body mass had non-normal residuals, so we log-transformed body mass and used a one-way analysis of variance (ANOVA); similarly, we also log-transformed flight bout speed and rank-transformed total distance flown to test the effects of nematode parasitism, pre-flight body mass, and temperature. The data for number of flight bouts was overdispersed (i.e. the mean to variance ratio was larger than expected), so we fit a negative binomial distribution to these data. The negative binomial distribution is similar to a Poisson distribution, but includes a term modelling the dispersion of the data.

We also tested the effect of nematode parasitism and diel period on distance flown by wasps using a linear mixed-effects model (LMM). In this model, we included an offset term to account for the unequal light:dark ratio during the 24-h flight period. We diagnosed this model for violations as before and found that the residuals had a non-normal distribution and heterogeneity in the variability of flight among individual wasps. We accounted for this residual structure by log transforming the response variable (total distance flown) and fitting a random effect for each wasp. The F -statistics, degrees of freedom, and P -values for the LLMs were calculated based on Satterthwaite's approximations.

Results

Of 128 male *S. noctilio* tethered to flight mills, we recorded a total of 79 successful flights from 52 parasitized and 27 non-parasitized wasps. Of these flights, 16, 26, and 37 wasps flew at 15, 20, and 25 °C, respectively. Pre-flight body mass of male *S. noctilio* ranged from 0.0120 to 0.2327 g, with a mean of 0.0576 ± 0.0053 (SE) g. Male *S. noctilio* flight bout speed varied between 0.22 and 2.73 km/h (Fig. 1). One parasitized male wasp had the farthest total flight distance of 19.1 km at 20 °C in contrast to 9.41 km at 25 °C observed for a non-parasitized male individual. On average, total distance flown was 2.87 ± 0.49 km for males. Male wasps had 17 ± 2 bouts of flight. The maximum total number of flight bouts was 116 bouts of flight at 25 °C by a parasitized male wasp and 83 bouts of flight at 25 °C for a non-parasitized male wasp.

A total of 89 female *S. noctilio* were also flown, and we recorded 53 successful flights from 39 parasitized and 14 non-parasitized wasps. Female *S. noctilio* mass ranged from 0.0240 to 0.3299 g, with a mean of 0.1093 ± 0.0101 g. Female *S. noctilio* flight bout speed varied between 0.24 and 2.19 km/h (Fig. 2). A parasitized female wasp had the farthest total flight distance of 20.77 km in contrast to 11.35 km observed for a non-parasitized female individual. Mean total distance flown was 2.77 ± 0.53 km for females. Female wasps had 29 ± 3 bouts of flight. The maximum total number of flight bouts was 112 bouts of flight by a parasitized female wasp and 68 bouts of flight for a non-parasitized female wasp.

There was no association between nematode parasitism and whether or not male *S. noctilio* flew ($\chi^2 = 0.16$, $P = 0.693$). Similar to males, there was no association between nematode parasitism and whether or not female *S. noctilio* flew ($P = 0.624$). Nematode parasitism had a significant effect on body mass for male wasps but not for females ($F = 26.69$; $df = 1, 76$; $P < 0.001$ and $F = 3.42$; $df = 1, 51$; $P = 0.070$, respectively) (Fig. 3).

Nematode parasitism and pre-flight body mass had no effect on flight bout speed of male *S. noctilio* ($F = 0.04$; $df = 1, 74$; $P = 0.834$ and $F = 2.01$; $df = 1, 74$; $P = 0.161$,

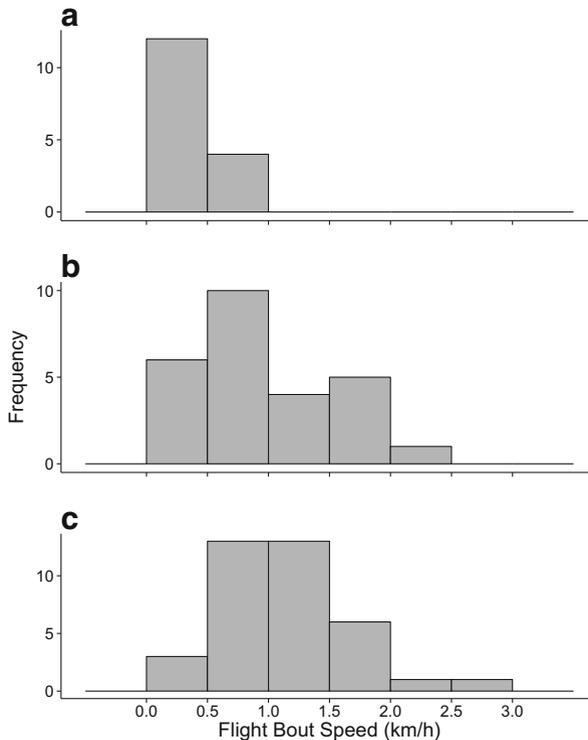


Fig. 1 Histogram of flight bout speed by 16, 26, and 37 male *S. noctilio* flown at 15 °C (a), 20 °C (b), and 25 °C (c), respectively, during bouts of flight while tethered to a flight mill

respectively). However, temperature had a significant effect on flight bout speed of male *S. noctilio* ($F = 25.23$; $df = 1, 74$; $P < 0.001$) (Fig. 4). This model explained 23 % of the observed variability in the data. Similarly, nematode parasitism and pre-flight body mass had no effect on flight bout speed of female *S. noctilio* ($F = 2.72$; $df = 1, 50$; $P = 0.105$ and $F = 0.69$; $df = 1, 50$; $P = 0.410$, respectively). This model explained 12 % of the observed variability in the data.

Nematode parasitism also did not have an effect on the total distance flown ($F < 0.01$; $df = 1, 74$; $P = 0.960$) but pre-flight body mass and temperature had significant effects on the total distance flown ($F = 28.53$; $df = 1, 74$; $P < 0.001$ and $F = 41.65$; $df = 1, 74$; $P < 0.001$, respectively) for male *S. noctilio*. This model explained 46 % of the observed variability in the data. The total distance flown by females was not affected by nematode parasitism ($F = 0.73$; $df = 1, 50$; $P = 0.397$) but was affected by pre-flight body mass ($F = 6.81$; $df = 1, 50$; $P = 0.012$). This model explained only 9 % of the observed variability in the data.

The number of flight bouts taken by male wasps was not affected by nematode parasitism ($F = 0.40$; $df = 1, 74$; $P = 0.531$). Pre-flight body mass and temperature had significant effects on the number of flight bouts taken by males ($F = 11.82$; $df = 1, 74$; $P < 0.001$ and $F = 56.55$; $df = 1, 74$; $P < 0.001$, respectively) (Fig. 5). Nematode parasitism had no effect on the number of flight bouts ($F = 1.01$; $df = 1, 50$; $P = 0.318$), but pre-flight body mass did

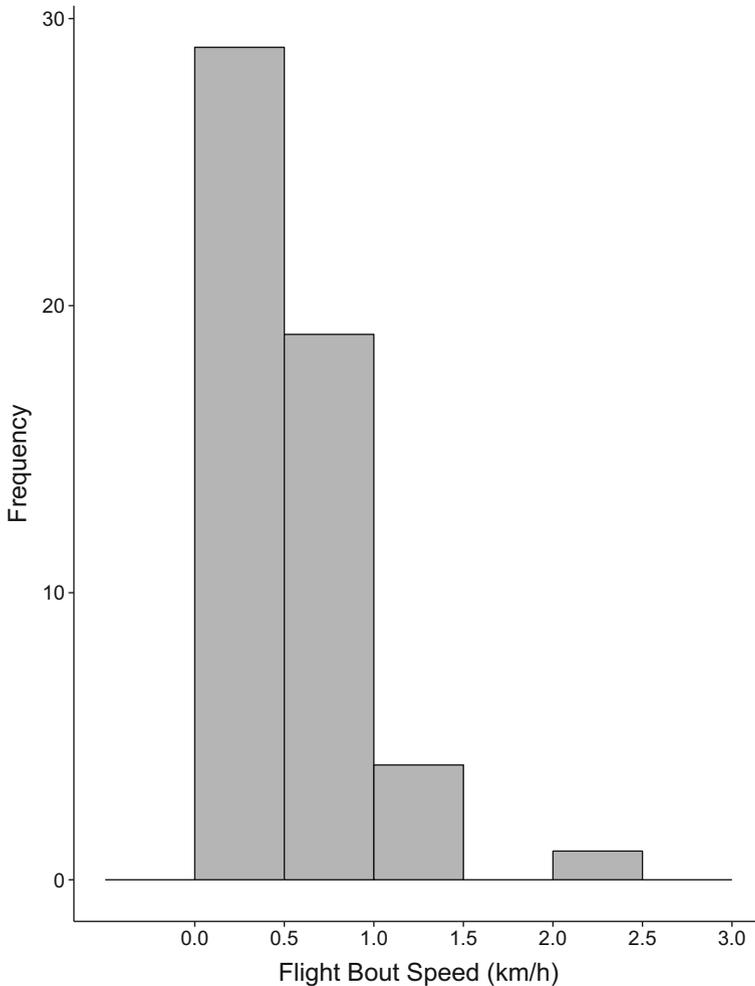


Fig. 2 Histogram of flight bout speed by 53 female *S. noctilio* during bouts of flight while tethered to a flight mill

have an effect on the number of flight bouts ($F = 11.41$; $df = 1, 50$; $P = 0.001$) for female *S. noctilio* (Fig 6).

Diel period and nematode parasitism had a significant effect on total distance flown for male *S. noctilio* ($F = 491.18$; $df = 1, 25$; $P < 0.001$ and $F = 4.67$; $df = 1, 24$; $P = 0.041$, respectively). Moreover, parasitized males were found to be flying farther distances than non-parasitized males. Diel period also had a significant effect on total distance flown by female wasps ($F = 415.50$; $df = 1, 52$; $P < 0.001$). Unlike in males, total distance flown for females was not affected by nematode parasitism ($F = 0.01$; $df = 1, 51$; $P = 0.904$).

Discussion

In general, there was no consistent effect of nematode parasitism on *S. noctilio* body mass, and flight behavior in male and female *S. noctilio* was not negatively affected by

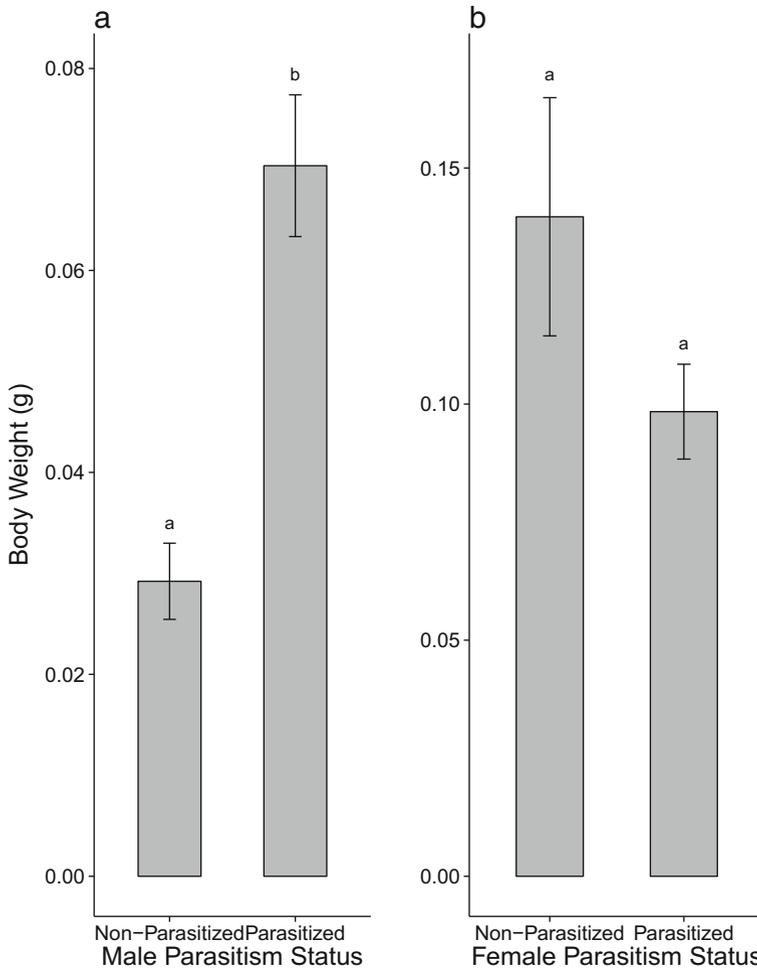


Fig. 3 Parasitized male *S. noctilio* were heavier than non-parasitized males (**a**) whereas parasitized female *S. noctilio* mass did not vary significantly from non-parasitized females (**b**). Lowercase letters indicate statistically significant differences between parasitized and non-parasitized wasps ($P < 0.05$, one-way ANOVA)

parasitism by *D. siricidicola*. Greater pre-flight body mass increased flight performance of male and female *S. noctilio* such that heavier wasps commonly flew faster, farther, and more frequently. Increasing temperature had similar effects on male *S. noctilio* wasp flight performance. An effect of diel period was observed on both male and female flight behavior with both males and females flying farther during the photoperiod than the scotoperiod.

Parasites exploit their hosts' resources and usually negatively influence their insect hosts. However, our results do not support this general observation. We found that male *S. noctilio* parasitized by *D. siricidicola* were heavier than those not parasitized and, in contrast, parasitized females were marginally, but not significantly, smaller (see Fig. 3). It is unclear at this time if males were larger when parasitism occurred (i.e. perhaps

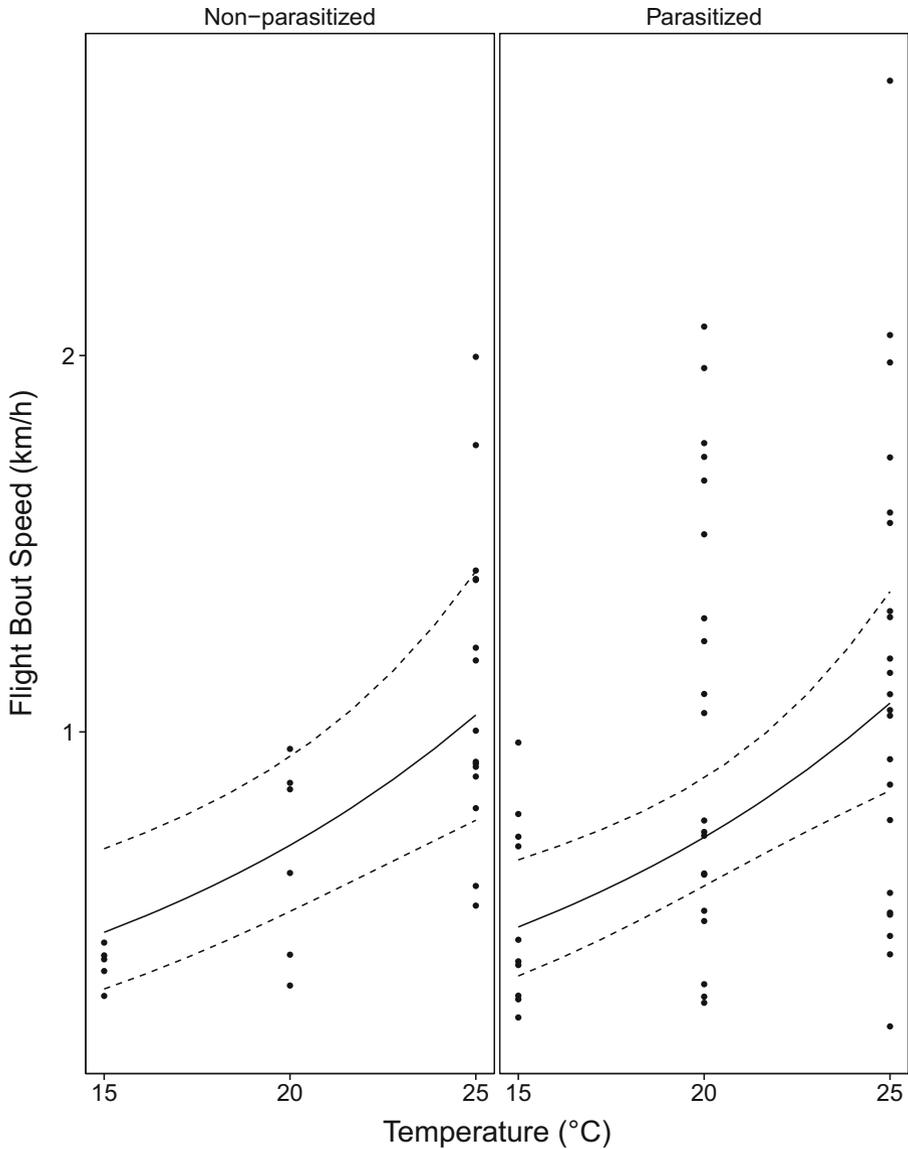


Fig. 4 Flight bout speed of non-parasitized and parasitized male *S. noctilio* increased with temperature. The solid lines and dotted bands show the fit and 95 % confidence intervals, respectively

large males are more apparent in the environment and suffer more parasitism), or if carrying nematodes in the abdominal cavity increased the mass of male wasps. Although parasitism of *S. noctilio* by *D. siricidicola* has been shown to reduce fat reserves in larvae and adults (Zondag 1969) and to result in sterilization (Bedding 1967, 1972; Zondag 1969), we saw a limited negative effect of nematode parasitism on wasp flight behavior. We found that male wasps parasitized by the nematode flew a greater total distance whereas non-parasitized female wasps flew a greater total distance. The

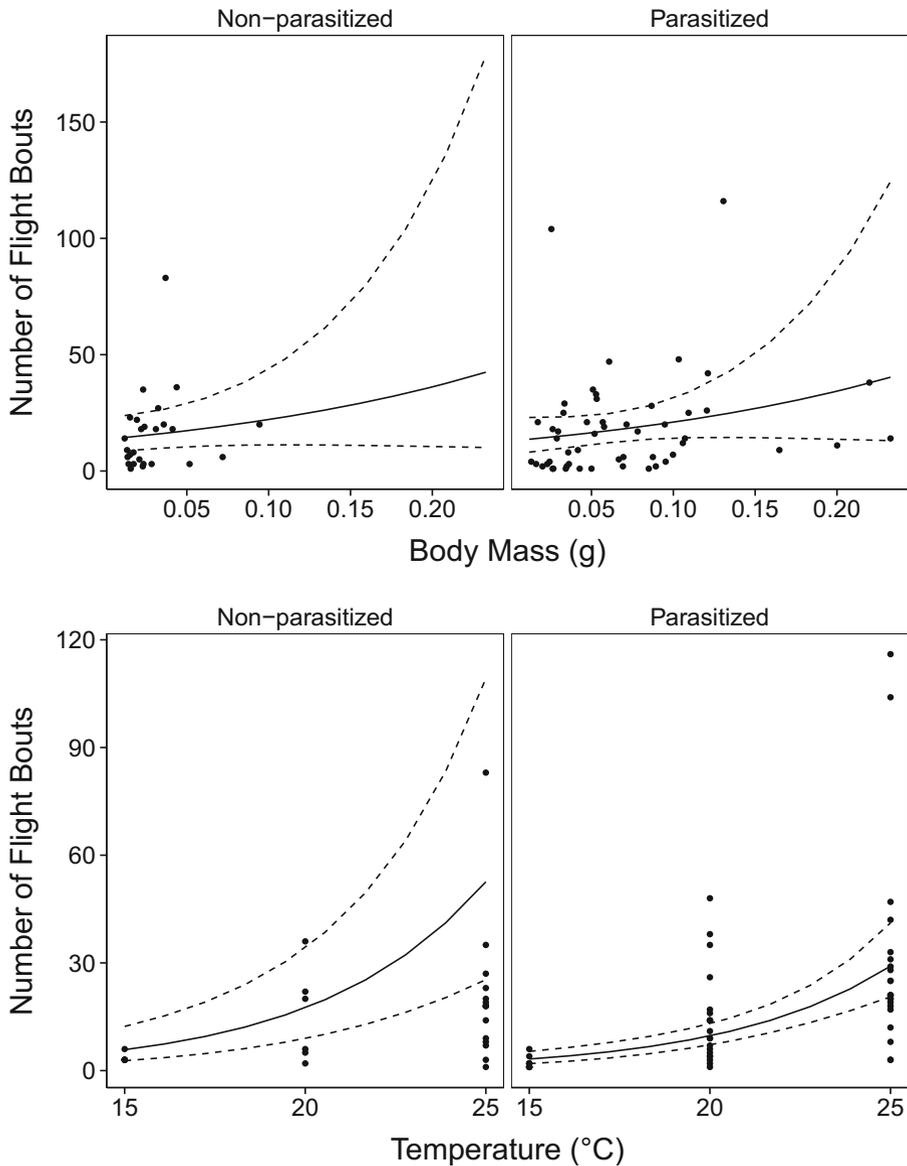


Fig. 5 Number of flight bouts by non-parasitized and parasitized male *S. noctilio* increased with body mass and temperature. The solid lines and dotted bands show the fit and 95 % confidence intervals, respectively

population of individuals that did not fly may differ in terms of size and parasitism, and the patterns we had observed might not have emerged if we included those wasps that did not fly. As nematodes are usually dispersed by female wasps through their infected eggs (Zondag 1969), the limited impact of nematode parasitism on wasp flight is likely advantageous for *D. siricidicola* dispersal and ultimately host location.

Significant size variation exists in *S. noctilio*, and this does not appear to be related to parasitism by *D. siricidicola*. Body-fat reserves gained during the larval stages of

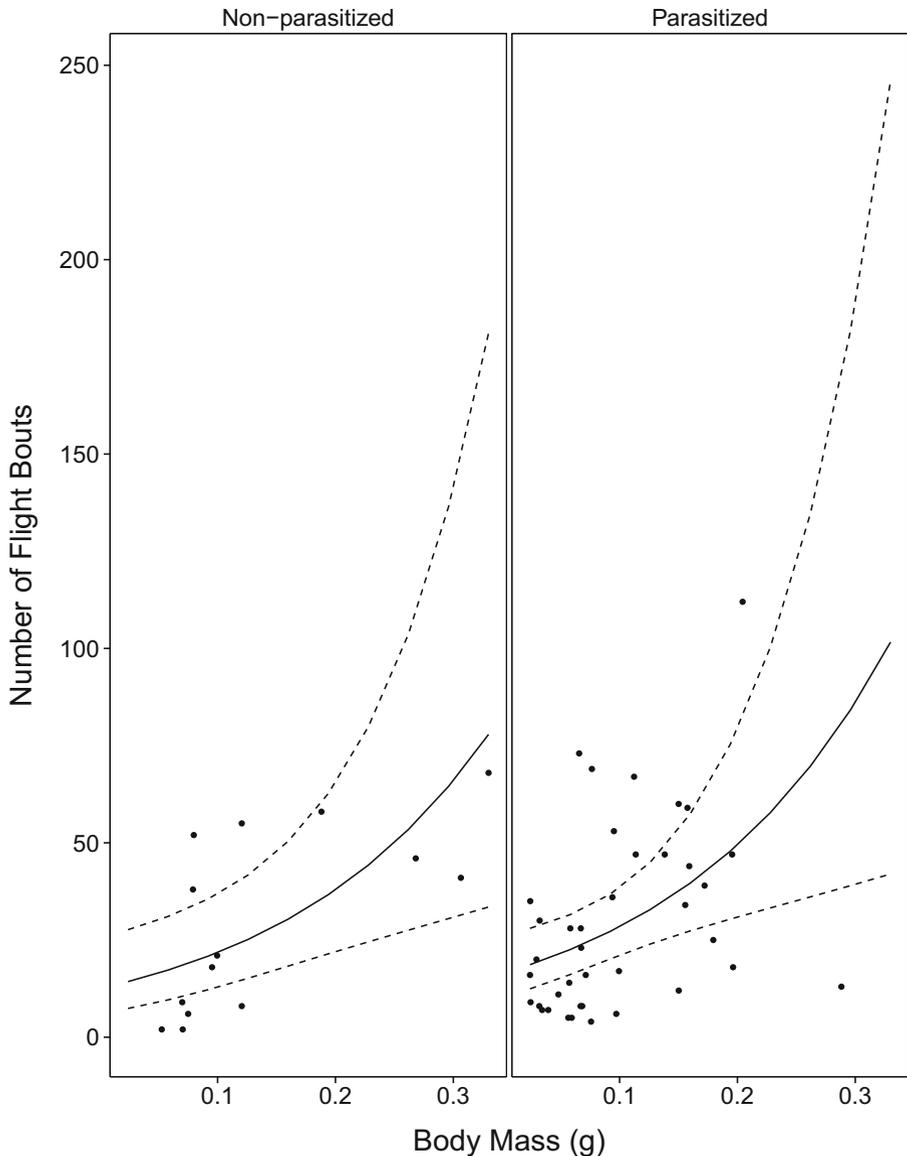


Fig. 6 Number of flight bouts by non-parasitized and parasitized female *S. noctilio* increased with body mass. The solid lines and dotted bands show the fit and 95 % confidence intervals, respectively

S. noctilio relate directly to adult body mass (Bruzzone et al. 2009). It has been suggested that the large variation in wasp size may help explain variation in flight performance in *S. noctilio*, where larger wasps fly faster and farther than smaller ones (e.g. Bruzzone et al. 2009). Villacide and Corley (2008) reported that parasitism of *S. noctilio* by *D. siricidicola* negatively impacted female *S. noctilio* by reducing their body size, and that smaller, parasitized females flew slower and shorter distances than those not parasitized. However, Haavik et al. (2016) found that larger, parasitized male

wasps flew farther (but not faster) than those that were smaller and not parasitized. [Bruzzone et al. \(2009\)](#) also showed that larger female *S. noctilio* consistently flew faster and farther whereas smaller wasps flew slower and shorter distances, often flying periodically or in pulses. Whether these wasps were parasitized or not was not determined, but in either case, it is clear that wasp size is an important factor influencing flight in *S. noctilio*.

In our study, initial body mass was a significant predictor of the total distance and number of flight bouts flown for both male and female *S. noctilio*. Our results are consistent with the general hypothesis that there is a positive correlation between wasp size and flight bout speed, total distance flown, and number of flight bouts flown in *S. noctilio*. Unfortunately, body mass explained little variation in our data (see Figs. 5 and 6). Thus, we conclude that body mass alone has low biological importance in explaining the flight capability of *S. noctilio*, and there are likely other important factors affecting flight, such as temperature and diel period.

It is well known that temperature affects insect flight behavior ([Taylor 1963](#)). Increasing temperatures result in decreased fecundity, developmental time, size, and nematode sterilization for *S. noctilio* ([Yousuf et al. 2014](#)), further altering its dispersal and flight capabilities, and thus spread and control. It is not surprising that we observed a positive relationship between temperature and flight bout speed, total distance flown, and the number of flight bouts flown for male *S. noctilio*. Temperature alone did not explain much variation in our data (see Figs. 4 and 5), which suggests that it works additively with other factors to affect flight behaviour in male wasps. Consistent with our study, [Lantschner et al. \(2014\)](#) reported a direct influence of temperature on flight behavior in *S. noctilio* in that wasps were more active in areas with higher temperature, likely up until a certain threshold temperature. Increased flight capacity may mean that males increase their number of matings over a lifetime because they have added bouts of flight as well as disperse greater distances because they fly faster, farther, and more often. The variable effects of temperature on *S. noctilio* should be considered together when modeling to predict rates of dispersal and spread.

A distinct relationship between diel period and amount of flight was displayed by both male and female *S. noctilio*, where there was greater total distances flown by wasps during the photoperiod as opposed to the scotoperiod. Although both male and female *S. noctilio* also flew during the scotoperiod, *S. noctilio* flight activity appears to be primarily diurnal in nature. The flight activity during the scotoperiod may have been due to an artefact of the experimental design (e.g. absence of landing cues as a consequence of being tethered to a flight mill), or perhaps that *S. noctilio* see well enough to be able to fly during the scotoperiod. We also found that parasitized male wasps flew farther than non-parasitized males. However, since nematodes are not transmitted by male wasps ([Bedding 1972](#); [Zondag 1975](#)), this would not translate into an effect on the dispersal of nematodes across the landscape.

Male *S. noctilio* fly to the top of the canopy after emergence to form leks ([Madden 1988](#); [Martínez et al. 2014](#)). We show that they are also capable of long-range dispersal. We also found that the impact of large body sizes, temperature, and photoperiod was more important than the impact of nematode parasitism on wasp flight, but each factor alone has little biological importance. Our finding that parasitism by *D. siricidicola* did not negatively impact flight in female *S. noctilio* suggests that the nematode should be able to spread throughout *S. noctilio* populations and sterilize wasps, which is

consistent with observations of the nematode functioning as an effective biological control agent in the Southern Hemisphere. Future studies could determine the temperature thresholds for flight in *S. noctilio* and the role of light intensity on flight activity.

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Authors Contribution LJH and JDA conceived and designed the experiment, LJH conducted the experiment, JMG and CJKM analyzed the data, and all authors contributed to writing the manuscript.

Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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