

Determinants of mating success in a lek-mating species

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Funding information

Natural Resources Canada; Tree Protection Cooperative Programme; United States Department of Agriculture–Forest Service Forest Health Protection (USDA-FS FHP); South African Department of Forestry, Fisheries and the Environment

Abstract

1. Leks are male-biased aggregations formed for mating, where sperm is the only resource acquired by visiting females.
2. One of the many advantages of leks is the possibility to efficiently assess the quality of potential mates by comparing aggregated individuals of the same sex with one another.
3. When direct mate choice occurs in a lekking species, it is often exhibited by females, but some studies have also demonstrated the presence of male mate choice.
4. We investigate mate choice in the lek-forming European woodwasp, *Sirex noctilio*.
5. We determine the importance of age and size as predictors of mating success.
6. We demonstrate that mating is not random and that male and female traits affect mating success.
7. Age plays an important role in mating success in both males and females, with older males mating more and younger females being more attractive and more receptive to mating.
8. Relative male size seems to play a role in mating success, with males being more successful when attempting to mate with females that are larger than they are.

KEYWORDS

Hymenoptera, leks, male mate choice, mating behaviour, woodwasp

INTRODUCTION

In the animal kingdom, leks are defined as male-biased aggregations formed for mating, where sperm is the only resource acquired by visiting females (Höglund & Alatalo, 1995). There are many advantages to lek formation, from reduced predation risks to increased mating chances or easy mate location (Field et al., 2002; Höglund & Alatalo, 1995). Another advantage of lek formation is efficient mate choice as many potential mates of varying quality are grouped together and can be easily compared. Depending on the species, male quality can refer to a wide variety of traits such as genetic quality, genetic compatibility, sperm availability and quality or quality of parental care. In leks, mate choice is primarily

done by females that use male traits such as the characteristics of visual, auditory or olfactory displays (Alcock, 1987; Alem & Greenfield, 2010; Andersson, 1991; Cheng et al., 2022; Gibson, 1996; Grafe, 1997), size or other morphological traits (Clutton-Brock et al., 1989; Ryder et al., 2010), the male's level of heterozygosity (Ryder et al., 2010) or hierarchy within the lek (Gosling & Petrie, 1990; Jarrige et al., 2016; Ryder et al., 2011) to choose a mate. However, studies have also demonstrated the presence of male mate choice in some lekking mammals (Bro-Jørgensen, 2011), birds (Karvonen et al., 2000; Petrie et al., 1992; Sæther et al., 2001), fish (Werner & Lotem, 2003) and insects (Goubault & Burlaud, 2018; Shelly et al., 2012). In these species, males use female traits such as size (Goubault & Burlaud, 2018;

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Werner & Lotem, 2003), age (Mainguy et al., 2008; Shelly et al., 2012) or mating status (Bro-Jørgensen, 2007) to discriminate between low and high quality females.

The invasive woodwasp *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) lays eggs in the wood of various pine species where the larvae bore galleries and feed on the wood before emerging as adults (Slippers et al., 2012). During egg laying, females inject a symbiotic fungus and a phytotoxic mucus into the wood. Together, the mucus and fungus provide adequate conditions for larval development. The mucus stresses the tree by altering the water balance. This encourages the growth of the fungus that obstructs the xylem and further disrupts water translocation (Madden, 1988). *Sirex noctilio* causes economic loss across the Southern Hemisphere by killing trees in pine plantations. In South Africa, *S. noctilio* has been responsible for tree mortality of up to 10% and 35% in the Western Cape and KwaZulu-Natal respectively (Hurley et al., 2007). In the Western Cape, climate is characterized by rainy winters and dry summers and *S. noctilio* mostly attacks *P. radiata*, as it is the most readily available host. In KwaZulu-Natal, rain occurs during the summer while winters remain mostly dry. In this region, *P. patula* is mostly available to *S. noctilio*. In South Africa, control strategies against *S. noctilio* involve silvicultural practices and biological control using parasitoid wasps and a parasitic nematode, *Deladenus siricidicola* (Slippers et al., 2012). The study of this species and further development of regulation strategies is still obstructed by the difficulty of rearing this species in captivity. One of many aspects that prevent rearing is the difficulty to realize mating in captivity. A deeper understanding of mating behaviour in *S. noctilio* could facilitate the development of successful laboratory rearing protocols which would benefit future research programmes (van der Merwe et al., 2023).

After emerging from the wood, male *S. noctilio* are attracted to light and fly to the canopy to aggregate and form small swarms called leks (Madden, 1988). These aggregations usually form on warm sunny days in the early morning or late afternoon (Dolezal, 1967). Females join these leks, and mating is initiated when a female comes close enough to a male, allowing the male to sense the contact pheromones on the cuticle of the female (Böröczky et al., 2009). To initiate mating and fertilize the female, a male must grasp the female with his front legs, bend his abdomen to reach underneath the female, and open his claspers. The claspers are located on the sides of the male genitalia and allow males to lock themselves on the females' genitalia to prevent the mating from being interrupted before fertilization. On average, copulation lasts around 50 s (Lu et al., 2022). Females mate with multiple males (Caetano & Hajek, 2017) and fly away to find a host into which to lay eggs. Previous observations of the wasps in captivity have suggested that males and females do not mate with all the individuals they encounter, suggesting the presence of both female and male mate choice in this species.

In *S. noctilio*, both males and females exhibit marked size variation that positively correlates with resource availability during larval development (Garnas et al., 2020; Neumann et al., 1987). Females are generally larger and measure between 10 mm and 44 mm in length, while the males measure between 9.3 and 34.9 mm in length (Ryan & Hurley, 2012). In insects, body size is a trait commonly used by males to choose a mate because it is a good indicator of fecundity (Beukeboom, 2018; Bonduriansky, 2001). For example, males of the

lesser wax moth, *Achroia grisella*, preferentially mate with larger females (Goubault & Burlaud, 2018). In female *S. noctilio*, body size is correlated with greater egg count (Madden, 1974) and greater dispersal capacity (Gaudon et al., 2016). In insects, male size is often positively correlated with sperm production and availability (Pech-May et al., 2012). As a result, it should be in each individual's interest to mate with the largest conspecific they encounter. However, a peculiar behaviour is often observed in *S. noctilio*. Large males tend to struggle to bend their abdomen enough to be able to copulate with a small female. This suggests that the relationship between mating success and size is not straightforward in *S. noctilio* and deserves investigation.

Male *S. noctilio* usually emerge a few days to a few weeks before females and have a life span of approximately 12 days during the warm summer months and can extend to up to two weeks during the colder fall months (Haavik et al., 2013; Morgan & Stewart, 1966; Neumann et al., 1987; Rawlings, 1948). This is an interesting behaviour because while they are waiting for the females to emerge, males are exposed to predators, parasites and to abiotic stresses that can reduce life span. A possible advantage of emerging early would be to display 'good genes' to a potential mate (Brooks & Kemp, 2001). In many insects, females are able to determine the age of a potential mate because courtship displays involving olfactory, auditory and visual signals tend to differ with age (Kaltenpoth & Strohm, 2006; Simmons & Zuk, 1992; Thanda Win et al., 2013). As such, we would expect that females would prefer mating with older males. On the other hand, females have a shorter life span of approximately 5 days in the summer but can extend to up to two weeks in the fall (Neumann et al., 1987). Males would benefit from mating preferentially with young females that have more time to use their sperm.

To guarantee that they have enough time to lay eggs, many females within the Hymenoptera switch from a mate location phase to a host location phase at some point during their lives and stop responding to male courtship. Because adult *S. noctilio* do not feed, the size of fat reserves accumulated as larvae influences lifespan, meaning that larger females generally live longer (Arrese & Soulages, 2010; Bruzzone et al., 2009; Villacide & Corley, 2012). As such, smaller females should prioritize host location over mate location earlier than larger females. Therefore, it is possible that the effect of size on mating success might differ among age groups. The objectives of this study were to determine which of the two sexes exhibit mate choice and to assess how size, age and the interaction between size and age influence receptivity and mating success in this species.

METHODS

Obtention of *S. noctilio*

We collected logs of *P. patula* and *P. radiata* in the South African provinces of the Western Cape and KwaZulu-Natal between September 2018 and January 2019. We brought the logs to the Forestry and Agricultural Biotechnology Institute Biocontrol Centre of the University of Pretoria and placed them indoors in emergence cages (130 cm

× 50 cm × 50 cm) made from metal frames and plastic mesh. The logs were maintained at $23 \pm 10^\circ\text{C}$; 12 L:12D.

We collected *Sirex noctilio* adults from the emergence cages daily between 07:00 and 09:00, placed them in ventilated individual plastic containers (12 cm × 12 cm × 5 cm) and kept them at $23 \pm 10^\circ\text{C}$ with a photoperiod of 12L:12D until they were used for bioassays. The bottom of each container was covered in pieces of pine bark because *S. noctilio* adults struggle to gain traction on the smooth surface of plastic containers. We sprayed the pine bark with distilled water every two days to prevent dehydration of the wasps. Under these conditions, males lived up to 20 days and females up to 12 days, indicating that the wasps were not stressed and could be used for behavioural tests. During the collection of adults, if emergence cages contained more than one sex, we discarded the individuals in that cage to ensure that all individuals used for behavioural tests were naïve.

Bioassays

We conducted a total of 21 bioassays in a wooden cage (31 cm × 32 cm × 42 cm) with one glass screen wall and a door on the ceiling. We placed the cage outdoors on a table in the shade. We determined the ideal size and placement of the cage based on preliminary trials that indicated which conditions would maximize mating success in captivity. A similar protocol was also used by Caetano and Hajek (2017). We chose to introduce one female along with eight males in the cage to recreate the densities of individuals previously observed within leks in the field. We first introduced one female into the cage and kept her under a small plastic cage (10 cm × 10 cm × 5 cm). This allowed the female to recover from the stress of handling. The placement of the small plastic cage in the cage was standardized across bioassays. We then randomly selected eight males and painted a dot of oil-based paint (Dala oil paint) on the back of the thorax using a different colour for each male (Gangwere et al., 1964). We then introduced the males into the cage.

During the first few minutes after being introduced into the cage, males usually exhibit aggressive behaviours towards females and each other. To prevent injuries to the female, we only removed the small plastic cage isolating her 5 min after the introduction of the males. We did so quickly through the door on the ceiling of the cage. The cage was large enough that this action did not disturb the wasps, which, at that point, had settled and showed very little movement. The bioassays lasted 20 min, starting from the removal of the small plastic cage over the female.

We covered all walls, except for the glass screen, with paper and changed the paper after each bioassay to avoid contamination through the deposition of contact and volatile pheromones. Furthermore, we cleaned the glass screen with 70% ethanol after each bioassay. We drew a grid on the floor of the cage to facilitate scoring the location of individuals. We conducted all bioassays between 08:00 and 12:30 on days with cloud cover below 50% to guarantee that low temperatures would not interfere with mating success (Lu et al., 2022). The temperature varied between 22 and 32°C .

Data collection

We recorded all bioassays using a video camera (Canon LEGRIA HF G26). Because the dots of paint on the males were not always visible on the video, we also continuously orally described the location of the males in the cage. From the video, we recorded the number of contacts between all the males and the female, the number of mating attempts made by each male towards the female and the number of matings between the female and each male.

When placed in a cage with a female, males have rarely been observed to walk towards the female in a straight line. Males must come into contact with a female to detect her contact pheromones (Böröczky et al., 2009; Dolezal, 1967). We defined a contact between a male and a female as a contact between the male antennae and any part of the female body. We only used bioassays during which each male came into contact with the female at least once ($n = 20$).

We defined a mating attempt as a male bending his abdomen forward and opening his claspers within one second of a contact with a female. We defined a mating as a male being visibly locked to a female for more than 20 s. We recorded the age of each male and female before placing them into the cage. Across all bioassays, the youngest female was zero days old, meaning that she emerged less than 24 h before the start of the experiment, while the oldest female was nine days old. Across all bioassays, male age ranged from 0 to 12 days. After each bioassay, we gave each individual an identification number, placed them in 90% ethanol and later measured the width of their pronotum (mm) as a proxy for size (Haavik et al., 2016; Madden, 1981). We took the measurements using a pair of digital calipers. Female pronotum width ranged from 1.96 to 6.57 mm. Male pronotum width ranged from 1.5 to 6.1 mm.

Analysis of female attractiveness and female receptivity

Female attractiveness was defined as the number of attempts a female receives from the males, and female receptivity was defined as the proportion of attempts that lead to a mating. Both female attractiveness and female receptivity could be influenced by the age and size of both sexes, among other factors. Therefore, we investigated the effect of age, size and their interactions on female attractiveness and female receptivity by constructing a series of models that predict female attractiveness and female receptivity.

Because eight males were tested at a time, the behaviour of males within a bioassay is non-independent, and neither is the response of a female to each male. To account for the fact that male behaviour and female response are non-independent, we built generalized linear mixed effects models and added the female identification number to the models as a random effect. The `glmmTMB` function from the `glmmTMB` package (Brooks et al., 2017) in R (R Core Team, 2023) was used to build the models. Since female attractiveness is a count variable, we used a Poisson distribution. Female receptivity is a binomial variable that includes the number of attempts by a

male leading to a mating (success) and the number of attempts by a male leading to a rejection of the male by the female (failure). Therefore, we fitted generalized linear mixed models with a binomial distribution to explain female receptivity.

We fitted nine models explaining female attractiveness (model set I; Table 1) to be compared and the same nine for female receptivity (model set J; Table 2). Each model set had one null model that does not use any factor to predict attractiveness or receptivity. Null models describe a situation where mating attempts and mating are random. Each model set also contained eight models containing different combinations of seven parameters that might have affected female attractiveness and female receptivity. We included female pronotum width (mm), female age (days), male pronotum width (mm), male age (days) and male to female pronotum width ratio. To test for an effect of an interaction between size and age, we also included the interactions between female age and female pronotum width and between male age and male pronotum width in our models. We used a model selection approach to identify parameters that affect female attractiveness and female mating success as recommended by Bolker et al. (2009) and Rhodes et al. (2009). We calculated Akaike weights from the models' AIC_c because the AIC_c is corrected for sample size (Burnham et al., 2011) and determined a 95% confidence interval of models that best fit the data (Rhodes et al., 2009). When more than one model fell into the 95% confidence intervals, we used model averaging to obtain averaged parameter estimates (Burnham & Anderson, 2002).

RESULTS

Female mating success and male mating skew

Of the 15 females that mated (71.4% of the females), 66.7% of them mated more than once. Among them, the average number of matings per female was 2.6 ± 0.57 (mean \pm SE, $n = 15$). On average, $20.4\% \pm 12.1\%$ ($n = 20$) of contacts between a male and a female led to an attempt by the male (200 attempts after 1109 contacts). On average, 24% of the males obtained 100% of the matings.

Female attractiveness

Through model comparison and model averaging, we first demonstrated that mating attempts performed by males are not random (Table 1 and Supporting Information). We found that the seven parameters tested affect female attractiveness. The absolute values of the averaged parameter estimates for Model I (APEI) show that the parameter with the strongest effect on female attractiveness is the male to female size ratio ($APEI_{\text{male/female size ratio}} = -3.42$), followed by female size ($APEI_{\text{female size}} = -0.76$), male size ($APEI_{\text{male size}} = 0.62$), female age ($APEI_{\text{female age}} = -0.47$), male age ($APEI_{\text{male age}} = 0.16$), the interaction between female age and female size ($APEI_{\text{female age} \times \text{female size}} = 0.1$) and, finally, the interaction

TABLE 1 Summary of the generalized linear mixed models predicting female attractiveness.

Model	Model rank	k	AIC_c	ΔAIC_c	wi	Evidence ratio	Intercept	Female age		Female size	Male size/ Female size		Female age: Female size		Male age: Male size	
								Female age	Male age		Male size	Female size	Female size	Male size	Female size	Male size
I1	9	1	504.92	19.31	3.50E-05	15.606	0.09									
I2	3	7	487.6	1.99	0.2	2.7	2.08	-0.55	0.12	-0.37	-1.34	0.16				
I3	7	7	494.8	9.19	5.50E-03	98.83	4.07	-0.44	-0.7	-0.7	-3.74	0.122				
I4	8	7	495.1	9.49	4.80E-03	114.82	-0.07	0.07	0.25	-0.76	-2.2					-0.05
I5	5	7	493.3	7.69	1.20E-02	46.68	3.2		0.24	-0.93	-5.53					-0.05
I6	1	8	485.61	0	0.55	1	4.13	-0.46	0.13	-0.93	-4.32	0.14				
I7	6	8	493.71	8.09	9.60E-03	57.18	2.93	0.07	0.27	-0.76	-5.57					-0.05
I8	4	9	491.03	5.41	0.04	14.98	0.47	-0.56	0.28	-0.14	-0.12	0.16				-0.06
I9	2	10	487.8	2.19	0.18	2.99	3.76	-0.46	0.29	-0.93	-4.31	-0.06				0.14
Averaged parameter estimates								3.38	-0.47	-0.76	-3.42	0.1			0.02	

Note: Values in the eight columns on the right are parameter estimates predicted by the models. Models in bold fall into the 95% confidence interval. The averaged parameter estimates are obtained by averaging and weighing estimates across the models that fall within the 95% confidence interval. Abbreviations: k, number of parameters estimated; wi, Akaike weight.

TABLE 2 Summary of the generalized linear mixed models predicting female receptivity.

Model	Model rank	k	AIC _c	ΔAIC _c	wi	Evidence ratio	Intercept	Female		Male size/		Female age:		Male age:			
								age	size	Female size	Male size	Female size	Male size	Female size	Male size		
J1	8	1	136.12	4.72	3.10E-02	10.61	-1.58										
J2	1	7	131.4	0	0.33	1	3.32	-0.43	-0.94				8.40E-02				
J3	9	7	136.5	5.1	2.60E-02	12.81	1.86	-0.3	-0.36				3.50E-02				
J4	2	7	132.4	1	0.2	1.65	-0.64	-0.11					1.5			2.20E-03	
J5	5	7	133.9	2.5	9.40E-02	3.49	0.85		-0.4				-0.53			0.02	
J6	3	8	133.61	2.21	0.11	3.01	2.6	-0.43	-0.75				-0.94	0.09			
J7	6	8	134.21	2.81	8.10E-02	4.07	1.32	-0.12	-0.48				-0.81			-1.9E-03	
J8	4	9	133.84	2.44	0.1	3.39	1.73	-0.43	-0.58				0.09			-1.4E-02	
J9	7	10	136.1	4.7	3.10E-02	10.49	2.54	-0.44	-0.77				-2.0E-01	0.09		-1.5E-02	
Averaged parameter estimates							1.64	-0.27	-0.55				-0.27	-0.57	0.05		1.80E-04

Note: Values in the eight columns on the right are parameter estimates predicted by the models. Models in bold fall into the 95% confidence interval. The averaged parameter estimates are obtained by averaging and weighing estimates across the models that fall within the 95% confidence interval. Abbreviations: k, number of parameters estimated; wi, Akaike weight.

between male age and male size ($APEI_{\text{male age} \times \text{male size}} = 0.02$) (see last row in Table 1). $APEI_{\text{male/female size ratio}} < 0$, indicating that as male size decreases relative to female size, the number of mating attempts increases. This means that males attempt to mate more with females that are larger than them. $APEI_{\text{female size}} < 0$, indicating that males attempt to mate more with smaller females. $APEI_{\text{male size}} > 0$, indicating that larger males attempt to mate more than smaller males. $APEI_{\text{female age}} < 0$, showing that males attempt to mate more with younger females. $APEI_{\text{male age}} > 0$, which means that older males attempt to mate more. $APEI_{\text{female age} \times \text{female size}} > 0$ and $APEI_{\text{male age} \times \text{male size}} > 0$, indicating that the effect of female and male age on the number of mating attempts is stronger in larger individuals.

Female receptivity

Through model comparison and model averaging, we found that the seven parameters tested affect female receptivity (Supporting Information). The absolute values of the averaged parameter estimates for model J (APEJ) show that the parameter with the strongest effect on female attractiveness is the male to female size ratio ($APEJ_{\text{male/female size ratio}} = -0.57$), followed by female size ($APEJ_{\text{female size}} = -0.55$), male size ($APEJ_{\text{male size}} = -0.27$), female age ($APEJ_{\text{female age}} = -0.27$), male age ($APEJ_{\text{male age}} = 0.13$), the interaction between female age and female size ($APEJ_{\text{female age} \times \text{female size}} = 0.05$), and finally, the interaction between male age and male size ($APEJ_{\text{male age} \times \text{male size}} = 1.8E-4$) (see last row in Table 2). $APEJ_{\text{male/female size ratio}} < 0$, indicating that as male size decreases relative to female size, the proportion of mating attempts leading to a successful mating increases. This means that females are more receptive to males that are smaller than them. $APEJ_{\text{female size}} < 0$, indicating that smaller females are more receptive than larger females. $APEJ_{\text{male size}} < 0$, indicating that females are more receptive to smaller males. $APEJ_{\text{female age}} < 0$, showing that younger females are more receptive than older females. $APEJ_{\text{male age}} > 0$, which means that females are more receptive to older males. $APEJ_{\text{female age} \times \text{female size}} > 0$ and $APEJ_{\text{male age} \times \text{male size}} > 0$, indicating that the effect of female and male age on the proportion of mating attempts leading to a successful mating is stronger in larger individuals.

DISCUSSION

We found that females are polyandrous with two thirds of the females that mated, mating more than once. This corroborates findings by Caetano and Hajek (2017). We also showed that 24% of the males obtained 100% of the matings. This was expected as mating skews are common in lekking species (Widemo & Owens, 1995). Interestingly, we found that only 20.4% of the contacts between a male and a female led to a mating attempt by the male. This suggests that males also exhibit choice and do not attempt to mate with all the females they encounter. Male mate choice has rarely been

demonstrated in lekking insect species (Goubault & Burlaud, 2018; Sæther et al., 2001; Shelly et al., 2012; Werner & Lotem, 2003), but *S. noctilio* is a new example.

Male to female size ratio has the strongest effect on female attractiveness and female receptivity. This means that regardless of their size, males attempt to mate, and mate more with females that are larger than them. This corroborates our observation that large males struggle to bend their abdomen enough to copulate with small females and could explain why females number 17 and 18 never mated. All the males encountered by female number 17 were larger than her, while six males out of eight were larger than female number 18. In *S. noctilio*, there is a trade-off between fast development and size (Lombardero et al., 2016). Individuals that have access to limited or poor-quality resources such as dry wood or bolts with a small diameter can either emerge early and at a smaller size, taking the risk of being outcompeted by larger males during mate choice, or can emerge the following year at a larger size but take the risk of dying before mating due to predation or adverse weather conditions. However, the size constraint on pairing among males and females might provide an advantage for small males that emerge early.

The factor with the second strongest effect on female attractiveness and female receptivity was female size. Smaller females were both more attractive and mated more than larger females. Our observation that smaller females were more attractive to males could be a result of assortative mating. To avoid sperm competition with large males, small sperm-restricted males would only attempt to mate with small females. This may be a case of 'prudent choice' where individuals of lower quality intentionally reject high-quality mates (Taborsky et al., 2009). As a result, while large females would only be courted by large males, small females would be courted by males of all sizes. In addition to being more attractive, small females were also more receptive than large females. This result seems counterintuitive because smaller females produce fewer eggs and need less sperm (Morgan & Stewart, 1966). This observation may be the result of a convenience polyandry (Thornhill & Alcock, 1983) which is frequently observed in insects, including the Hymenoptera (Fernández-Escudero et al., 2002; Trontti et al., 2007). Here, small females might accept mating to avoid harassment and injuries (Boulton et al., 2018). This may stem from a conflict of interest between the sexes and especially between small males and small females. If small females copulate preferentially with large males, small males might have to resort to coercion to guarantee mating.

The third factor with the strongest effect on female attractiveness and female receptivity was male size. We found that large males attempted to mate more, but females were more receptive to smaller males. Large males have more sperm available (Pech-May et al., 2012). This would probably explain why they attempt to mate more than small males. However, as mentioned earlier, large males struggle to copulate with females that are too small, decreasing their chance of successful mating. This explains why we observe that small males are more likely to mate.

Female age had some effect on female attractiveness and receptivity, although age had a weaker effect than size. Younger females were both more attractive to males and mated more than older

females. This observation can be explained by two non-mutually exclusive phenomena. First, males might prefer mating with younger females, like in *Ephestia kuehniella* (Lepidoptera: Pyralidae) (Xu & Wang, 2009) or *Empis borealis* (Diptera: Empididae) (Svensson et al., 1989). This is because younger females have more time to use sperm after fertilization and have more energy resources to disperse and locate high-quality hosts. Second, males might not recognize older females as potential mates. Female *S. noctilio* have biologically active cuticular hydrocarbons that trigger mating attempts from males (Böröczky et al., 2009; Faal et al., 2022). Perhaps older females have reduced titres or a different profile of cuticular hydrocarbons as in *Drosophila melanogaster* (Kuo et al., 2012). Because Hymenoptera species are haplodiploid, females can produce male progeny without being fertilized. After reaching a certain age, whether they are mated or not, *S. noctilio* females switch their focus from mate location to host location for egg laying (Morgan & Stewart, 1966). This succession of behaviours is similar to other hymenopteran species in which mates and hosts are separated in the landscape (Guertin et al., 1996). The mechanisms that trigger a switch from a mate-searching to a host-searching phase in unmated hymenopteran females are still unknown, but it is likely that this switch would be characterized by a change in behaviour and physiology. In *S. noctilio*, those physiological changes might include qualitative and/or quantitative changes in the cuticular hydrocarbon profile of females.

Older males attempted to mate and mated more than younger males. This could be explained by two phenomena that are not mutually exclusive. First, it is possible that males are sexually immature at emergence and need a few days to reach sexual maturity. This phenomenon has been observed in other hymenopteran species and is linked to delayed sperm maturation after emergence (Moors et al., 2009; Poidatz et al., 2018; Quimio & Walter, 2000). Second, male *S. noctilio* might become more eager to mate as they age or might become less choosy with time (Bonduriansky, 2001). This phenomenon has been observed in other insect species (e.g., *Propylea dissecta*; Pervez & Richmond, 2004, *Drosophila pseudoobscura*; Dhole & Pfennig, 2014, *Drosophila melanogaster*; Dukas & Baxter, 2014 and *Cimex lectularius*; Wang et al., 2016). To determine which of these two phenomena contributes to the effect of age on male motivation to mate in *S. noctilio*, sperm production and maturation in relation to age should be investigated.

Females choosing to mate with older males is common among insects (Avent et al., 2008; Somashekar & Krishna, 2011; Zuk, 1987). Females can determine the age of a male because courtship displays involving olfactory, auditory and visual signals can differ with male age (Kaltenpoth & Strohm, 2006; Simmons & Zuk, 1992; Thanda Win et al., 2013). By estimating male age, females can also estimate male fitness because, by surviving longer, older males demonstrate genetic superiority (Brooks & Kemp, 2001; Manning, 1985). This hypothesis is particularly relevant considering that in *S. noctilio*, males emerge a few days before females. While they are waiting for females to emerge, males are exposed to predators and fluctuating environmental conditions that can significantly reduce their lifespan and prevent them from reproducing.

Although the effects of age on female attractiveness and female receptivity were weaker than the effects of size, it is important to note that insects do not age at a constant rate when temperatures vary (Promislow et al., 2022). While we attempted to keep wasps at a constant temperature, individuals that lived through warmer days likely aged faster than individuals that lived through cooler conditions. This is due to the fact that insects lose more water on warmer days and use greater amounts of their energy reserves because of increased metabolic rates (Addo-Bediako et al., 2001; Arrese & Soulages, 2010; Clarke & Fraser, 2004). While there might be a linear relationship between physiological state (i.e., water and energy reserves) and mating success, changes in temperature prior to the experiment might affect a potential linear relationship between age and mating success. We also found that the effect of male age was weaker than the effect of female age. Perhaps this is because the effect of male age is non-linear. While male mating success increases within the first few days after emergence because they become sexually mature or less picky, male willingness to mate and attractiveness might decrease again as they approach death.

Finally, we found a weak and perhaps negligible effect of the interactions between female age and female size and between male age and male size. We found that the effect of age on female attractiveness and receptivity was stronger in larger individuals. This means that (1) the number of mating attempts and the number of matings decreased faster with age in larger females than in smaller females and that (2) the number of mating attempts and the number of matings increased faster with age in larger males than in smaller males.

CONCLUSIONS

The results of this study demonstrated that, in *S. noctilio*, mating is not random and that both males and females exhibit mate choice. We found that size and age affect mating success but that the relationship between those traits is a complex one. Age seems to play a role in both sexes, with older males being more successful and younger females being more attractive and more receptive to males. Males might need to reach sexual maturity to mate, while older females probably switch their behaviour from mate to host location. Our results also suggest that the male to female size ratio influences mating success, with males smaller than the female being more likely to mate. Females number nine and ten were one day old or younger and mostly encountered males smaller than them in the cage. Despite these seemingly favourable conditions, these females never mated. This would indicate that females use other male traits to select males. These traits could be related to genetic compatibility (Thiel et al., 2013), male motor performance (Byers et al., 2010) or colouration (Allison et al., 2021). In natural conditions, females might use other male characteristics such as mating status (Li et al., 2023) or male hierarchy within the lek (Izzo & Tibbetts, 2012). Male mate choice is rarely investigated in lekking species (Sæther et al., 2001; Shelly et al., 2012; Werner & Lotem, 2003). For this reason, mate choice by males should receive more attention in *S. noctilio*.

Past research on the biology of *S. noctilio* has been limited by our poor understanding of the reproductive biology of this species. Studies that required populations reared in the laboratory or behavioural observation of mating behaviour are examples of areas that would benefit from a better understanding of male and female mate choice and willingness to mate. The future development of new management strategies might also benefit from our findings. For example, gene drive technologies (van der Merwe et al., 2023) and sterile insect techniques rely heavily on the availability of lab-reared males that are as attractive to females as wild males. As such, we recommend any study that requires individuals to mate in captivity or in the field to use females that have emerged within the last 48 hours and males that are one to two days old. We also recommend that, besides extremely small males, protocols should use males representing a variety of sizes to match the variety of sizes found in females. This is especially important for populations reared in the laboratory as standardized rearing protocols might lead to a reduction of the size variation among males.

AUTHOR CONTRIBUTIONS

Joséphine Queffelec: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; software; validation; visualization; writing – original draft; writing – review and editing. **Jeremy D. Allison:** Conceptualization; funding acquisition; investigation; resources; supervision; validation; writing – review and editing. **Bernard Slippers:** Conceptualization; funding acquisition; investigation; resources; supervision; validation; writing – review and editing. **Jaco M. Greeff:** Conceptualization; data curation; formal analysis; investigation; methodology; software; supervision; validation; writing – original draft; writing – review and editing.

ACKNOWLEDGEMENTS

This work was supported by members of the Tree Protection Cooperative Programme (TPCP); the Department of Forestry, Fisheries and the Environment (DFFE); Natural Resources Canada; and the United States Department of Agriculture–Forest Service Forest Health Protection (USDA-FS FHP). We thank members of the TPCP and the South African Sirex Control Programme for assistance with field work and sample collection.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data underlying the results of this study are openly available on the Open Government portal at <https://doi.org/10.23687/6e5122f6-098e-47e1-a43c-7908f28cf5fe>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Distribution of male age within each bioassay. Orange dots represent the age of the males that mated successfully. Points are scattered around values to avoid superposition.

Figure S2. Distribution of male pronotum width within each bioassay. Orange dots represent the pronotum width of the males that mated successfully.

How to cite this article: Queffelec, J., Allison, J.D., Slippers, B. & Greeff, J.M. (2025) Determinants of mating success in a lek-mating species. *Agricultural and Forest Entomology*, 27(4), 643–652. Available from: <https://doi.org/10.1111/afe.12692>