

Could different environmental conditions select for different flight characteristics in sexual and asexual parasitoid *Venturia canescens*?

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Abstract

In the parasitoid *Venturia canescens* Gravenhorst (Hymenoptera: Ichneumonidae), asexual and sexual wasps coexist in the field in the Mediterranean basin, but only the asexual strain is present indoors. The sexual strain dominates outdoors despite the demographic costs associated with the production of males and mate location. The present study tests whether females of the sexual and asexual strains of *V. canescens* differ in flight characteristics in line with the differences of their preferred habitats and enquires whether these differences might contribute to the persistence of sexually reproducing individuals in the vicinity of asexual counterparts. The results show that sexual female wasps are smaller than their asexual counterparts. The size of wasps has a strong influence on flight parameters, with larger animals generally being better fliers. In wasps of approximately the same size, sexual wasps fly faster than their asexual counterparts under experimental laboratory conditions, in terms of both the average speed over the observation period as well as the longest single flight. Sexual wasps also perform fewer flights to cover the same distance. Sexual wasps have higher wing loading than asexual ones of the same size, which could have contributed to the observed differences in speed between individuals of both reproductive modes. There are no significant differences between the two reproductive modes in the parameters related to the distance traversed or the time spent in flight. This study shows clear differences in the flight behaviour of sexual and asexual *V. canescens*. Together with previous results, this finding suggests differential adaptations to their preferred habitats. These differences might ease the competition between modes of reproduction through niche and habitat differentiation and might help to explain their coexistence on a geographical scale.

Introduction

The maintenance of sexual reproduction is perceived as a major paradox in evolutionary biology. Males only indirectly contribute to the next generation. As a consequence, demographically, when compared with asexual reproduction, sexual reproduction has a competitive disadvantage [the ‘two-fold cost of sex’ for animals with equal sex ratios (Maynard Smith, 1978)]. In spite of this, sexual reproduction predominates in nature. It has been suggested that

sexual reproduction accelerates the rate of evolutionary changes (Müller, 1932; Crow & Kimura, 1965) and that by recombination it prevents the accumulation of deleterious mutations (Müller, 1964; Haccou & Schneider, 2004). However, these long-term arguments cannot account for the coexistence of sexually and asexually reproducing competitors observed in some systems (Semlitsch et al., 1997; Belshaw et al., 1999; Beukeboom et al., 1999; Simon et al., 2002; Belshaw & Quicke, 2003). This calls for short-term explanations for the compensation of the cost of producing males (Williams, 1975).

In the Mediterranean basin, the parasitoid *Venturia canescens* Gravenhorst (Hymenoptera: Ichneumonidae) offers an opportunity to assess the respective costs and

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benefits of sexual reproduction. The parasitoid has two strains with different modes of reproduction: asexual reproduction (obligate thelytoky) not induced by *Wolbachia* bacteria (Beukeboom & Pijnacker, 2000) and sexual reproduction by obligate arrhenotoky (the haplo-diploid reproduction common to Hymenoptera). Both strains forage for the same resources under natural conditions (Beukeboom et al., 1999; Schneider et al., 2002; Amat, 2004). Whilst the sexual strain largely predominates in nature (Schneider et al., 2002; Amat, 2004), only the asexual strain develops in indoor environments (mills and stores). In nature, both strains of *V. canescens* attack larvae of various pyralid moths (Lepidoptera: Pyralidae) in desiccated fruits (Salt, 1976). Host larvae are normally sparse and homogeneously distributed, and generally one fruit harbours only one or two such larvae (Driessen & Bernstein, 1999). Indoors, asexual *V. canescens* attacks host larvae feeding on or near the surface of stored products (Ahmad, 1936; Waage, 1979). In mills and stores, host populations may reach high densities (Bowditch & Madden, 1996); therefore, the reproductive success of parasitoids would depend more on oviposition capacity than on frequent dispersal.

In *V. canescens*, flight is often associated with food and host searching (Desouhant et al., 2003, 2005) as well as, in the case of sexual strains, with mating (Metzger, 2010). Biochemical analyses have shown that *V. canescens* in the field frequently consumes food (Casas et al., 2003) and maintains fairly constant metabolic reserves. This suggests that *V. canescens* moves frequently in search of food resources and oviposition sites. Anthropogenic environments, such as mills and stores, are most often free of sugar-based food resources. It is conceivable that when their energy reserves decline, thelytokous *V. canescens* are forced to perform long flights in search of metabolic resources whenever food sources are scarce in the near surroundings of mills and stores.

The differences between their preferred environments lead to the hypothesis that sexual and asexual strains of *V. canescens* might have evolved different flight characteristics. To cope with their environments, individuals of the sexual strain should be more frequent and faster fliers (being more frequently exposed to the risks that this entails), and their flying behaviour would be less dependent on their physiological state (e.g., age). Asexual individuals would be expected to initiate flight less frequently and to perform longer flights at lower metabolic reserves. Abundant literature suggests that trade-offs between different life-history traits (competition, dispersal, extinction, etc.) and different forms of spatial heterogeneity (Neuhauser, 1998) can broaden the conditions for the coexistence of competitors (Levins & Culver, 1971; Hastings,

1980; Tilman, 1994; Amarasekare, 2003). Flight capacity is known to be normally affected by wing loading (body mass per wing area) and wing-beat frequency (Barker & Krebs, 1995). A low wing loading is associated with a superior flying ability (Wainright, 1994) and is thought to do so because flight becomes more energetically efficient with decreasing wing loading (Angelo & Slansky, 1984). In this context, knowledge of the flight behaviour of females from the sexual and asexual strains of *V. canescens* can aid the understanding of the process that makes the co-occurrence of both modes of reproduction possible under field conditions.

To test the flight capacity of contrasting groups of the same insect species, computer-linked flight mills were used, as they provide quantification of different flight parameters such as distance, duration, and velocity. Laboratory flight proved to be a successful model system for providing comparative data (Dorn et al., 1999; Hughes & Dorn, 2002), and several studies report a strong correlation between activity patterns in the laboratory and in the field (Keil et al., 2001). Here we test whether the sexual and asexual strains of *V. canescens* differ in their flight characteristics in line with the differences of their preferred habitats and to enquire whether these differences might contribute to the persistence of sexually reproducing strains in the vicinity of their asexual counterparts, either directly by easing competition or indirectly through niche separation.

Materials and methods

Biological details and cultures

The sexual and asexual strains originated from a laboratory culture founded with wasps collected near Valence, in south-east France (44°58'57"N, 4°58'16"E) in 2004. Wasps of both strains were reared on fourth and fifth instars of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) at 25 °C, 70 ± 5% r.h., and L12:D12 for two generations prior to the experiments. The host larvae were reared on semolina in climatic chambers and were maintained in a constant environment of 25 ± 1 °C, 70 ± 5% r.h., and L16:D8. Cultures were kept separately in clear plastic boxes (16 × 14 × 7 cm) containing 200–250 g of semolina in paper sentinels with 250–300 host eggs. This set-up allowed host larvae to develop with excess food throughout the larval stage. The paper sentinels were transferred individually to plastic rearing boxes (30 × 30 × 30 cm) before the expected time of wasp emergence. Wasps were collected daily at emergence between 16:00 and 20:00 hours (GMT + 1) and kept individually in plastic vials (3 × 9 cm). All wasps were supplied ad libitum with a 50% (vol/vol)

honey–water solution. To standardise mating status, each sexual female was kept in vial with two males for 24 h. After this period, the males were removed.

Flight-testing technique

The flight mill, consisting of 30 individual units, was established in a climate chamber maintained at 25 °C, 60% r.h., and L16:D8 photoperiod. The flight activity of wasps was monitored over a 23-h period. Detailed descriptions of the apparatus can be found in Schumacher et al. (1997), Hughes & Dorn (2002), and Hughes et al. (2004).

Each female wasp was anaesthetised for 30 s with CO₂. Then, an insect pin was tethered to the dorsal side of the thorax using a quick-drying solvent-free glue (Cyanolit; 3M AG, Rüşchlikon, Switzerland). The experiments started 3 h after exposing the wasps to CO₂. The pin to which the wasp was secured was pushed perpendicularly through a flight arm. The distance between the axis and wasp attaching point was 10 cm, resulting in a 62.8-cm revolution circumference. The sequence of revolutions was interpreted in terms of single flights and breaks. Following Hughes & Dorn (2002), a break was defined as a period longer than 3 s without a revolution and a single flight was defined as the period between two breaks. The duration, distance, and velocity of each flight were calculated. Thus, the overall flight performance was characterised by nine parameters: total distance flown (TD), total time flown (TT), longest single flight distance (LSFm), longest single flight time (LSFs), mean flight velocity (Vel), velocity of the longest single flight (LSFv), mean distance flown (MD), mean time per flight (MT), and total number of flights (TNOF).

Experimental design

To examine the age-dependent differences in flight patterns between the two strains, females of different ages (48, 96, 144, 192, 240, and 288 h since adult eclosion) were compared for each strain in a factorial design. *Venturia canescens* feeds frequently under field conditions to maintain a fairly constant level of carbohydrate reserves (Casas et al., 2003; Lucchetta, 2007). As wasps cannot feed on the experimental flight mill, to maintain conditions as naturally as possible, the analysis of flight parameters of both strains was restricted to the first 3 h of observation. Longer flight periods might have reflected the effect of depletion in metabolic reserves, which is likely to differ between the reproductive modes (Pelosse et al., 2007).

A total of 293 wasps were initially tested, but only 202 (118 asexual and 84 sexual) were included in the final analysis because the others had died before the end of the test. They were excluded from the analysis as it was not possible

to assess whether they had died from exhaustion or mishandling while setting-up the test.

Assessment of wasp size

The body size of wasps was assessed by measuring the length of the left hind tibia (Bernstein et al., 2002). Digital images of the detached tibias of all wasps were taken from a frontal view under an Olympus stereomicroscope SZX12 (Olympus C&S, Praha, Czech Republic) with the digital camera Olympus 5050Z (Olympus C&S). The length of individual tibias (in millimetre) from digital images was assessed using the image analysis software SigmaScan Pro 5 (SPSS, 1999).

To preserve the original set of experimental animals for future histological analysis, a complementary set of 50 sexual and 50 asexual *V. canescens* wasps originating from the same strains as used in the flight experiment was used to estimate the wing loading. Adults of less than 12 h after eclosion (without access to food) were anaesthetised for 30 s with CO₂, and weighed to the nearest 0.001 mg on electronic laboratory scales (Mettler AE 240-S; Mettler Instrumente AG, Zürich, Switzerland). A similar digital image analysing technique as that described above was used to quantify the wasps' left forewing and hind-wing surfaces (in mm²). Multiplying by two, the total wing area of each animal was obtained. The length of the left hind tibia was assessed as described above. To facilitate the graphical representation of the results, all of the figures showing the dependence of flight parameters on the size of animals were drawn at their natural logarithmic scales per millimetre of tibia length.

Statistical analysis

The tibia length of wasps from the two strains of *V. canescens* was compared with a two-sample t-test. Analyses for the influence of wasp age (Age), hind tibia length (Size), and the mode of reproduction (Strain) on different flight parameters (see Table 1) were conducted using linear models assuming a normal distribution of residuals (R freeware statistical package; R Development Core Team R, 2007). The data were first fitted to an initial model, and then least significant variables were progressively removed from the model until obtaining a minimal appropriate model (i.e., a simplified model in which all terms are significant). Single factors or variables incorporated into the significant interaction were maintained in the minimum adequate model (Crawley, 1993). The initial model fitted to the data was $\ln[\text{Flight parameter}] = [\text{Strain}] * \ln[\text{Size}] + [\text{Strain}] * [\text{Age}] + [\text{Strain}] * [\text{Age}]^2$, where * represents the sum of the influences of one two-way interaction and the two single variables. The $[\text{Age}]^2$ term accounted for the possible non-linearities in the influence of

Table 1 Parameter estimates and levels of significance for the minimum appropriate linear models fitted to assess the influence of various features of the females on the flight parameters of *Venturia canescens*

	TD	TT	LSFm	LSFs	Vel	LSFv	MD	MT	TNOF
Intercept	-0.366 ns	1.832*	-1.269 ns	-0.358 ns	-1.563***	-1.734***	-0.669 ns	0.797 ns	2.110**
Strain (S)					0.0492**	0.0591*			-0.3751*
Age	1.848×10^{-2} *	1.85×10^{-2} **	2.360×10^{-2} ***	2.412×10^{-2} ***		3.37×10^{-4} **	1.234×10^{-2} *	1.236×10^{-2} *	
ln[Size]	6.796***	6.408***	6.311***	5.549***	0.488***	0.8683***	3.317**	2.929*	2.811**
Age ²	-5.140×10^{-5} **	-5.115×10^{-5} **	-6.762×10^{-5} ***	-6.813×10^{-5} ***			-3.586×10^{-5} *	-3.56×10^{-5} *	

Strain: mode of reproduction [Strain (S) denotes the effect of sexual reproduction when compared with asexual animals (Intercept)]; Age: Age²: a linear and a quadratic component of the age of the animal; ln[Size]: logarithm of the length of the left hind tibia. Flight parameters: TD, total distance flown in 3 h; TT, total time in flight in 3 h; LSFm and LSFs, distance traversed and time spent in the longest single flight, respectively; Vel, mean flight velocity; LSFv, velocity of the longest single flight; MD, mean distance per flight; MT, mean time per flight; TNOF, total number of flights. All dependent variables were ln-transformed. The interaction between independent variables did not have a significant effect in any case. ns, not significant, *P<0.05, **P<0.01, ***P<0.001.

post-emergence age. The examination of the residuals confirmed the fit to a normal distribution.

Results

The size of wasps (as estimated by the length of the hind tibia) had a strong influence on all of the flight parameters, with larger animals generally being better fliers (Table 1). Sexual *V. canescens* were significantly smaller than their asexual counterparts (Welch two-sample t-test: $t = 4.1$, d.f. = 200, $P < 0.00001$): the mean (\pm SE) left hind tibia lengths of the asexual and sexual *V. canescens* were $1.982 (\pm 0.012)$ and $1.897 (\pm 0.017)$ mm, respectively.

The age of wasps influenced the total distance flown, the total time in flight, the distance traversed in the longest single flight and the time invested in it, the velocity of the longest single flight, the mean distance per flight, and the corresponding time per flight (Table 1). The minimum adequate model for total distance flown in the first 3 h of *V. canescens* females per millimetre of tibia length, $[TD]/[Size]$, as the function of age (time since wasp emergence, h) was $\ln[TD]/[Size] = 4.131 + 2.040 \times 10^{-2} [Age] - 5.828 \times 10^{-5} [Age]^2$; $F_{2,198} = 6.11$, $P = 0.003$, adjusted $R^2 = 0.0486$. The total number of flights and the mean flight velocity were independent of age (Table 1; Figures 1 and 2). The flight parameter most clearly affected by the mode of reproduction was the mean flight velocity (Figure 2), for which sexual females flew faster than asexual ones of the same size. A similar result was obtained for the velocity of the longest single flight. The minimum adequate models for the longest single flight velocity performed in the first 3 h of *V. canescens* females per millimetre of left tibia length, $[LSFv]/[Size]$, as a function of age (time since wasp eclosion, h) was for asexual mode of reproduction $\ln[LSFv]/[Size] = -1.891 - 3.280 \times 10^{-4} [Age]$ and for sexual mode of reproduction $\ln[LSFv]/[Size] = -1.826 - 3.280 \times 10^{-4} [Age]$. Intercepts for both reproductive modes differed significantly ($F_{2,198} = 7.412$, $P < 0.001$, adjusted $R^2 = 0.0603$). Sexual females needed fewer flights to cover the same total distance (Table 1; Figure 1). As shown by Figure 3, wing loading was also strongly influenced by the mode of reproduction. For the same wasp size, sexual females had higher wing loading than asexual ones.

Discussion

This work shows that some flight parameters of *V. canescens* clearly depend on the mode of reproduction. Sexual wasps fly on average, as well as during the longest single flight, faster than their asexual counterparts of the same size and perform fewer flights to cover the same distance.

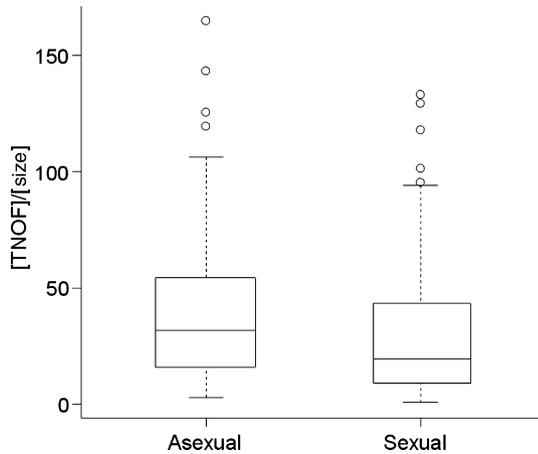


Figure 1 Comparison of the total number of flights performed in the first 3 h of *Venturia canescens* females flown per millimetre of tibia length, [TNOF]/[Size], between the two modes of reproduction. Box-plots showing the median, the 25 and 75 percentiles (box), 1.5 times the interquartile range of the data (horizontal lines), and individual outliers (open circles). Adjusted $R^2 = 0.0404$, $F_{1,199} = 9.428$, $P = 0.002$.

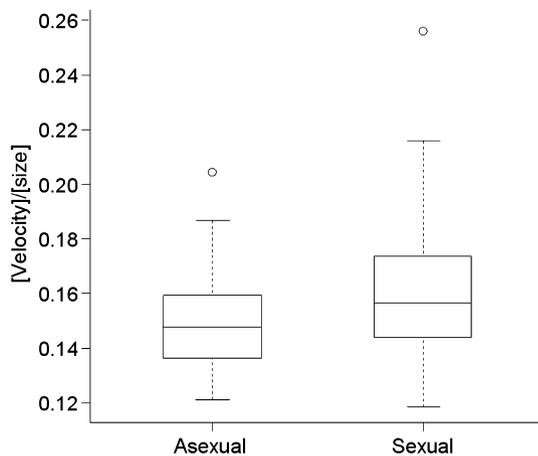


Figure 2 Comparison of the velocity performed in the first 3 h of *Venturia canescens* females flown per millimetre of tibia length, [Velocity]/[Size], between the two modes of reproduction. Box-plots showing the median, the 25 and 75 percentiles (box), 1.5 times the interquartile range of the data (horizontal lines), and individual outliers (open circles). Adjusted $R^2 = 0.0808$, $F_{1,199} = 18.58$, $P < 0.001$.

In contrast, there are no significant differences between reproductive modes in the parameters related to the distance traversed or the time spent in flight.

Based on the differences between their preferred environments, it had been hypothesised that arrhenotokous wasps would be more frequent and faster fliers and that

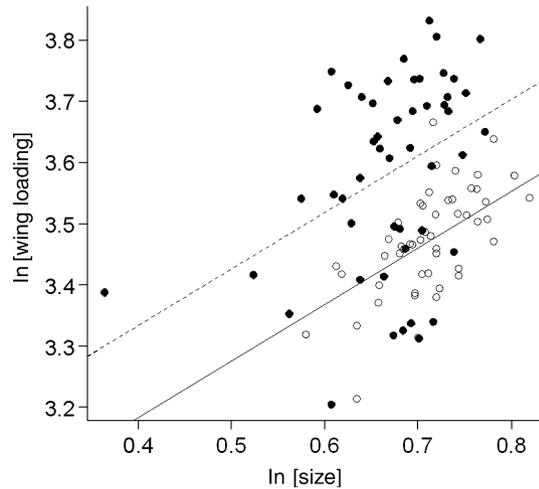


Figure 3 Line plot for the wing loading of *Venturia canescens* females as a function of the wasp's size (estimated by the hind tibia length). Lines correspond to the fitted minimum adequate model; the dots correspond to the actual data. Open circles and solid line (—○—) represent the asexual mode of reproduction (minimum adequate model: $\ln[\text{Wing loading}] = 2.8143 - 0.9237 \ln[\text{Size}]$); filled circles and dashed line (---●---) represent the sexual mode of reproduction (minimum adequate model: $\ln[\text{Wing loading}] = 2.9643 - 0.9237 \ln[\text{Size}]$). Intercepts for both reproductive modes differed significantly ($F_{2,97} = 23.08$, $P < 0.001$, adjusted $R^2 = 0.3085$).

their flying behaviour would be less dependent on physiological state (age). Differential flight behaviours between the sexual and asexual strains of *V. canescens* might enhance adaptation to their respectively preferred environments, alleviating competition between asexual and sexual reproduction, either directly or through niche differentiation, and thereby facilitating the coexistence of sexual and asexual sub-populations (Schneider et al., 2003). The present findings partially confirm these expectations, showing that sexual females initiated fewer flights than asexual individuals and that both strains are similarly influenced by age.

Our results show that asexual females were larger than their sexual counterparts and that size had a strong influence on the flight parameters, with larger individuals being better fliers. If differences in size are maintained under natural conditions, they could offset the advantages in flight of the sexual strain, thus compounding the problem of the coexistence of both strains. The actual size of adult *V. canescens* is known to depend on rearing conditions, host body mass, instar, and species (Harvey et al., 1994; Harvey & Thompson, 1995; Harvey, 1996; Harvey & Vet, 1997; Bernstein et al., 2002). Thus, the actual realisation under field conditions of the potential differences in flight efficiency of both modes of reproduction cannot be

elucidated without a specific reference to the host species attacked by each strain. *Venturia canescens* can develop, with varying degrees of success, from at least 14 host species (Salt, 1975). In this study, to standardise conditions, animals of both modes of reproduction were reared on the same strain of *E. kuehniella*, a common pest in granaries and flour mills, but not a common host of the sexual strain. The smaller size attained by sexual females might stem from the fact that they were not reared on one of their usual hosts. These qualifications do not negate that within the trade-off imposed by limiting resources, sexual wasps are better adapted to outdoor conditions and are (all else being equal) better fliers.

Earlier work has already shown differences between sexual and asexual *V. canescens* in line with what might be expected from their preferred environments. For instance, in a mark-release-recapture experiment, sexual females leave release points sooner than asexual ones (Amat, 2004). Experimental results reveal that during larval development, sexual *V. canescens* allocate more energy to metabolic reserves, particularly glycogen, than asexual ones, independent of resource availability during ontogeny (Pelosse et al., 2007). In Hymenoptera, glycogen is usually allocated to flight (Vogt et al., 2000; Harrison & Fewell, 2002) after decomposition in simple sugars (van der Horst, 2003). Other than size, differences in flight velocity between strains might be based on physiological differences. For instance, both strains could have different temperature optima for flight or different muscle performance under the same temperature. This could be translated into differences in wing-beat amplitude and frequency, leading to differences in velocity (Marden, 1995; Marden et al., 1997). Asexual *V. canescens* allocate more energy to egg production and tend to exploit host patches more thoroughly than sexual wasps (Pelosse et al., 2007). This is not unexpected. The lack of food sources in an indoor environment should select for animals that are able to realise a maximum fecundity in the short period of approximately 3 days. This is the time for which they have a basic energy budget at emergence (Casas et al., 2003). Extending this period demands that asexual wasps commute between habitats, leaving their indoor environment to renew their metabolic reserves and then returning (Beling, 1932). It is not known what distance could prevent parasitoids from commuting, with regards to the cost in terms of mortality risk and time and energy invested, but at least part of the escaping population disperses in nature (C Bernstein & J Lukáš, personal observation).

In nature, individuals of both strains of *V. canescens* explore wider environments, renew fuel for flight when necessary (Casas et al., 2003), and search for hosts that are scarce and homogeneously distributed. This calls for

higher flight efficiency from sexual wasps that live exclusively under field conditions. The fact that sexual *V. canescens* cover similar distances as asexual females in fewer flights, together with the fact that they are faster fliers, suggests that for the same size, the former are more efficient fliers. These facts should have been reflected in the mean distance or mean time per flight. The lack of significant evidence in this sense may be due to the high variability in the data.

No age*strain interaction relates to the observed flight performance factors. The age of the wasps has a non-linear effect (parameters initially increase and then decrease) on the total flight distance, the distance of the longest single flight, and the mean flight distance. The same effect is observed for the respective flight duration parameters. King (1993) observed a similar non-linear effect of age on total flight duration of *Nasonia vitripennis* (Walker), and other studies confirm this tendency for the flight performance of mosquitoes (Rowley & Graham, 1968; Nayar & Sauerman, 1973). Similarly, newly emerged adults of *Libellula pulchella* Drury spend less time flying and made longer-duration flights when compared with mature adults (Marden et al., 1996). These age-dependent changes related to flight distance could be explained by a trade-off with resource allocation. Willers et al. (1987) attributed a decline in flight performance of *Heliothis virescens* (Fabricius) to the onset of oviposition, which led to a loss of energy sources and a reduction of long flights by older mated females. In *V. canescens*, the velocity of the longest single flight decreases linearly with age and the overall velocity and the total number of flights are independent of age. This is in concordance with Marden et al. (2003), who reported that long-lived *Indy* mutations of *Drosophila melanogaster* Meigen show no significant difference in maximum flight velocity compared with normal-lived controls, although other monitored flight performance parameters are influenced by age. Moreover, a stable flight speed is maintained even under conditions of nutritive stress for this *Drosophila* mutation. A study of the energetic status influence on the flight parameters of both *V. canescens* strains might be a promising avenue for further research.

A trade-off between flight characteristics and life-history traits has been reported for *Cydia pomonella* L., based on selections for individuals with high and low mobility (Gu et al., 2006). Females of the less mobile strain are larger, and this strain has a greater net reproductive rate and a higher intrinsic rate of natural increase, hence a higher fitness (Gu et al., 2006). The present results show that the flight parameters of *V. canescens* are also significantly influenced by body size, but, in this study, larger insects

are generally better fliers. Although size directly affects metabolic reserves, the relationship between size and flight capacity might be affected by different parameters, as indicated by diverging findings. For instance, smaller individuals of *D. buzzatii* Patterson & Wheeler fly significantly longer than larger ones (Gu & Barker, 1995), whereas major differences in the size of *Cactoblastis cactorum* (Berg) do not significantly influence the distance traversed (Sarvary et al., 2008). The present study with *V. canescens* documents that sexual females (the faster fliers) had higher wing loading than asexual ones of the same size. For fundamental aerodynamic reasons (Alerstam et al., 2007; Dudley et al., 2007), flight speed among animals is expected to increase with wing loading. This expected relationship is often observed in different insect groups (Fischer & Kutsch, 2000; Dudley & Srygley, 1994; Oberdörster & Grant, 2007). Consequently, wing loading may account, at least partially, for the observed differences in speed between individuals of both reproductive modes.

The present study shows clear differences in the flight behaviour of sexual and asexual *V. canescens*. This finding, together with previous studies (Amat, 2004; Amat et al., 2006, 2009; Lucchetta et al., 2007; Pelosse et al., 2010), suggests differential adaptations to their preferred habitats. These differences might ease the competition between modes of reproduction through niche and habitat differentiation and might contribute to explaining their coexistence on a geographical scale.

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