Flight variability in the woodwasp *Sirex noctilio* (Hymenoptera: Siricidae): an analysis of flight data using wavelets

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SUMMARY

We describe flight variability in the woodwasp *Sirex noctilio* Fabricius, 1793 (Hymenoptera: Siricidae) by studying tethered females in a flight mill device and analyzing output data by a time series methodology. Twenty-eight wasps were flown during 24 h-long periods, under controlled temperature and lighting conditions. The maximum distance recorded was 49 km, and mean velocity was 0.37 m s^{-1}. All wasps lost weight during flight (mean weight loss of 10.0% of initial body mass). By using a wavelets analysis on the flight mill time series output, we identified three distinct flight patterns: regular (long acceleration–deceleration spells), periodic (alternation of acceleration–deceleration spells without resting) and pulsating (resting spells interrupted by bursts of flight activity). The first two flight patterns are indistinguishable using traditional flight mill data analysis. Flight patterns for each individual were significantly dependent on wasp body mass, suggesting a relationship with the resources used in flight and their availability. Large females flew sequentially through a regular-periodic-pulsating sequence but medium sized wasps flew mostly with periodic and pulsating patterns. The smallest wasps flew only in a pulsating pattern, being incapable of long, sustained flight. Variability in size and behavior can have significant consequences on population dynamics by determining local and regional dispersal. An important outcome of our work is the introduction of wavelet analysis to study tethered flight data series for the first time. This methodology allowed us to uncover and statistically test individual variability in insect flight characteristics.

Key words: insect flight, flight mill, insect dispersal, time series.

INTRODUCTION

In insect ecological and behavioral studies, a recurrent question concerns flight capacity. How far an insect can fly is important to explain individual dispersal and the spatial structure of populations. Dispersal strongly influences population dynamics in meta-populations (Hanski and Gilpin, 1997) and can determine the survival of a population during environmental changes (Watt et al., 1997) and play an important role in species interactions (Commins et al., 1992). In systems where insects become pests, dispersal capabilities can determine the rate of invasion into new patches (Liebhold et al., 1995; Lavandero et al., 2004). Most of these parameters can be analyzed using flight mills.

Although flight mill experiments are common in insect dispersal studies, data analyses have focused mostly on the main characteristic of flight. Typically, total distance traveled, total flight duration, and average flight speed are measured (e.g. Weber and Ferro, 1996; Vogt et al., 2000; Yamanaka et al., 2001; Luo et al., 2002). Occasionally, other characteristics related to the continuity of the flight, such as the extension of continuous flight, or flight interruptions, the length of pulses or pauses between successive flights have also been quantified (Shirai and Kosugi, 2000; Ishiguri and Shirai, 2004; MacQuarrie and Boitau, 2003; Blackmer et al., 2004; Wanner et al., 2006). However, because the insects are forced to fly in a flight mill as a result of permanent stimulation by lack of tarsal contact (Edwards, 2006), classical analysis of flight mill data tend to overestimate the flight distance and the total flight time by a factor of ten or more, compared with other laboratory studies such as those

carried out in flight chambers (Shirai and Kosugi, 2000; Yamanaka et al., 2001; Blackmer et al., 2004) or field methods such as mark–release–recapture (Botero-Garces and Isaacs, 2004). To our knowledge, a detailed exploration of the complete data set obtained from tethered flight studies using some modern time series analyses has never been performed.

Wavelets analysis is a time series analysis method commonly applied in mathematics, physics, engineering, and more recently in signal analysis and data compression (Graps, 1995; Torrence and Compo, 1998). In biological studies, wavelets have been used to analyze data series in physiology [e.g. the analysis of chrono-biological signals (Chan et al., 2000)], and for the analysis of spatio-temporal series in ecological work (Keitt and Urban, 2005; Perry et al., 2002). Although other simpler time series analysis (such as autocorrelation or Fourier analysis) would be useful to analyze flight mill data, wavelets are particularly appropriate do describe changes in the series frequency composition (to describe changing periods) and to find discontinuities, as may commonly occur in insect flight behavior.

The method involves approximating a given function $f(x)$, as a linear combination of different expressions $[g_i(x)]$ of a simple function used as a template $g(x)$ (the mother wavelet), so that $f'(x)=\Sigma[c_ig_i(x)]$, where $f'(x)$, which is the approximation of $f(x)$, and c_i are coefficients estimated by the method. The functions $g_i(x)$ are obtained by shifting and rescaling the same mother wavelet. In contrast to standard Fourier analysis, the mother wavelet is not a sinusoidal function (Pinsky, 2001). To rescale and shift the function

g, *f* is divided into its different frequency components, and thus a *wavelet transformation* is obtained (namely the representation of *f* in terms of **g**). Because it allows time–frequency simultaneous representations, wavelet analysis is the best-suited method for multi-resolution analysis, and is superior to Fourier for analysis of functions that present discontinuities (Graps, 1995; Chan et al., 2000). Although the windowed Fourier transformation (WFT), could also allow a time–frequency representation of the data, the main advantage of wavelets over WFT, is the ability to perform multi-scale analysis [i.e. from the Nyquist frequency to 1/2 of the length of the series, whereas WFT is limited by the size of the window (Pinsky, 2001)].

The outcome of a wavelet analysis (the wavelet transformation) is represented as three dimensional or contour plots. The time domain is represented in the *x* axis, the position in the *y* axis is a function of the period of $f'(x)$ (i.e. higher *y* indicates a lower frequency), and the *z* axis represents the fit of $g_i(x)$ [i.e. the fraction of the variance of *f* explained by $c_i g_i(x)$, or the wavelet coefficient].

In our case, the position in the *y* axis is thus a function of the duration of periods of acceleration and deceleration, and the *x* axis is time since the first lap of the insect in the flight mill. Since the wavelet coefficients represent the fit of the transformation at different frequencies, they characterize the flight behavior in terms of the dominant frequencies. For example, if in an observation lasting for 2h, in the first hour the animal flies in periods of acceleration and deceleration of 10s, and of 20s in the second hour, using wavelets we would obtain a plot with higher coefficients at *y*=10, in the first hour, and at *y*=20, in the second.

Our case-study was the adult woodwasp, *Sirex noctilio* Fabricius 1793 (Hymenoptera, Siricidae), which is a phytophagous insect that attacks conifers. Native to Eurasia, *S. noctilio* has recently invaded several regions of the world such as Australasia, South America, South Africa and North America (Hurley et al., 2007). In most invaded areas, it has become one of the most economically significant pests of softwood forests (Madden, 1988). Adult *S. noctilio* wasps are short lived and do not feed. Females lay eggs within tree cambium during the summer and larvae develop later in the year, drilling galleries and feeding on decomposed wood and hyphae of the symbiotic fungus *Amylostereum areolatum* (Coutts, 1969).

In the case of *S. noctilio*, information on flight characteristics has important applied implications. Local and regional distribution as well as the ability to invade new forests is strongly tied to female flight capacity. In turn, the spatial consequences of dispersal may relate closely to the observed population dynamics (Berryman, 1987; Corley et al., 2007). At a local scale, healthy pine trees can resist only a limited number of attacks by *S. noctilio*, and so limited dispersal may lead to aggregated attacks that could overwhelm initially healthy trees. Finally, biological control of this pest, largely based on the sterilizing parasitic nematode *Beddingia siricidicola* (Bedding, 1972), rely on female-host, and therefore parasite, dispersal within treated forests.

In this work, we describe the flight of the *S. noctilio* females in laboratory conditions. We studied, by means of a flight mill device, standard flight characteristics such as speed, distance covered and total flight time during 24h-long assays. In addition, we used wavelets analysis to explore the data series in detail, looking for recurrent changes in frequency composition and for possible discontinuities indicating different flight patterns.

MATERIALS AND METHODS
Insect rearing and preparation
We used recently emerged (24–48h) female *S. noctilio* wasps, obtained from 1m long billets of naturally infested *Pinus contorta* var. latifolia trees, which we collected from plantations located in North Western Patagonia, Argentina.

The flight mills
To study *S. noctilio* flight, we used a set of two flight mills, based on the model of Schumacher et al. (Schumacher et al., 1997). A vertical steel needle in the center of this structure, supported by the magnetic field generated by two cylindrical neodimian magnets acted as an axle, to which a short, light wooden horizontal rod was attached. Wasps were then attached to one end of the balanced wooden rod with an entomological pin. The wasp was attached at 6cm from the axis, resulting in a rotational length of 127.3cm (Fig.1).

Each mill was mounted within a hardwood, square box with a transparent Perspex roof, to minimize external odors and air fluxes while allowing overhead light in. Overhead lighting was provided by a 40W fluorescent lamp, set for a 16h:8h L:D light regime.

The rotation of the mills was detected by infrared optical sensors connected through a circuit to the parallel port of a microcomputer. Data were collected by the use of a specific Python script. Each rotation was recorded once, each time the beam of light generated by a LED was interrupted by the end of
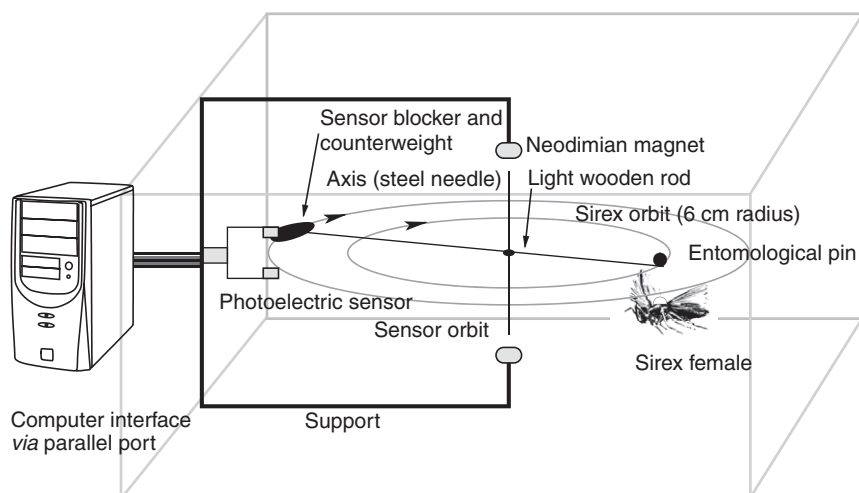
Fig. 1. Scheme of the flight mill used for this study.

Computer interface *via* parallel port

the wooden rod opposite to the one where the insect was held. For each flight mill, the program recorded every rotation, and then calculated flight speed (in $m s^{-1}$), accumulated flight distance (m) and total flight time (s).

Because in the population studied, *S. noctilio* mass was strongly correlated with all the other measures of size (J.M.V., unpublished data), we used the wasp mass as the estimator of body size. We weighed all wasps (Scientech Inc., 5649 Arapahoe Avenue, Boulder, CO, USA; s.d.: 0.1 mg) and placed them individually inside an air-tight Perspex box. Wasps were CO_2 anesthetized for 5 min before fixing an entomological pin to the back of the thorax, and they were left to recover for 1 h before experiments. Because *S. noctilio* wasps are unusually large and robust insects, a reliable attachment of the pin to the thorax was needed. We did so by sticking a plastic bead to the head of a pin with a two component epoxy adhesive to increase its surface area and once dried, we attached the newly headed pin to a wasp, using cyanoacrylate glue.

The wasps flew in the mills for 20 h, and weighted again after the experiment. The time between the two weight measurements was fixed at 24 h.

Wavelet analysis and flight classification
Wavelet selection
To analyze our data, we chose the discrete stationary wavelet transformation, and following Torrence and Compo (Torrence and Compo, 1998), we adopted as a mother function the 4 waveform, from Daubechies (Daubechies, 1988). This waveform best fits the shape of the oscillations in sections of the data series where it could be observed. Other waveforms [Haar (square waveform), Coiflet (symmetric) and Daubechies] with moments higher than 4, were also tested in preliminary analyses. The main criterion was the sensitivity of the analysis to reveal changes in the frequency composition of the series. Both Haar and Coiflet had less sensitivity than the Daubechies, whereas other Daubechies waveforms up to 10 moments, showed the same results as the 4 moment waveform. Thus, we chose that simplest waveform.

The standardized wavelets coefficients were tested for significance with the χ^2-test, with two degrees of freedom and a $P < 0.05$ criterion, against the null hypothesis of white noise (see Torrence and Compo, 1998). Before the wavelet analysis, the data series that consisted of series of irregularly separated events (the recorded times in which the wasp activated the sensor), was first re-sampled to a series of speed data uniformly separated by 1 s, which was then the resolution of the study (and the resolution for the frequency analysis, the Nyquist frequency was 0.5 Hz or the 2 s long period). After re-sampling the series was de-trended using the residuals of a linear regression of speed as a function of time. The wavelet analysis and data processing were performed using a Python script, with the pywavelet module for discrete wavelet transform (v. 0.1.2; http://www.pybytes.com/pywavelets).

Because the data analysis was mostly exploratory, and we did not have *a priori* knowledge of which kind of pattern we were liable to find, we performed the data analysis in two steps. Firstly, we analyzed the series in search of characteristic patterns in the flight displayed by all the wasps. Secondly, according to the patterns found, we classified individuals in different categories. This classification was based on both the main frequencies of periods of acceleration–deceleration and discontinuities in the series.

We performed two one-way ANOVAs with *a posteriori* Tukey contrasts to test for differences in mass, and mass loss between wasps that performed different flight patterns. Also, we tested the relationship between the initial mass and a proportion of mass lost,

using a Pearson correlation coefficient. ANOVA, contrasts and correlations were calculated using the R statistical environment (R Development Core Team, 2006).

RESULTS
General flight parameters
The flight parameters of *S. noctilio* were highly variable between individuals, with only three of 29 females being able of performing long flights of more than 30 km. The average distance flown by a wasp during the 1 day-long trial was 17395.8±14241.9 m (mean ± s.d.) with a maximum of 49731.5 m (mean ± s.d.) and a minimum of 1081.2 m. The average speed for all wasps was $0.37\pm0.39\,m s^{-1}$ (mean ± s.d.); however, most of the time individuals remained at rest, and during flight, speed was highly variable (Table A1, Appendix).

Wavelets analysis
Frequency composition
Contrary to the general flight parameters, the spectral composition of *S. noctilio* flights, were less variable. All the individuals showed a significant periodical pattern at some point of their flight. Periods varied from 4 s to nearly 40 min (2^2 to 2^{11} s), with a peak of significance for the flights of approximately 20 min span (2^{10} s), which was the dominant period in all females studied. Whenever the wavelets plot showed the presence of significant periods, these always shorter to begin with and then slowly got longer. We called the time interval during which the period gets longer as the elongation of flight period (EFP). Under sustained flight conditions, at some moment EFP is interrupted by an abrupt change towards a shorter period, after which EFP restarts (Fig. 2). That pattern was clearer in longer than in shorter flights, perhaps because the flight was too short in the latter, to fully develop that pattern. However, at the beginning of flight, some females showed a flight pattern without any periodical pattern.

Classification of flights
The flights were classified according to the scheme displayed in the Fig. 2, into three categories, regular, periodical and pulsating. Fig. 2 shows three distinct examples of flight patterns, which were displayed recurrently by groups of individuals (shown schematically in Fig. 2). To describe these patterns, we divided the frequency domain (y axis) into four different sections (of different period, from longer to shorter) as follows: acceleration–slowdown (deceleration) at the beginning of the flight (AS; lasting longer than 1 h), inter-flight periods (IE; longer than 30 min), intra-flight periods (IA; periodic variation of speed without resting, with a period between 4 s and 30 min), and noise (NO; less than 4 s). AS and IE shared the same frequency domain. However, whereas AS occurred during the insect flight, IE was registered when the studied insect remained at rest. According to the presence of significant wavelet coefficients in a combination of areas of the y axis, we divided the time domain (x axis), into three different patterns of flight: regular, periodic and pulsating, as shown in Fig. 2.

The higher frequencies corresponded to periods of less than 4 s. The patterns at this scale were difficult to differentiate from noise (since the series was re-sampled to a 1 s frequency in order to perform the wavelets analysis, the limit of the resolution of this study was too close) and they were ignored in the analysis.

The regular flight pattern was characterized by the presence of significant coefficients only in the acceleration–slowdown domain, representing a single, long sustained flight with a changing (but slowing) speed, with slight acceleration only at the beginning of
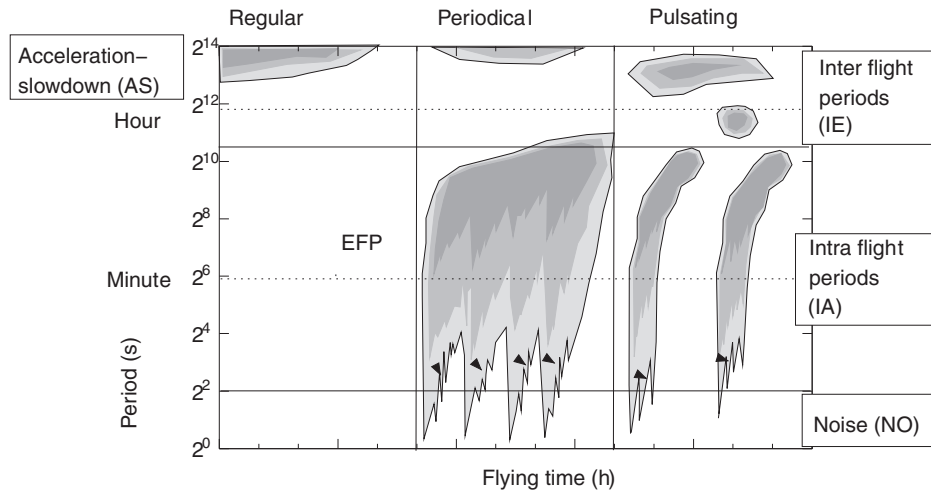
Fig. 2. Schematic representation of the criteria used to classify the *S. noctilio* flight using the wavelets power spectrum. Shading indicates the value of the positive wavelets coefficient (darker is higher). The three types of flight were classified as follows: the frequency domain was divided into four different areas, acceleration–slowdown (AS), inter and intra flights (IE and IA, respectively), and noise (NO). The grey areas represent the expected significant wavelets coefficients for each kind of flight. The upper area of the graph is shared between the AS and IE, the difference is that AS corresponds to a single period slow change in the average speed at the beginning of the flight, whereas IE is the period between different flight pulses. The higher frequencies (bottom of the figure) correspond to periods of less than 4 s, which here were considered as noise. The arrows indicate the presence and location of elongation of flight period (EFP).

flight, and a steady slowdown after reaching the maximum flight speed (Fig. 3A; Re sector).

Periodical flight in its turn, was characterized by significant coefficients both in the AS and in the IA areas. This implies a long, sustained flight without resting, but with a periodically variable speed. Flight span between two consecutive pauses was longer than an hour (Fig. 3A,B; Pe sector). Several consecutive periods of EFP were observed in most of the periodical flights.

Finally, pulsating flight had significant coefficients in the inter- and intra-flight areas, a pattern that may be interpreted as a representing a flight pattern composed of short pulses of flights (spans shorter than 1 h), followed by longer pauses (Fig. 3A–C; Pu sector). In most of the flight pulses a single EFP period was observed. In individuals that only performed this type of flight, the EFP pattern was less clear.

Classification of individuals

Individuals that performed regular flights were classified as regular fliers (Re), whereas the wasps that performed periodical flights were periodical fliers (Pe) and those that performed only pulsating flights, were classified as pulsating fliers (Pu).

Among 28 *S. noctilio* females flown, five wasps were classified as Re, 13 as Pe and 10 as Pu. In those cases where regular fliers also displayed another type of flight, the regular type was performed always first, and encompassed more than 40% of the total flight time. Finally, all Pe also showed a pulsating pattern towards the end of the flight assay.

The flight pattern displayed by female *S. noctilio* wasps was strongly dependent on the mass of the individuals before trials. The Re were significantly heavier than the rest (4887±121 mg; mean ± s.d.) and Pe were heavier than Pu (2796±111 mg and 1624±53 mg, respectively). Re wasps also flew much faster and longer distances than Pe, whereas Pe flew faster and longer distances than those classified as Pu (Table 1).

Even though the proportion of mass loss was significantly correlated with initial wasp mass ($r=0.421$, $N=28$, $P=0.032$), we found no differences in mass losses between the three groups (Re

11.21±12.11%, Pe 11.83±46.53%, Pu 7.08±39.61%; ANOVA $F=1.66$, $P=0.21$).

DISCUSSION

Our results show that *S. noctilio* woodwasps have a variable flight behavior, which relates to initial body mass. Woodwasps of different sizes, not only differ in the total distance flown, speed (maximum and average) and length of individual flight, but probably more importantly in the flight pattern, in terms of frequency composition as revealed by the wavelets transformations. Heavier females were capable of longer and faster flights than lighter individuals that displayed only periodical or pulsating flight patterns, the latter including long pauses and variable speeds. By contrast, independent of body mass, and flight speed, during the same kind of flight, the frequency composition was the same across all the individuals.

Total distance flown by woodwasp females in the flight mills ranged between a minimum of 1 to a maximum of 50 km. In turn, recent field studies suggest that *S. noctilio* dispersal within a forest is very limited, less than 150 m (Corley et al., 2007). However, the comparison between field data and standard flight parameters obtained from basic flight mill data should be carried out with caution. Our results also show that heavier individuals flew longer distances than the smaller ones. These flight differences closely relate to the type of flight displayed and in consequence to wasp dispersal potential.

It is known that for animals in general, reproductive and locomotion potential strongly depend on body mass. The association between individual size and dispersal is mediated by complex hormonal interactions as observed in several mammals and birds (Dufty and Belthoff, 2001). In insects, while hormonal regulation influences dispersal and reproduction, body size may be a key factor determining the proportion of teneral resources (those with which the individual is born or emerges) assigned either to offspring production or to movement (Jervis and Ferns, 2004). For many species such as *S. noctilio*, whose adults do not feed, body-fat reserves will relate directly to body mass.
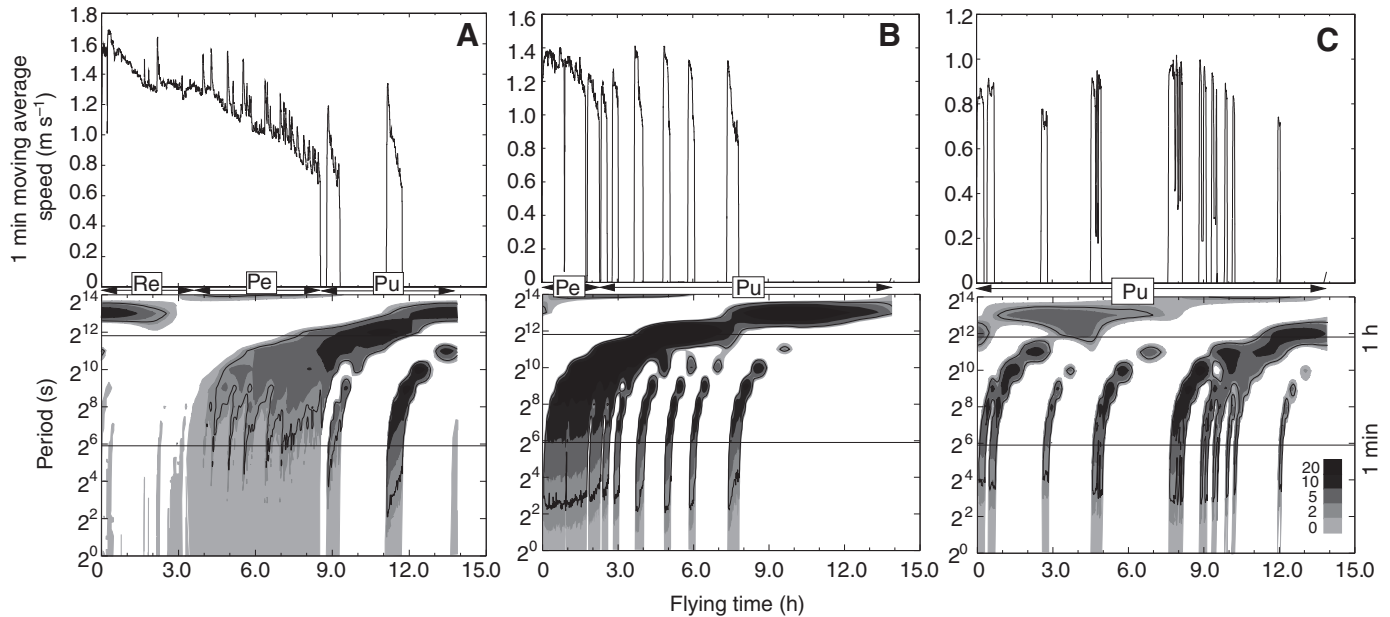
Fig. 3. First 50,000 s (13 h 53 min) of flight recorded for typical *S. noctilio* females, according to the flight patterns established using the wavelets transformation of flight mill data series: (A) a regular flier, (B) a periodic flier and (C) a pulsating flier. For the sake of clarity, instead of the raw data, the upper plots in each part show the 1 min moving average speed as a function of time, and the lower plots show the wavelets power spectrum. Shading indicates the value of the positive wavelets (darker is higher) coefficient where the black contour line is the upper limit of the confidence interval (*P*=0.05), corresponding to a coefficient value of 2.9997. Shaded areas within the black contour lines indicate significant wavelet transform. The arrows below the plots indicate the time during which each flight pattern was performed: regular (Re), periodic (Pe) and pulsating (Pu). To help interpret the length of periods (which are in a logarithmic scale on the *y*-axis), lines indicating 1 min- and 1 h-long periods are plotted.

Based in the flight variability we suggest that the relation body mass–distance flown for *S. noctilio* may not be a continuous variable, in which the larger individuals fly longer distance than smaller ones following some relation (for example, lineal or quadratic). For instance, it may occur that Pe and Pu are incapable of any kind on uninterrupted long-distance flights in the field. Thus, the pattern found by Corley et al. (Corley et al., 2007), might be a consequence of a local dispersal of individual Pe and Pu, whereas Re may disperse over larger spatial scales.

Madden (Madden, 1974) showed that trees vary widely in their suitability for *A. areolatum* and hence for *S. noctilio* larval development. Suitable trees are detected by female wasps at a distance, following chemical cues (Coutts, 1969). Long sustained flights in experimental conditions, might be akin to persistent hovering in search of these cues in natural conditions. The state-dependent changes in flight pattern might be explained by the fact that, for resource-limited animals, the best strategy should be to alight in a nearby tree and use the final resources for the oviposition activity.

Individual variations in dispersal capacity can have consequences on wasp population dynamics at different spatial scales. Regular fliers (the larger wasps) are probably responsible for *S. noctilio* dispersal on a regional scale. This is because such wasps are capable of sustained flights at an almost constant speed for several hours, suggesting that in the field, they could perform long distance flights, even over flying areas that lack suitable hosts.

Differences with classical analyses

The results obtained here differ from those that can be expected from classical flight mill data analyses. The latter analyses are simple and straightforward but they have the disadvantage of missing a large part of the information. For instance, information on recurring patterns and on their periodicity may remain undetected by classical analyses. In addition, statistical testing of within time series characterizations is not possible through classical methods of analysis. Note also that many conventional outputs such as the duration of the longest flight or the definition of stops are subjected to arbitrary classification carried out by the observer, limiting inter-study comparisons.

Time series analyses, by contrast, allow detailed study of time-dependent data such as the output generated by flight mills, including statistical hypothesis testing. For instance, the application

Table 1. Descriptive statistics of the main characteristics observed for *S. noctilio* females displaying three distinct flight patterns, as determined by wavelets transformation of flight mill data series

	Re (*N*=5)	Pe (*N*=13)	Pu (*N*=10)
Total distance flown (m)	31937.2±8761.3	20837.1±11382.6	3270.4±2210.1
Longest single flight (s)	20245±8634	11176±7513	2155±979
Maximum flight speed* (m s^{-1})	1.44±1.62	1.05±0.34	0.59±0.19
Mass (mg)	4887±121	2796±111	1624±53
Mass loss (%)	11.21±12.11	11.83±46.53	7.08±39.61

Values are mean ± s.d.

*Maximum sustained speed during 1 min (i.e. the average speed during the minute in which the flight was fastest).

Re, regular flier; Pe, periodical flier; Pu, pulsating flier.

of windowed Fourier analyses allows the appropriate characterization of frequency composition and the identification of changes in frequency composition. Wavelets analysis, in turn, while generally similar to Fourier methods has several additional advantages. Unlike windowed Fourier methods, wavelets are not limited to the study of sinusoidal waves, and are not limited either to the size of the window that is set (i.e. multi-resolution and multi-scale analyses). Time series methods are also easily plotted allowing visualization of statistical results. Through time series analysis, otherwise undetectable flight patterns are easily distinguished allowing unbiased comparisons between and within species and a much clear understanding of flight in insects.

An important outcome of our study is that it shows, for the first time, the suitability of modern time series analysis (such as wavelets, but other methods can be useful, depending in the characteristics of the series) for analyzing tethered flight data series. In our study, wavelet analysis made it possible to uncover individual variability in *S. noctilio* flight characteristics, which otherwise would have remained undetected.

Although general, standard parameters such as mean speed or distance flown by individuals are important in understanding flight and dispersal potential of insects, the characteristics of such flight, as determined by the frequency composition of such parameters, may be central to understanding the ecological consequences of flight. Strong variations in size and behavior can have significant consequences on population dynamics by determining actual local and regional dispersal and consequently the management of pest species.

LIST OF ABBREVIATIONS

AS	acceleration–slowdown
EFP	elongation of flight period
IA	intra-flight periods
IE	inter-flight periods
Pe	periodical flier
Pu	pulsating flier
Re	regular flier

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APPENDIX

Table A1. Main flight parameters and classification of the *Sirex noctilio* females used in the experiment according to the kind of flight performed

Individual	Total distance flown (m)	Longest single flight (s)	Maximum sustained speed (m s⁻¹)	Mass (mg)	Type of flight Re	Type of flight Pe	Type of flight Pu	Final classification
sn61	1081.2	1251	0.36	1248			+	Pu
sn11	1206.0	1465	0.63	1468			+	Pu
sn56	1556.9	1995	0.72	2612			+	Pu
sn47	1730.4	826	0.25	1177			+	Pu
sn52	1891.4	4319	0.53	2004			+	Pu
sn44	3661.7	2826	0.42	1299			+	Pu
sn49	3772.9	2483	0.64	1309			+	Pu
sn53	3937.3	1809	0.57	2208			+	Pu
sn69	6893.3	2567	0.65	1496			+	Pu
sn17	6973.2	2015	0.76	1381			+	Pu
sn55	2629.1	7170	0.42	1623		+	+	Pe
sn71	7209.2	5315	0.63	3452		+	+	Pe
sn41	11249.8	6990	1.05	1292		+	+	Pe
sn59	16811.1	6106	1.23	2131		+	+	Pe
sn76	17022.7	7438	1.13	4427		+	+	Pe
sn78	21643.1	29706	0.85	2722		+	+	Pe
sn22	21892.2	6246	1.32	2261		+	+	Pe
sn64	23149.5	7307	0.87	2045		+	+	Pe
sn79	23233.6	16615	1.08	4438		+	+	Pe
sn25	23888.0	11219	1.20	1737		+	+	Pe
sn43	26121.7	12335	1.47	3507		+	+	Pe
sn15	26293.2	6204	1.32	3058		+	+	Pe
sn67	49731.5	22648	1.41	3693		+	+	Pe
sn45	24636.4	7199	1.19	3964	+			Re
sn05	29113.1	20004	1.53	4030	+			Re
sn70	23462.0	18967	1.37	5439	+	+		Re
sn33	40578.9	30706	1.57	4199	+	+	+	Re
sn36	41896.9	24352	1.56	6804	+	+	+	Re

The main flight parameters shown are the most commonly used in classical analyses. Maximum sustained speed is the maximum value of the on minute moving average (as shown in the upper panels of Fig. 3).

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