

# Territorial dynamics and contest behaviour in the solitary wasp *Stizus continuus* (Hymenoptera: Apoidea: Crabronidae)

Josep D. Asís<sup>1)</sup>, J. Tormos & Severiano F. Gayubo

(Área de Zoología, Facultad de Biología, Universidad de Salamanca,  
37071 Salamanca, Spain)

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## Summary

Territorial and agonistic behaviour in male sand wasps (*Stizus continuus*) was investigated in order to determine the influence of body size on territory maintenance and the strategies used to reduce the costs associated with territoriality. Size is the decisive factor in the capacity of males to defend a territory against other competitors: (1) in the disputes observed, the largest male was usually the winner; (2) territorial males were larger than those never seen occupying territories; (3) the size of males occupying territories that were left vacant when their inhabitants were removed experimentally was smaller. To optimize their territorial behaviour, males only defend sites in the nesting area and only when virgin females are emerging (from 0700 to 1300), and reduce the time spent perching (as opposed to patrolling) as temperature increases during the morning. To reduce costs associated with contests, males fight only with rivals of similar size and show a greater tendency to fight with larger males when virgin females are most likely to emerge (from 0800 to 1000). This suggests that males may be able to estimate the size of rivals immediately before an attack (face-to-face hovering), and leave when the opponent is significantly larger.

*Keywords:* agonistic behaviour, Crabronidae, Hymenoptera, male strategies, pair-wise assessment, *Stizus*, territoriality.

## Introduction

The defence of mating territories by male wasps is common (Eberhard, 1969; Alcock, 1978, 1979a; Smith & Alcock, 1980), including at least 15 genera

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<sup>1)</sup> Corresponding author's e-mail address: asis@usal.es

of sphecid wasps (see reviews in Alcock, 1975; Alcock et al., 1978; Evans & O'Neill, 1988). Depending on the characteristics of each species, these territories are established in areas where females emerge, feed, and nest, as well as at so-called landmark mating areas (Thornhill & Alcock, 1983).

The defence of those territories is adaptive only when the benefits in terms of reproductive success are greater than the costs. Different authors have called attention to the possible costs associated with territorial defense, such as a greater risk of predation (Gwynne & O'Neill, 1980; O'Neill & Evans, 1981; Alcock, 1996a), increased energy expenditure (Eickwort, 1977; Hastings, 1989a), which may be related to reduced longevity (Alcock, 1979b, 1996a), the risk of physical injury (Eickwort, 1977; Alcock, 1996a), and severe physiological stress (O'Neill & O'Neill, 1988). These costs may be outweighed in emergence areas if the females: (1) only copulate once in their lives; (2) are receptive immediately after emergence; (3) tend to cluster spatially; and (4) the number of competing males is not excessively high (Alcock et al., 1978; Thornhill & Alcock, 1983).

Different authors have analysed strategies adopted to maximize the advantages of territoriality in certain situations and reduce the costs involved. However, many such studies have focused on the analysis of a specific factor (e.g. temperature, body size, male temporal adjustment to the emergence patterns of the females), offering evidence concerning the role of such a factor, although without considering the possible joint influence of others (O'Neill & O'Neill, 1988; Larsson, 1989, 1991; Villalobos & Shelly, 1994; Alcock, 1996a, 1996b; Coelho, 2001).

The aim of the present study is to perform a multivariable analysis of the strategy shown by a spheciform wasp; namely, *Stizus continuus* (Klug). *S. continuus* is a southern European species often associated with coastal salt-marshes. Females form local aggregations where they dig multi-celled nests in the soil and capture the nymphs and adults of Orthoptera to feed their larvae. After completing their development, larvae pupate inside a cocoon constructed with silk and grains of sand. Adult males defend small territories against other congeners, and are often associated with the holes produced by the emergence of adults from underground cells. When a virgin female emerges from her cell, males compete intensely to copulate with her (Asís et al., 1988).

Very little is known about the reproductive behaviour of males of the genus *Stizus* (Tsuneki, 1976; Asís et al., 1988), although the existence of

territoriality has been mentioned in *S. continuus* (Asís et al., 1988). Starting out from the data pointing to the existence of physical interactions between the males of *S. continuus*, the general hypothesis is that size must play an essential role in access to females. Additionally, and owing to the supposedly high cost of this type of activity, there must be adaptations, relative to the temporal adjustment with the emergence of virgin females, to size, and to the thermal conditions of the nesting area, that will allow the characteristics of each individual to be optimized. A specific issue examined in the present work is how males adjust their territorial behaviour to different biotic (e.g. the presence of virgin females) and abiotic factors (e.g. temperature in the nesting area), depending on their size, while at the same time reducing the possible costs associated with the maintenance of territories and with interactions with other conspecifics.

## Methods and materials

The study was conducted at 'Mallada Llarga', in the Natural Park of 'Dehesa del Saler' (Valencia, Spain), in August-September 1998 and June-September 1999, in two areas in which the females established their nests: area A, approximately 180 m<sup>2</sup>, and area B, of about 120 m<sup>2</sup>. A large part of the surface of both areas is bare sandy soil, although about 35% is occupied by vegetation, mainly comprised of *Arthrocnemum fruticosum* (Chenopodiaceae) and *Juncus maritimus* (Juncaceae). These areas are separated by approximately 100 m by a barrier of *Pinus pinaster* (Pinaceae) and *Phragmites australis* (Gramineae). Despite their proximity, the two areas seem to be relatively isolated, as suggested by the fact that even though regular visits were made to both areas, only 18 males were found outside the area where they had been marked (and presumably emerged).

The population exhibits two likely generations during summer: the first, from the end of May to the beginning of July, and the second, from the end of July to the beginning of September. Between these two periods, an important decrease in wasp activity was observed, with no new emergence holes appearing in the area (C. Polidori, P. Mendiola, J.D. Asís, J. Tormos, F. Andrietti, unpubl. data).

Four hundred and eighty-three males were marked, analysing the head size of those of each area, year, and generation independently: 150 from the

1998 2<sup>nd</sup> generation, area A (1998A2<sup>nd</sup>); 180 from the 1999 1<sup>st</sup> generation, area A (1999A1<sup>st</sup>); 65 from the 1999 2<sup>nd</sup> generation, area A (1999A2<sup>nd</sup>), and 88 from the 1999 2<sup>nd</sup> generation, area B (1999B2<sup>nd</sup>). The individuals were marked as soon as they were seen in the area for the first time. Each specimen was marked with a unique combination of four colored dots on the thorax (UniPaint Marker, Mitsubishi Pencil Co., Japan). At the same time, head width was measured to the nearest 0.01 mm with a digital caliper, after which the specimen was released back into the study area. Head width has been used on several occasions to estimate the total weight of wasps (O'Neill, 1983a; O'Neill & Evans, 1983; Asís et al., 1996). In a sample of 26 individuals (1999B1<sup>st</sup>), head width and weight were highly correlated ( $r = 0.935$ ,  $df = 24$ ,  $p < 0.0001$ ). The unmarked males detected in the study area were captured, measured, marked immediately, and released. The manipulation apparently did not produce any effect on the activity of the specimens, and several of the males that had been captured and labeled immediately after their emergence were observed interacting with other males on the same day. The marking date was used as an estimator of the age of the specimens (Hastings, 1989b).

To facilitate data acquisition, area A (with a greater number of specimens) was divided into 44 squares of  $2 \times 2$  m and area B (with fewer individuals) into 15 of  $3 \times 3$  m. Twenty-five of these squares in area A and 10 in area B were inspected over two minutes every hour from 0700 to 1300 in 1998 (area A) and from 0700 to 1230 in 1999 (areas A and B). After the two-min observation period, the number, identity, and location of both territorial and non-territorial males was noted. Considering a territory as the area within which a particular male stayed preferentially and from which other males were expelled, its size is very variable. Approximate measurements of 12 of such territories revealed a mean size of  $1.73 \pm 1.45$  m<sup>2</sup>. A male was considered territorial if he remained in a territory from more than 75% of the time (i.e. 90 s) for three inspections in a particular day (perched, patrolling, or interacting with other males). Although on some occasions the territorial males abandoned the territories for more than 2 min, the 90 sec interval allowed a reasonable idea about the identity of truly territorial males to be obtained.

Censuses of the number of emergence holes in area A (1998A2<sup>nd</sup>, 1999A1<sup>st</sup>) were carried out every hour, from 0600 to 1315 in 1998 and from 0630 to 1215 in 1999. The new holes were marked with colored pins to

facilitate the identification of recent holes. Because the emergence of two individuals from the same hole was observed very infrequently, the number of emergence holes can be considered as a reasonable estimate of the number of individuals (males and females) emerged. This conclusion is supported by the existence of a correlation between the number of emergence holes and the number of males marked each day (1999A1<sup>st</sup>) ( $r = 0.628$ ,  $N = 12$ ,  $p < 0.05$ ).

To determine the general pattern of activity of territorial males over the course of the day, the time spent by males (for 1998A2<sup>nd</sup> aggregation) (1) patrolling their territory or broader zones of the nesting area; (2) perching on the ground; and (3) interacting with other insects was counted. This activity was recorded on a cassette recorder, later calculating the amount of time (over 5 min samples) devoted to each activity. Forty-four five min samples were obtained with 14 males at different times of the morning over 15 days. General linear models were conducted to analyse male activity patterns: interacting, patrolling and perching. The time of day, temperature and size were used as variables. To avoid pseudoreplication, only one observation per male, selected at random, was used.

To analyse the interactions between males, the categories described by Lin (1963) in the wasp *Sphecius speciosus* (Drury) and by Eickwort (1977) in the bee *Hoplitis anthocopoides* (Schenk) were employed. These authors observed the following: (1) pursuits in flight, without physical contact; (2) contacts including collisions or *butts*; (3) face-to-face hoverings, in which two males face each other in flight and almost touch; (4) *grapples*, that is, fights where the adversaries fall to the ground and use their mandibles to bite one another. *Grapples* represent the maximum level of aggression with a duration that may vary from a few seconds to some minutes. Over periods of five min the number of pursuits, butts, face-to-face hoverings, and grapples were counted. Eighty-eight five min samples were obtained with 20 males over 16 days (1998A2<sup>nd</sup>). The number of pursuits was analysed with a general linear model, using temperature, male size, and the time of day as explanatory variables; a single observation per male, selected at random, was used. Sixty-four pairs of fighting males were also captured to analyse the size differences between contenders (1999A1<sup>st</sup>, 1999B2<sup>nd</sup>). We used a logistic regression to analyse the number of face-to-face hovering that ended in a grapple, with *time* and *size* (10<sup>th</sup> root transformed) as variables.

We performed removal experiments to determine the re-occupation of the territories that remained vacant and evaluate the role of the body size on territorial defense (see O'Neill, 1983b). The analysis was done with 33 territorial males (1998A2<sup>nd</sup>, 1999B2<sup>nd</sup>), holding the original occupant during 30 min in a small container (30 × 40 × 20 cm) maintained in shadow. Later release of the original occupant allowed information about the possible *residence effect* on the occupation and maintenance of territories to be obtained, on the presumption that both the original individual removed and the new occupant *believed* themselves to be the owners (Waage, 1988). In disputes for dominance over territories similar criteria to those employed by Hastings (1989a) were used to assess territory takeovers.

Once every hour the temperature to the nearest 0.1°C was measured with a digital thermometer at ground level. Times are given in GMT. Statistical analyses were performed using XLStat 6.0 and Minitab 13.0.

## Results

### *Male size*

The size of the males in the different areas and generations was not homogeneous. Males of the first generation were larger than those of the second one (ANOVA;  $F_{1,504} = 9.18$ ,  $p = 0.003$ ), and males coming from the B aggregation were smaller than those observed in A (ANOVA;  $F_{1,504} = 8.75$ ,  $p = 0.003$ ), while the influence of the year was not significant (ANOVA;  $F_{1,504} = 1.88$ ,  $p = 0.171$ ) (Table 1).

For the 1998A2<sup>nd</sup>, 1999A1<sup>st</sup>, and 1999B2<sup>nd</sup> populations, we analysed the possible effect of date of emergence on body size by analysis of covariance with the date of emergence as a covariate, population as a random factor and male head width as the dependent variable. No differences were observed with respect to the date of emergence (ANCOVA;  $F_{1,414} = 1.77$ ,  $p = 0.184$ ).

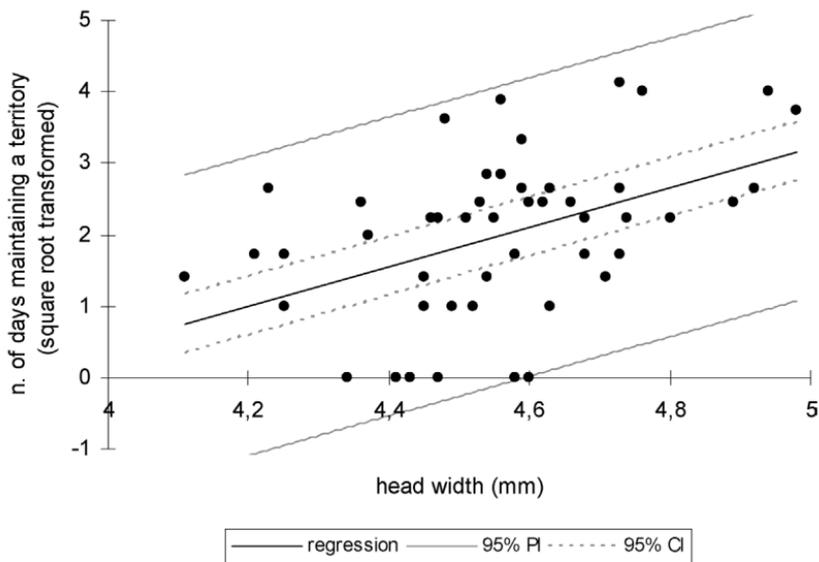
Most (72.0%) of the 150 marked males in the 1998A2<sup>nd</sup> population were recaptured at least once. Of the 108 recaptured males, about half ( $N = 49$ ) visited the nesting area without interruption from the day when they were marked until their disappearance. The rest ( $N = 59$ ) did not visit the area continuously, leaving it for one or several days (mean = 1.6 d, range = 1-8 d,  $N = 76$ ). The number of days spent in the nesting area, for males resighted at least 3 times, was  $10.4 \pm 5.8$  days (range = 3-29,  $N = 50$ ). No significant

**Table 1.** Head width (mm) of *Stizus continuus* males in the five populations studied. Measurements for the 26 males from 1999B1<sup>st</sup>, which were captured to analyse the correlation between head width and body weight, are also included.

Population	<i>N</i>	Mean head width ± SD	Range
1998A2 <sup>nd</sup>			
all males	150	4.51 ± 0.18	4.08-4.98
territorial males	85	4.55 ± 0.19	4.11-4.98
males found in copula	12	4.60 ± 0.10	4.45-4.76
1999B2 <sup>nd</sup>			
all males	88	4.39 ± 0.22	3.79-4.89
territorial males	36	4.48 ± 0.20	3.91-4.87
males found in fights	40	4.47 ± 0.17	4.11-4.78
males found in copula	15	4.52 ± 0.16	4.28-4.78
1999A1 <sup>st</sup>	180	4.56 ± 0.27	3.71-5.06
1999B1 <sup>st</sup>	26	4.43 ± 0.26	3.81-5.01
1999A2 <sup>nd</sup>	65	4.46 ± 0.19	3.85-4.87

correlation was observed between the size of the males and the number of days spent in the nesting area ( $r = 0.172$ ,  $df = 48$ , NS).

Almost 60% of the males marked in 1998A2<sup>nd</sup> were at some time observed occupying territories in the nesting area. For the males of 1998A2<sup>nd</sup>, the occupation of a particular territory varied between 1 and 17 days in succession (mean =  $4.67 \pm 4.57$  d,  $N = 57$ ). The number of days that a male maintained a territory (square root transformed) was positively related with its size ( $b = 2.77$ ,  $R^2 = 0.216$ ,  $F_{1,48} = 13.22$ ,  $p < 0.001$ ) (Figure 1). The comparison of head widths between mated and unmated males, and territorial and non-territorial males (for 1998A2<sup>nd</sup> and 1999B2<sup>nd</sup>), was analysed as an ANOVA with *area* as a random factor and *in copula* (or *territorial*) as the main effect. Males found in copula were larger on average than those never seen mating, in both areas ( $F_{1,235} = 9.38$ ,  $p = 0.002$ ), and the same was true for territorial males as regards those never found occupying territories ( $F_{1,223} = 19.38$ ,  $p < 0.001$ ) (Table 1). For 1999B2<sup>nd</sup> males, Student's *t* test also revealed that the males found in disputes were larger than those never seen fighting ( $t_{86} = 3.44$ ,  $p < 0.001$ ).

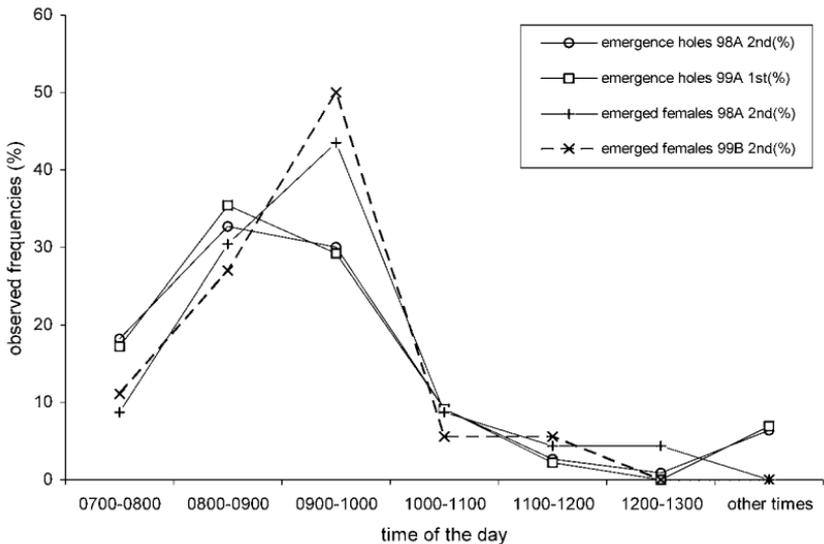


**Figure 1.** Number of days that males maintained a territory (square root transformed) vs. male size (1998A2<sup>nd</sup>). The regression line, prediction intervals (PI) (95%) and confidence intervals (CI) (95%) are provided ( $F_{1,48} = 13.22$ ,  $p < 0.001$ ,  $R^2 = 0.216$ ).

### Adult emergence schedule

The daily pattern of the emergence of adults, estimated from the number of new emergence holes observed for the 1998A2<sup>nd</sup> ( $N = 278$ ) and 1999A1<sup>st</sup> ( $N = 344$ ) populations, is shown in Figure 2. About 90% of the emergences occurred between 0700 and 1100, and more than 60% were concentrated between 0800 and 1000. In the case of females, for the 1998A2<sup>nd</sup> and 1999B2<sup>nd</sup> populations most emergences were also concentrated between 0800 and 1000 (more than 75%), although the pattern was slightly different from that obtained for the overall adult population (Figure 2).

When an adult female emerged, males competed intensely for her, using legs, wings, and mandibles in an attempt to displace rivals. When a male managed to mount the female, the couple flew off, leaving the nesting area with copulation presumably occurring elsewhere. In cases in which a virgin female was not detected by any male ( $N = 3$ ), she remained for a few seconds next to the emergence hole, grooming herself, and then left the area shortly thereafter, flying off towards the neighboring bushes or trees. Two of those females were mated by non-territorial males.

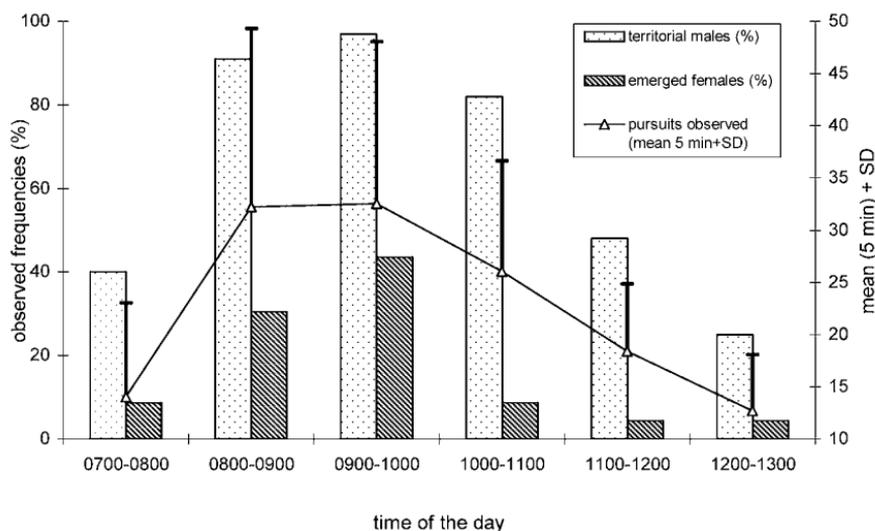


**Figure 2.** Percentage of adults (males and females) and of females of *Stizus continius* emerging at different times of the day. The emergences of adults are separated for 1998A2<sup>nd</sup> ( $N = 278$ ) and 1999A1<sup>st</sup> ( $N = 344$ ). Female emergences correspond to 1998A2<sup>nd</sup> ( $N = 23$ ) and 1999B2<sup>nd</sup> ( $N = 18$ ).

The owners of each territory were responsible for most of the copulations observed (21/27), although males from neighboring territories (4/27) or even non-territorial males (2/27) also mated. Copulations only occurred with recently emerged females, and a male mating with a nesting female was never observed.

### Male activity

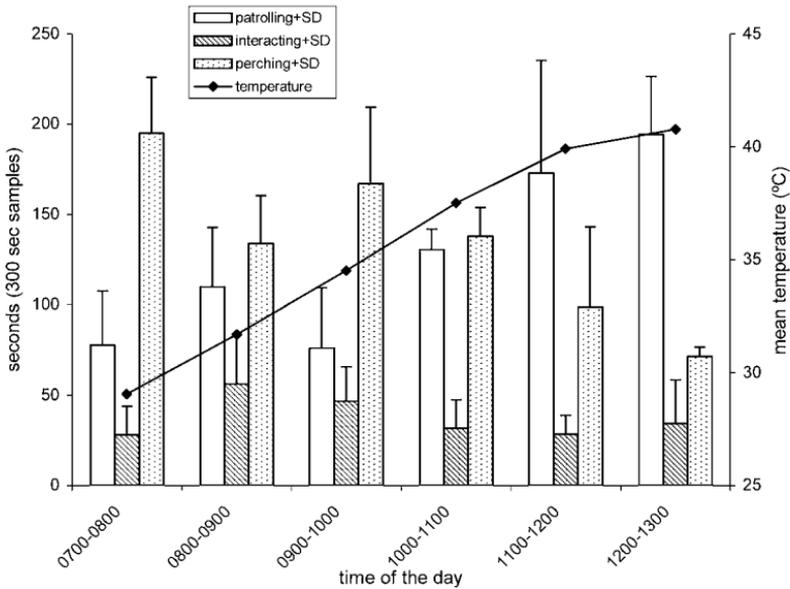
Males first appeared in the nesting area at about 0630, and more than 50% of the territories were occupied by 0730. The maximum occupation of territories occurred between 0900 and 1000 (Figure 3). This pattern of occupation was observed in both 1998A2<sup>nd</sup> and in 1999A1<sup>st</sup> (Kolmogorov–Smirnov  $D$  test;  $D = 0.143$ ,  $N_1 = 7$ ,  $N_2 = 7$ , NS). By noon, few territorial males remained; by about 1230 only a few isolated males were seen patrolling the nesting area, although between 1500 and 1600 the number of males increased again. These males flew over the area and entered small holes (usually emergence holes) to spend the night, closing them from the inside. Most males retired before 1630.



**Figure 3.** Percentage of territorial males and emerging females of *Stizus continuus* and number of pursuits observed (in five-min samples) as a function of the time of day for the 1998A2<sup>nd</sup> aggregation.

The activity pattern observed for 14 territorial males (1998A2<sup>nd</sup>) varied throughout the morning, with an increase in the time devoted to *patrolling*, together with a decrease in the amount of time spent *perching*; the amount of time spent *interacting* with other insects was greater between 08:00 and 10:00 (Figure 4). A general linear model analysis revealed that *temperature* was a factor in the amount of time devoted to *patrolling* ( $F_{1,10} = 7.30$ ,  $p = 0.022$ ) and *perching* ( $F_{1,12} = 28.09$ ,  $p < 0.001$ ): increases in temperature were accompanied by a tendency to patrol, while the time devoted to perching decreased. Also, the *time of the day* and its quadratic term entered in the minimal adequate model (the model in which all terms are significant, see Grafen & Hails, 2002) for *patrolling* ( $F_{1,10} = 5.89$ ,  $p = 0.036$  for *time*;  $F_{1,10} = 5.42$ ,  $p = 0.042$  for *time*<sup>2</sup>), their coefficients ( $-126.9$  for *time* and  $6.5$  for *time*<sup>2</sup>) revealing a non linear relationship, with an increase in the time devoted to patrolling at the beginning and end of the morning, when female emersions are scarce. A general linear model including the 45 samples and *male identity* as a variable gave the same results and revealed that *male identity* was not significant.

Regarding the time spent by the males in interacting, the model revealed, as a single significant variable, the time of day and its quadratic and cubic terms ( $F_{1,10} = 12.99$ ,  $p = 0.005$  for *time*;  $F_{1,10} = 11.57$ ,  $p = 0.007$



**Figure 4.** Time spent by *Stizus continuus* males (1998A2<sup>nd</sup> aggregation) in patrolling, interacting with other insects, and perching, as a function of the time of day. Samples were of five-minute intervals. Mean surface temperature ( $N = 28$ ) along the morning is also shown.

for  $time^2$ ;  $F_{1,10} = 10.17$ ,  $p = 0.01$  for  $time^3$ ), with increases in the time devoted to interacting between 08:00 and 10:00 and also around 1200 (Figures 3 & 4); temperature and size did not enter the minimal adequate model.

During the early morning hours, the duration of perching events (mean  $\pm$  SD =  $7.95 \pm 7.54$  s,  $N = 129$ ) was greater than that observed at the end of the day (mean  $\pm$  SD =  $4.39 \pm 3.59$  s,  $N = 152$ ). In a general linear model analysis with *perching duration* (log transformed) as the dependent variable, and *temperature*, *time of the day* and *male size* as explanatory variables, only *temperature* was significant ( $F_{1,12} = 6.76$ ,  $p = 0.023$ ), while the other variables did not enter the minimal adequate model. Perching duration decreased with the increase in temperature. A general linear model including the 88 samples and *male identity* as another explanatory variable gave the same results, and *male identity* had no influence.

### Removal experiments

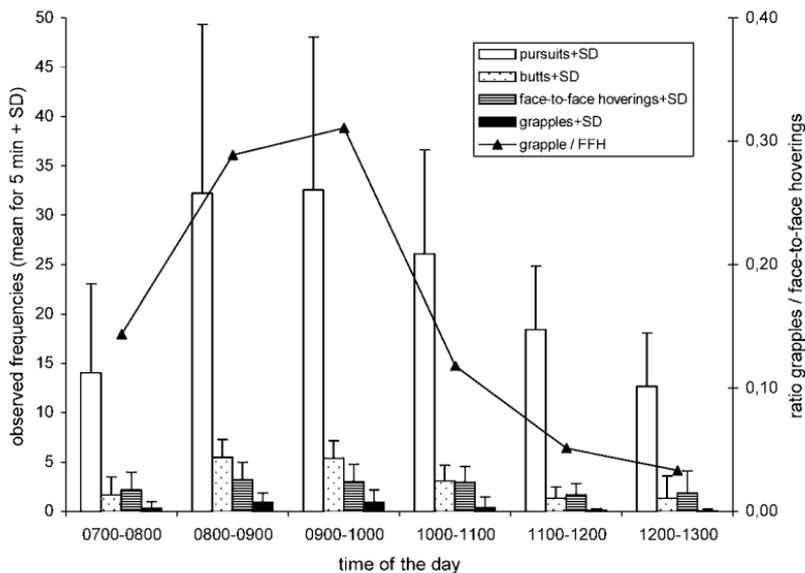
Upon removal of 33 territorial males, the territory was occupied by another male on 32 occasions with the size of the *secondary* males being smaller

than that of the original one (paired  $t$ -test;  $t_{30} = 4.60$ ,  $p < 0.001$ ). When the original male (usually larger) was released, in 24 out of 32 times it re-occupied the territory, displacing the *secondary* male. The males that finally occupied the territories were larger than the displaced ones (paired  $t$ -test;  $t_{29} = 5.00$ ,  $p < 0.0001$ ).

### Contest dynamics

To determine the possible influence of male size and age in territorial occupation, the results of 72 territorial disputes were analysed. The larger male nearly always won the dispute (60/72), and eventually the territory ( $\chi_1^2 = 32.00$ ,  $p < 0.001$ ). However, male age was not a factor; in 31 cases the younger male won and in 26 the older one did ( $\chi_1^2 = 0.44$ , NS). In the case of disputes in which the smaller male won, on five occasions this was the younger one and in three the older one.

The number of pursuits, butts, face-to-face hoverings, and grapples exhibited by 20 territorial males (the frequency of each of these types of behaviour in periods of five min) (Figure 5) varied through the morning. Interactions resulting in a simple pursuit (mean 4.51/min) were much more fre-



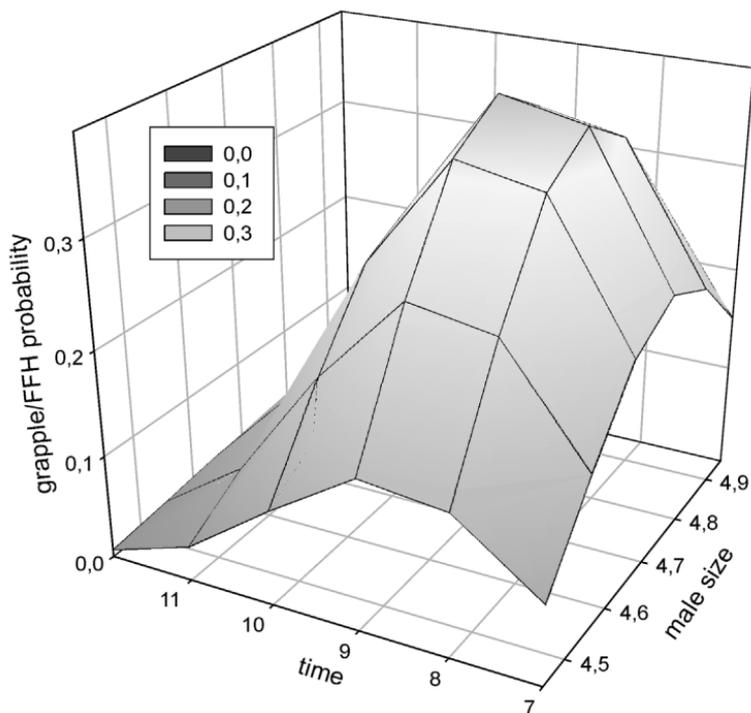
**Figure 5.** Interactions (mean for five-min samples) observed between *Stizus continuus* males (1998A2<sup>nd</sup> aggregation) as a function of the time of day. The grapple/face-to-face hovering ratio is also shown.

quent than those ending in butting (mean 0.65/min) or those ending in grappling (0.11/min). Overall, interactions were more frequent between 0800 and 1100, coinciding with the moment of highest presence of males in the territories (and with a higher number of emergences of females) (Figure 3). A general linear model analysis with the *number of pursuits* as the dependent variable and *temperature*, *time of the day*, and *male size* as explanatory variables, showed that the decisive factor was *time of day* ( $F_{1,17} = 15.91$ ,  $p = 0.001$  for *time*;  $F_{1,17} = 16.81$ ,  $p = 0.001$  for  $\text{time}^2$ ) while *temperature* or *male size* did not seem to have any influence. The number of pursuits increased between 08:00 and 10:00 (when there were more interactions and more females emerged), thereafter dropping off (Figure 5).

The mean value of the grapple/face-to-face hovering ratio was 1 grapple:4.83 face-to-face hoverings. However, this ratio was higher between 08:00 and 10:00. During this period, approximately 1 out of every 3.1 face-to-face hoverings would end in a grapple, whereas between 11:00 and 13:00 the ratio was 1 grapple:14.6 face-to-face hoverings. To analyse the differences in the likelihood that a face-to-face hovering might end in a grapple, a logistic regression of the number of face-to-face hoverings that turned into grapples, against *time* and *male size*, was performed. Both variables, as well as their quadratic terms, revealed a significant influence, reflecting non-linear relationships with the likelihood of grapple ( $\chi^2_{406} = 437.72$ ,  $p < 0.001$ ,  $R^2(\text{McFadden}) = 0.07$ ). The model revealed that the likelihood of grappling increased during the period in which the emergence of females was most frequent (08:00-10:00), with a greater trend in the males to attain maximum levels of aggression during that period. Additionally, the males with a size slightly larger than the mean tended to become involved in grapples more frequently than did the small or very large males (Figure 6).

### *Pair-wise assessment*

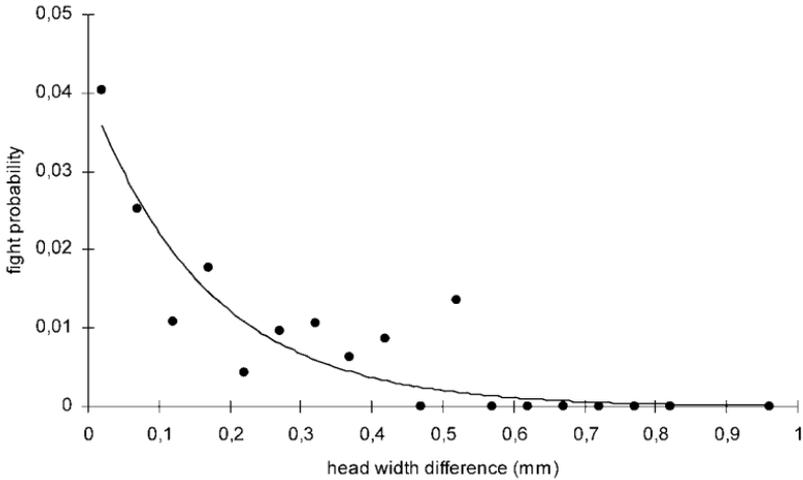
The males engaging in fights were usually territorial males, whereas the males never seen to occupy territories, even though interacting with the rest, rarely entered disputes ( $\chi^2_1 = 13.89$ ,  $p < 0.001$ ). The disputes almost always occurred between males of relatively similar sizes. In more than 75% of the fights observed ( $N = 64$ ) the difference in size (head width) of the males was less than 5% of the larger male and only in 3% of the cases did this difference surpass 10%. In three of the disputes, the smaller male



**Figure 6.** Likelihood of a face-to-face hovering developing into a grapple as a function of the time of day and male size, according to the model obtained with logistic regression.

was killed; two of those were appreciably smaller than the mean of their respective populations (head widths = 4.05 mm and 4.21 mm, population mean = 4.56 mm), and the differences between the contestants were 3.4%, 6.2%, and 17.2%.

The differences in size between the 35 pairs of males found in disputes, observed over 5 days (1999B2<sup>nd</sup>) were compared with all the possible differences between pairs of males for the 70 specimens detected during that same period in the area, assuming the same likelihood of encounter for all the males. We then analysed the number of disputes observed in each class of size difference for intervals of 0.05 mm (Figure 7). The number of disputes was seen to follow a negative exponential regression model ( $b = -5.95$ ,  $R^2 = 0.825$ ,  $F_{1,16} = 75.59$ ,  $p < 0.0001$ ), showing that the likelihood of dispute decreases with the increase in the difference in size among rival males. Furthermore, if the males are divided into two groups as a function of their size (larger or smaller than the mean), the disputes tended to occur between males belonging to the same size group ( $\chi^2_1 = 9.29$ ,  $p < 0.01$ ,  $N = 64$ ).



**Figure 7.** Fight (grapple) probability between males (calculated as the ratio between the number of disputes observed and the number of possible encounters among the 70 males present in the aggregation 1999B2<sup>nd</sup>) as a function of size difference (head width) of the pair of rival males. The regression line given in the text has been fitted.

**Table 2.** Differences in size (mm) of the males observed in disputes as a function of the time of day (1998A2<sup>nd</sup>).

Time of the day	<i>N</i>	Mean head difference $\pm$ SD	Range
0700-0800	14	0.06 $\pm$ 0.03	0.01-0.12
0800-0900	16	0.18 $\pm$ 0.13	0.03-0.42
0900-1000	12	0.18 $\pm$ 0.07	0.07-0.34
1000-1100	6	0.13 $\pm$ 0.19	0.00-0.52
1100-1200	3	0.14 $\pm$ 0.22	0.00-0.39

When differences in size between the males participating in 51 disputes as a function of the time of day were analysed, such differences were seen to be greater between 0800 and 1000, while in the disputes observed before and after this period the males were more similar in size (Kruskal–Wallis test;  $H = 15.41$ ,  $p < 0.01$ ,  $df = 4$ ) (Table 2).

## Discussion

The maintenance of territories by males as a reproductive strategy involves associated costs. However, these costs are particularly likely outweighed by

benefits when females can be monopolized via female defense polygyny (Alcock et al., 1978; Thornhill & Alcock, 1983).

In *Stizus continuus* virgin females are spatially clustered, making female defense territoriality profitable. The advantages conferred by possession of a territory seem evident since more than 90% of the virgin females were taken by territorial males. In 80% of the cases, it was the owner of the territory from which the female emerged that displaced rival males and flew off with the female. Non-territorial males (i.e. those that were never seen occupying territories) only secured 7% of the receptive females. Hastings (1989a) reported similar rates of success for the territorial males of *Sphecius grandis* (Say), a species with comparable physiological and eco-ethological characteristics.

In view of the potential advantage conferred by the possession of a territory, competition between males for their occupation must be intense, and manipulations such as removal of an owner male from its territory, should lead to rapid re-occupation by another male. This is precisely what happened in 97% of the cases.

### *Influence of body size*

Several factors determine the ability of a male to defend a territory (Thornhill & Alcock, 1983). Although there are examples of the influence of residency status (theoretical models in Stamps & Krishnan, 1999; Kemp, 2000) or age (Eickwort, 1977), in many cases the decisive factor is competitor size (Alcock, 1996c; Hernández & Benson, 1998). In view of the physical nature of the disputes observed between males of *S. continuus* for territorial possession, size could have been predicted to be the dominant factor. And indeed, in the disputes observed, the larger male was nearly always the winner, whereas the difference in age between the contenders did not seem to be important. Moreover, in several populations, territorial males were larger than males that were never seen occupying territories, and the replacement males occupying experimentally vacated territories were usually smaller than the original occupants. Additionally, in cases in which there might be uncertainty regarding residential status (such as, for example, in the situations created by the removal experiments) it was the larger male that expelled the *resident*. Also a correlation was observed between the size of the males and the number of days over which they maintained territories. In his study of *S. grandis*,

Hastings (1989a) also concluded that size was the key factor. For both *Stizus* and *Sphecius* (species in which disputes between males are physical), the results obtained are logical. In contrast, the size of the contenders does not seem critical to contest resolution in other sphecid wasps with non-physical interactions (Strohm & Lechner, 2000).

### *Male activity*

When female defense polygyny evolves males can be assumed to optimize this strategy by reducing the energy costs involved in the defense of territories. In *S. continuus*, this is accomplished by: synchronizing the presence of males in the nesting area with the period of emergence of the females; adapting the type of activity (perching – patrolling) to the environmental conditions (mainly temperature); and minimizing the risk of physical harm in confrontations with other males.

The ability of territorial males to anticipate the emergence of virgin females presumably reduces the costs associated with the maintenance of territories. The correlation between male territoriality and female emergence (Figure 3) has also been reported for other wasp species (Hastings, 1989a). In addition, it appears that, for any given day, males emerge before the females. This *intra-day* protandry has been reported, for example, for *Amegilla dawsoni* (Alcock, 1997), and is advantageous in the sense of maximizing a male's access to emerging females. Anyway, there's not, for the moment, any evidence supporting that males of *S. continuus* can mate within hours of their own emergence.

### *Influence of temperature*

Another important factor that determines the activity of sand wasps is temperature. In many species, the nests are established in dry and sunny places and, at least in temperate regions, activity is concentrated around the hottest part of the year. Several authors have highlighted the thermal stress experimented by both females and males. Females build their nests in the soil at times of high temperature (Willmer, 1985; Larsson, 1990), and males maintain their territories under demanding thermal regimes (O'Neill & O'Neill, 1988; Larsson, 1989, 1991; Villalobos & Shelly, 1994; Coelho, 2001). However, males of *Stizus continuus* spend less and less time perched in their territories as the morning progresses (falling from about 65% at 0700 to little

more than 20% at 1300), switching gradually from perching to patrolling. During the course of the morning, temperatures undergo a mean increase of nearly 12°C (Figure 4). During the last hour of the morning, males that stayed on the ground for long periods would surely overheat. Different authors have reported reductions in the time spent by males on the ground in different species of wasp (O'Neill & O'Neill, 1988; O'Neill et al., 1989; Coelho, 2001) (perching on plants, by contrast, does not change over the morning) as a strategy for reducing thermal stress and the analysis conducted on the duration of perching revealed that the decisive variable was temperature. A possible additional advantage of reduced perching time and increased patrolling would be that this latter activity allows males to inspect a larger area at a time when few virgin females are emerging. The fact that the *time* variable (and its quadratic term) significantly influence the amount of time devoted to patrolling could reflect this advantage, although it seems that temperature plays a decisive role in the change in behavioural strategy from perching to patrolling.

### *Contest dynamics*

In various hymenopterans, Eickwort (1977), Alcock (1979b, 1996a), and Hastings (1989a), among others, have shown that territorial defence may decrease longevity or result in physical damage to the contestants. Because fights rarely lead to death (although lethal combats does occur in *S. continuus*), mechanisms presumably exist for males to avoid extreme risk by assessing the power of potential opponents. For *Sphecius speciosus*, Lin (1963) reported different types of interactions among males, varying from simple *pursuit-fleeing* to fights in which the contenders fall to the ground and attack each other with their mandibles. The same range of behaviours occurs in *Stizus continuus*. The *pursuit-fleeing* interaction only involves energy expenditure, with little or no physical wear. Face-to-face hovering, if not accompanied by grappling, is also relatively *inexpensive*. However, grappling may cause physical damage or even death. Given the potential cost of physical combat, one would predict that face-to-face hoverings leading to grappling would be more frequent at times when there are more females available. This is precisely what was observed in this study (Figure 5): the grapple/face-to-face hovering ratio is greater between 0800 and 1000, the period in which the number of emerging females is highest.

### Pair-wise assessment

One of the mechanisms available for reducing dangerous behavioural patterns during competitive interactions is the estimation of the antagonist's *fighting ability* (Enquist & Leimar, 1990). In the fights observed between males of *S. continuus* that lead to a grapple, the difference in size of the antagonists was less than what would have been expected due to chance. Thus, grapples occurred most frequently between males of very similar size, and the likelihood of dispute was reduced when the difference between the sizes of rival males increased. Additionally, it seems logical to surmise the males of intermediate size would tend to exhibit a greater probability of fighting than the small males (who would back down from generally larger males) or the very large males (whose adversaries, generally smaller, would not become involved in a grapple). The model obtained points to a non-linear influence of size, such that the likelihood of a face-to-face hovering developing into a grapple is lower in the small and very large males (Figure 6).

Perhaps during the face-to-face hovering phase, males are able to gauge the adversary's size and decide whether to escalate the conflict. Thus, in the period when the greatest number of females emerge (hence increasing the possibilities of mating) the males would *risk* fighting with significantly larger adversaries. Coelho (1998) demonstrated in *Sphecius speciosus* that the buzz frequency is related to the body mass of an individual. The situation would probably be similar in *Stizus continuus*, although this issue has yet to be analysed. Coelho & Holliday (2001) have also suggested that males may assess their competitor's size just after the onset of grappling. Perhaps the acoustic information received from the rival during face-to-face hovering informs the male about the size of its opponent and determines whether to flee or continue fighting.

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