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Assessment between species: information gathering in usurpation contests between a paper wasp and its social parasite

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Costs associated with escalated fighting may be minimized where individuals are able to gather information regarding the likely outcome of conflicts. In particular, the ability to assess resource-holding potential (RHP) has been shown to be important in determining the dynamics of animal contests. While assessment rules have been investigated in contests in a range of species, little is known about the potential for assessment in contests between species. We examined the role of assessment in usurpation contests between the paper wasp *Polistes dominulus* and the social parasite *Polistes semenowi*. First, we investigated whether parasite clypeal patterns function as signals of RHP by staging contests with parasites in which the clypeal pattern was concealed with paint. Second, we examined the importance of body size as a determinant of RHP. Finally, we explored whether individuals use information about their own RHP, and that of their rivals, in deciding when to withdraw. We found no evidence that parasite clypeal patterns act to signal RHP to hosts: initial fights were neither longer nor more intense when the patterns were concealed. We also found no evidence for RHP assessment during contests: although body size predicted contest outcome, fight duration and intensity were not significantly related to either winner or loser size. We suggest that the high value of the nest to both parties, combined with the potential for 'divisive' asymmetries in RHP between hosts and parasites, may result in selection for escalated conflict over rival assessment during usurpation fights.

Contests over resources are widespread in nature, both between and within species. The outcomes of contests can have important fitness consequences, not only in terms of the resources gained or lost, but also in terms of the energetic cost of fighting and the risk of injury (e.g. Clutton-Brock et al. 1979; Mann et al. 2001; Briffa & Sneddon 2007). To minimize these costs, individuals may make strategic decisions based on their own resource-holding potential (RHP) and that of their rival (Arnott & Elwood 2009). Information acquired during contests about an individual's own performance, as well as its opponent's performance, is valuable as it allows rivals to assess the costs and benefits of continued fighting versus withdrawing from the contest (Arnott & Elwood 2009). Alternatively, or additionally, animals may assess rival ability prior to contests by attending to cues or signals of RHP (Maynard Smith & Harper 2003).

The type of information gathered by animals during contests, as well as the conditions under which information gathering occurs, has been the subject of much theoretical and empirical work (reviewed in Arnott & Elwood 2009). For example, by examining the relationship between winner and loser RHP and contest dynamics, it has been possible to deduce the likely assessment strategies used during contests (Taylor & Elwood 2003; Arnott & Elwood 2009). Information gathering may be limited to an assessment of an individual's own performance during a fight, with individuals withdrawing when an upper threshold is reached (self-assessment). Alternatively, individuals may base the decision to retreat on information about their own and their rival's RHP (mutual assessment). Furthermore, information gathered about other aspects of the contest, in particular the value of the contested resource, has been shown to have a critical role in shaping fight dynamics (Arnott & Elwood 2008). Resource value can affect an individual's fighting strategy via its effect on motivation: in cases where resource assessment is possible, individuals that place a greater value on the resource are expected to fight for longer and/or at greater intensities to secure the resource than individuals with lower motivation (Arnott & Elwood 2008). Indeed, in situations where the perceived value of the resource is so great that the benefits of winning outweigh the cost of escalated fighting, individuals are expected to persevere, irrespective of asymmetries in RHP (Enquist & Leimar 1990). While there is evidence that high resource value favours escalated fighting over self- and rival assessment in certain situations (e.g. Moore et al. 2008), in general some form of assessment based on signals/cues or performance during contests is expected to reduce the costs of fighting, and has

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been demonstrated in a wide range of taxa (e.g. Stuart-Fox 2006; Prenter et al. 2008; Tibbetts et al. 2010).

To date, studies of animal contests have focused largely on fights between conspecifics for resources. Members of the same species tend to occupy very similar ecological niches and therefore experience intense competition with one another over the limited resources available. Analysis of conspecific contests is aided by the fact that resources valuable to both contestants are readily identified, and factors determining RHP will be common to both contestants. Perhaps for these reasons, contests over resources between members of different species have been largely neglected (but see Macdonald et al. 2007; Tanner & Adler 2009). However, such contests play an important part in determining an individual's access to resources, with competition occurring between species, for example, for food and breeding sites (e.g. Becerril-Morales & Macías-Ordóñez 2009; Strubbe & Matthysen 2009). Thus, it is important to know which factors influence the outcome of contests between heterospecifics, and to what extent individuals are able to gauge the competitive abilities of heterospecific rivals.

Social parasites of primitively eusocial and eusocial Hymenoptera offer a good opportunity to study assessment strategies used in contests between heterospecifics. Following invasion of the host nest, social parasites take up residence with the hosts, on whom they depend to rear their offspring. Social parasites deploy a variety of deceptive strategies to subvert the host recognition system and so gain entry to the host nest, including chemical mimicry and dilution of cuticular compounds (chemical insignificance; Lorenzi 2006). However, a number of social parasites in the Vespinae and Polistinae adopt an aggressive usurpation strategy, engaging in prolonged fights with hosts (Reed & Akre 1983; Cervo 2006). While these aggressive interactions are well described for a number of species (e.g. Reed & Akre 1983; Zacchi et al. 1996), there has been little research into the factors determining fight outcome and dynamics, as well as the possible mechanisms of rival assessment used by hosts and parasites during usurpation.

In this study, we focused on the aggressive interactions that characterize host usurpation attempts by *Polistes semenowi*, one of three obligate social parasites within the paper wasp genus *Polistes*. *Polistes semenowi* is considered a specialist parasite of the European paper wasp, *Polistes dominulus* (Cervo 2006). *Polistes semenowi* targets host nests in the late pre-emergence phase of the colony cycle, when colony foundresses are the only adults present. The parasite invades aggressively, fighting with host foundresses until they submit (Zacchi et al. 1996). The original dominant foundress often remains in the colony, although her role as the principal egg-layer is now assumed by the parasite. In common with other *Polistes* social parasites, *P. semenowi* presents several morphological specializations, including enlarged femora and thickened mandibles, which are thought to enhance fighting ability (Cervo 2006).

In addition to the above adaptations for fighting, *P. semenowi* has conspicuous black patterning on the clypeus. Recent research into the function of clypeal patterns in the host species, *P. dominulus*, has demonstrated that these patterns play an important role in rival assessment (Tibbetts & Dale 2004; Tibbetts & Lindsay 2008). *Polistes dominulus* clypeal patterns are argued to function as status signals (or 'badges') that signal RHP (Tibbetts & Dale 2004), and there is evidence that they are useful in settling contests between unfamiliar rivals by making asymmetries in RHP apparent when rivals meet (Tibbetts & Dale 2004; Tibbetts & Lindsay 2008; but see Green & Field 2011). Although somewhat larger and less variable than host patterns, the clypeal patterns of the parasite may similarly function as signals of status. In the host, the active signal component of the pattern is its disruption, or 'brokenness' (Tibbetts 2010). In the parasite, however, melanin deposition is uniform across the clypeus and extends down to the mandibles. Noting this pattern, Ortolani et al. (2010) have alternatively proposed that the parasite clypeal patterns act as amplifiers (Taylor et al. 2000), highlighting a signal of RHP based on mandibular width. In an experiment in which heads of a second *Polistes* parasite, *Polistes sulcifer*, were presented to *P. dominulus* hosts, hosts showed more aggression towards heads painted to conceal the clypeal pattern (Ortolani et al. 2010). This finding raises the possibility that the clypeal patterns of *P. semenowi* function in parasite assessment by hosts during usurpation contests. If parasite clypeal patterns function as signals of RHP, either as status badges or amplifiers, then they may assist usurpation by reducing host aggressive responses.

In this study, we explored the potential for rival assessment in usurpation contests between *P. semenowi* and *P. dominulus* hosts. First, we tested the hypothesis that parasite clypeal patterns function to signal RHP in usurpation contests with hosts. We tested this by manipulating parasite clypeal patterns and observing the effect of the manipulations on the duration and intensity of fights with hosts. Signals of RHP based on clypeal patterns provide a potential mechanism for rival assessment prior to fighting; alternatively (or additionally), individuals may use information about rival RHP acquired during contests when deciding whether to persevere or retreat. Body size in *Polistes* wasps is often associated with social rank (Turillazzi & Pardi 1977; Cervo et al. 2008) and in *P. dominulus* body size affects the outcome of both intraspecific (Tibbetts & Shorter 2009) and interspecific (Ortolani & Cervo 2010) usurpation attempts. We therefore also analysed contest dynamics and outcome with respect to rival size to establish first whether size is a determinant of RHP in *P. dominulus–P. semenowi* contests, and second whether size information is used in strategic assessment during fights, as has been reported in other taxa (e.g. Morrell et al. 2005; Prenter et al. 2008).

METHODS

Polistes dominulus colonies parasitized by *P. semenowi* were located at sites around Conil de la Frontera and Zahara de los Atunes, Cádiz Province, Spain, in early May 2010. Because of the relative rarity of parasites in our study population (typically only 2% of host nests are parasitized), several hundred colonies had to be inspected to obtain the sample of 31 parasites used in the experiment. Parasites were removed from their host nests and placed in individual containers for 24 h prior to usurpation trials. To control for effects of resource value on the motivation of parasites to attack or hosts to defend, we presented parasites with similarly sized host colonies, in terms of nest size (mean $\pm$ SE $= 73.16 \pm 3.33$ cells), number of adult hosts (2.87 ± 0.10) and number of pupae (12.65 ± 1.17). Using intensive field surveys, we identified target host colonies with no prior history of parasitism; however, it is possible that colonies experienced brief usurpation attempts that were missed by the surveys. Therefore, to ensure that hosts and parasites had not previously interacted, parasites were presented with a host colony collected at least 3 km from where the parasite was found.

Parasite Manipulation

Prior to usurpation trials, parasites were marked with a spot of paint on the thorax to aid identification during video analysis. To test the importance of the clypeal pattern for agonistic interactions with hosts, parasites were randomly assigned to one of two treatment groups (Fig. 1). In Treatment 1 ($N = 14$), yellow paint was added to cover the black clypeus mark completely. In Treatment 2 ($N = 17$), yellow paint was added to the yellow genae to control for the presence of paint, the odour and spectral reflectance of which

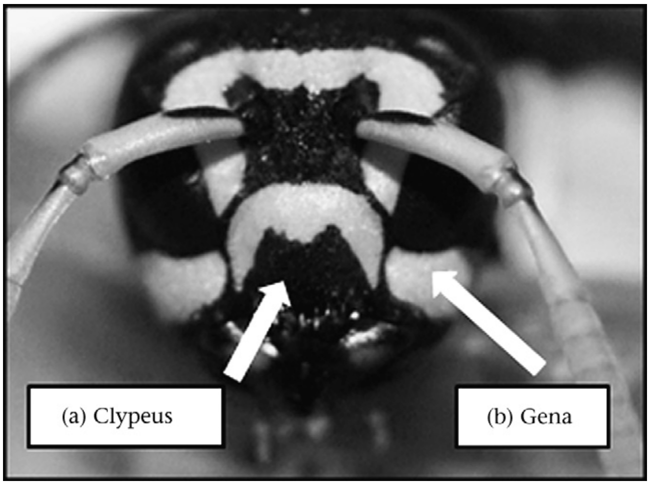

Figure 1. Head of *P. semenowi* (♀), with arrows indicating the (a) clypeus and (b) genae painted yellow in the experimental and control treatments, respectively.

are expected to differ from those of the cuticle. While it is possible that the presence of paint in general alters the behavioural response of the receiver, our experimental design allowed us to test for a specific effect of the parasite clypeal pattern on host behaviour over and above any general response to the presence of paint. Previous observations of manipulated parasites from established nests in the field have shown that such manipulations affect neither the parasite's ability to relocate its nest nor its subsequent behaviour towards hosts (J. P. Green, unpublished data).

Usurpation Trials

Thirty-one usurpation trials were carried out outdoors on warm, bright days between 1300 and 1600 hours (identified by Ortolani & Cervo (2009) as the time of peak activity in a related social parasite, *P. sulcifer*). In each trial, a single parasite was placed in a plastic cage (34 × 18 cm and 27 cm high) containing a target host nest and allowed to approach the nest and interact with hosts. In those trials where the parasite approached the nest within 2 h, we filmed all fights between parasites and hosts for 1 h following the initial approach (henceforth, 'observation period') using digital camcorders. Each parasite and host colony was used only once in the trials.

Morphological Measurements

Upon completion of usurpation trials all individuals were killed by freezing. Following Tibbetts & Dale (2004) and Ortolani & Cervo (2010), we used head width as a measure of body size. For each wasp, the head was removed and placed on a microscope slide. Head width was measured as the width at the widest point using a 16× binocular microscope. At the same time we recorded the presence or absence of clypeal patterns on the hosts. The presence or absence of clypeal patterns can be used as a simple indicator of host quality (Tibbetts & Lindsay 2008), and relates closely to the active signal component, brokenness: hosts without clypeal patterns have a lower brokenness (i.e. 0) than hosts with clypeal patterns.

Behavioural Analyses

For each trial, we recorded the total number of fights within the observation period. We also recorded the duration of each fight, with a pause of more than 30 s signifying the end of a fight. To investigate the effect of parasite clypeal patterns on aggressive interactions, we used data only from the initial encounter between parasite and hosts (i.e. the first fight, following the parasite's initial approach to the nest), as it has been suggested that familiarity between signaller and receiver can confound manipulative tests of signal function (Senar 1999). We obtained three measures from each initial fight: its duration and two measures of its intensity. To assess fight intensity, we distinguished between two classes of agonistic interactions observed during fights, according to likely energetic costs and risk of injury. 'Low-intensity' interactions were darting, antennating, chasing and lungeing (here defined as a rapid movement towards an individual resulting in physical contact). 'High-intensity' interactions were biting, grappling, 'dive bombing' (a behaviour shown by hosts during usurpation attempts in the wild where hosts fly into the parasite, pushing or biting on contact) and wrestling (wasps clasp legs tightly around one another attempting to sting and/or bite opponent). Fight intensity was then estimated in two ways: the number of high-intensity interactions occurring during it, and the total duration of these high-intensity interactions (as a proportion of total fight duration).

Statistical Analyses

All analyses were performed using the software R version 2.9.2 (http://www.r-project.org/). To test the signal function of the parasite clypeal patterns, we compared the duration and intensity of the first fight between the two treatment groups. The effect of the paint treatment on fight duration was analysed using a linear model (LM) with normal errors. Fight duration (log transformed) was fitted as the dependent variable with paint treatment fitted as a categorical independent variable. Recent work has suggested that, in *P. dominulus*, receiver responses to clypeal patterns depend on the RHP of receivers (Tibbetts et al. 2010). As a measure of receiver RHP, we recorded the proportion of hosts with clypeal patterns on each nest (i.e. within each trial). To test whether host responses to the parasite manipulations were dependent upon host RHP, we included the interaction between paint treatment and proportion of hosts on the nest with clypeal patterns as a covariate in the analysis. To examine the effect of parasite clypeal patterns on fight intensity, we compared both the number and duration of high-intensity interactions between treatments. A generalized linear model (GLM) with a quasi-Poisson error distribution was used to analyse the number of high-intensity interactions, as these data were in the form of overdispersed counts. The duration of high-intensity interactions was analysed as a proportion of the total fight duration. As these data also exhibited overdispersion, they were analysed using a GLM with quasibinomial errors. Paint treatment was fitted as an independent variable in both models and, as above, we also included the interaction between paint treatment and the proportion of hosts with clypeal patterns.

To investigate the influence of body size on RHP, we compared the sizes of winners and losers of usurpation contests. Parasites that succeeded in usurping nests were considered winners, and their defeated hosts losers; likewise, parasites that failed to usurp were losers, and their successful hosts winners. Measurements taken from winners and losers cannot be considered as independent because the outcome of a contest (i.e. who wins) is determined by the interaction between the two contestants (Briffa & Elwood 2010). Therefore, to explore the effect of size on contest outcome, we ran a general linear mixed model (GLMM) with normal errors in which 'trial number' was fitted as a random factor. Following Briffa & Elwood (2010), size was fitted as the dependent variable and outcome ('winner' or 'loser') as an independent variable. In the special case of interspecific contests, it is possible that the extent to which a trait influences contest outcome varies between the two species. To investigate whether the importance of size for contest outcome varies between parasites and hosts, we also fitted the interaction between outcome and contestant species (host or parasite).

Finally, we explored the relationship between winner and loser size and contest duration and intensity to test for possible assessment rules governing usurpation contests. First, we examined the relationship between winner and loser size and the duration and intensity of the first fight. Winners and losers were assigned based on whether the parasite was present on the nest at the end of the fight. The effect of winner/loser size on duration was analysed using a linear model with normal errors. Fight duration (log transformed) was the dependent variable, and winner and loser size the independent variables. As above, fight intensity was analysed as both the number and duration of high-intensity interactions using GLMs with quasi-Poisson and quasibinomial errors, respectively.

Second, we tested for a relationship between winner and loser size and the total number and duration of fights within the 1 h observation period. Here, winners and losers were assigned based on whether the parasite was present on the nest at the end of the observation period. The effect of winner–loser size on total duration was analysed using a linear model with normal errors. Total duration (log transformed) was the dependent variable, and winner and loser size the independent variables. Total number of fights did not follow a normal distribution due to many encounters involving only a single fight. We therefore used a GLM with Poisson errors with number of fights as the dependent variable, and winner and loser size as the independent variables.

For all analyses, model simplification proceeded by backwards deletion of nonsignificant terms until further removals led to a significant ($P < 0.05$) increase in deviance. This was assessed by comparing the models with and without the term in question, using tabulated values of F values for linear models with normal, quasi-Poisson or quasibinomial errors, χ^2 values for linear models with Poisson errors, and log likelihood tests for linear mixed models. Significance levels are reported for the addition of nonsignificant terms, and removal of significant terms, from the minimal adequate model. In all analyses, host head width was calculated as the mean head width of hosts within colonies. Substituting mean host head width for the head width of the largest host did not alter the results. Means are reported ± SE.

RESULTS

Usurpation attempts by the parasite (observed in 24/31 trials) were characterized by one or more approaches towards the host nest, resulting in physical fighting with the hosts. The initial fight continued until the parasite retreated (11/24 trials), or until the hosts withdrew, leaving the parasite alone on the nest (13/24 trials). Parasites that retreated after the initial fight were observed to make further approaches to the nest in six of 11 trials. Where parasites succeeded in taking over the nest after the initial fight, hosts returned and engaged the parasite in further fighting in eight of 13 trials. At the end of the observation period (1 h after the initial approach), 14 parasites were on the nest and 10 were off the nest.

For those trials in which parasites approached the nest, we examined the influence of the clypeal pattern manipulation on the dynamics of the ensuing fight. Duration of the initial fight was not influenced by the pattern manipulation (LM: paint treatment: $F_{1,23} = 0.35$, $P > 0.5$; treatment*proportion of hosts with clypeal spots: $P > 0.1$; Fig. 2). Independent of the pattern manipulation, fight duration tended to be positively related to the proportion of hosts on a nest with clypeal patterns, although this was not statistically significant ($F_{1,23} = 3.56$, $P = 0.07$). Manipulation of the clypeal pattern also had no effect on the intensity of the first fight, in terms of either the frequency of high-intensity interactions (GLM: $F_{1,23} = 0.31$, $P > 0.5$; treatment*proportion of hosts with clypeal spots: $P > 0.1$) or the proportion of time spent engaged in high-intensity interactions (GLM: $F_{1,23} = 0.04$, $P > 0.5$; treatment*proportion of hosts with clypeal spots: $P > 0.5$). Again, however, there was an independent effect of host clypeal patterns: relatively more time was spent engaged in high-intensity interactions when a higher proportion of hosts had clypeal patterns ($F_{1,23} = 6.55$, $P = 0.02$). The proportion of hosts on a nest with clypeal patterns also tended to be positively associated with the frequency of high-intensity interactions, although this was not statistically significant ($F_{1,23} = 3.60$, $P = 0.07$).

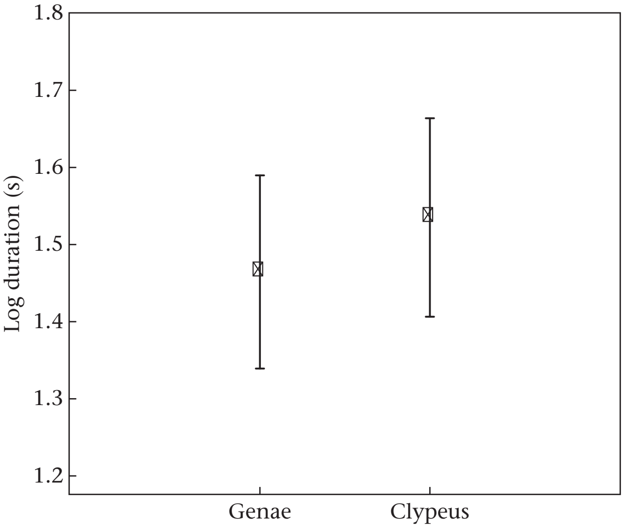

Figure 2. Duration of initial fights in relation to parasite manipulation (paint concealing the genae or clypeus). Points and bars show means ± 1 SE. $N = 24$ fights.

To explore the role of body size in RHP, we compared the sizes of winners and losers. Winners of the first fight (i.e. the fight following the initial approach by the parasite) were not significantly larger than losers (GLMM: $L_1 = 0.86$, $P > 0.1$; winners: 3.57 ± 0.02; losers: 3.54 ± 0.03 mm). However, in a second comparison of winner and loser size, this time based on whether nests had been usurped by the end of the observation period (i.e. 1 h after the first interaction), winners were significantly larger than losers (GLMM: $L_1 = 5.45$, $P = 0.02$; winners: 3.59 ± 0.02; losers: 3.51 ± 0.02 mm; Fig. 3). There was no significant interaction between outcome and species, indicating that the importance of size in determining fight outcome did not vary between species ($L_1 = 2.10$, $P > 0.1$). Two processes could account for the increase in size difference between winners and losers observed over the observation period. First, larger parasites that initially failed to usurp the nest may win against hosts in further fights. Although small sample sizes preclude statistical analysis, a comparison of mean head widths suggests this might be the case: average head width of parasites that subsequently usurped the nest was greater than that of parasites that lost the first fight and did not ultimately manage to usurp nests (3.69 ± 0.06 versus 3.52 ± 0.05 mm, $N = 3$ and 8, respectively). Additionally, or alternatively, smaller parasites may be more vulnerable to eviction from the nest if they are less able to resist further attacks from hosts following initial usurpation.

The importance of body size as a determinant of contest outcome indicates that information about own size and possibly rival size may be useful to individuals when choosing whether to persevere or retreat. To test for possible assessment rules, we

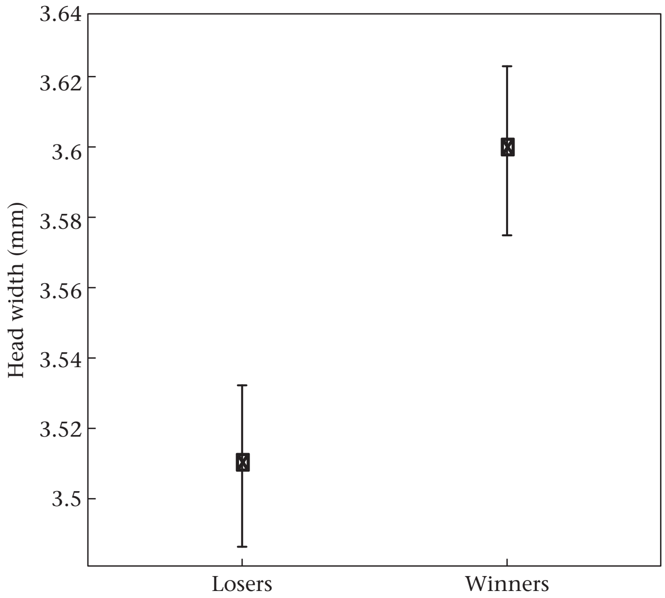

Figure 3. Mean head width of winners and losers, based on whether the parasite was on the nest at the end of the observation period (1 h after first approach). Points and bars show means ± 1 SE. $N = 24$ fights.

analysed the relationships between contest dynamics and the size of winners and losers. Focusing on the first fight, we found no significant relationship between fight duration and the size of winners (LM: $F_{1,23} = 0.00$, $P > 0.5$) or losers ($F_{1,23} = 0.00$, $P > 0.5$). We also found no relationship between the intensity of the first fight and the size of winners or losers, whether considering the frequency (GLM: winners: $F_{1,23} = 0.05$, $P > 0.5$; losers: $F_{1,23} = 0.16$, $P > 0.5$) or duration (GLM: winners: $F_{1,23} = 0.16$, $P > 0.5$; losers: $F_{1,23} = 0.01$, $P > 0.5$) of high-intensity interactions.

Total duration of all fights that occurred within the observation period was not significantly predicted by either winner size (LM: $F_{1,23} = 0.67$, $P > 0.1$) or loser size ($F_{1,23} = 0.20$, $P > 0.5$). Likewise, the total number of fights was not significantly predicted by size of either winners (GLM: $\chi^2_1 = 1.62$, $P > 0.1$) or losers ($\chi^2_1 = 2.27$, $P > 0.1$).

DISCUSSION

The Importance of Clypeal Patterns

We found no evidence that clypeal patterns in the social parasite *P. semenowi* function to minimize aggression from hosts during nest usurpation. Previous research into rival assessment in North American populations of *P. dominulus* has emphasized the importance of clypeal patterns as signals of RHP in settling contests between unfamiliar individuals (Tibbetts & Lindsay 2008; Tibbetts et al. 2010). While evidence for intraspecific status signalling via clypeal patterns in European populations is more limited (Cervo et al. 2008; Zanette & Field 2009; Green & Field 2011), results from a recent experiment have suggested that such patterns may be important in interspecific contests (Ortolani et al. 2010). Presentation experiments using heads of a related social parasite *P. sulcifer* demonstrated an increase in host aggression towards parasite heads that had been manipulated to conceal the clypeal pattern (Ortolani et al. 2010). This finding raises the possibility that parasite clypeal patterns could function as interspecific status badges, exploiting a mechanism of conflict resolution among hosts to dissuade hosts from aggressive retaliation during nest usurpation. Alternatively, the parasite's patterns may function as 'amplifiers' (Taylor et al. 2000), highlighting the width of the mandibles (Ortolani et al. 2010). Here, the clypeal pattern communicates fighting ability by amplifying a trait (mandible width) that is larger in *Polistes* social parasites than in their hosts and thought to confer superior fighting ability (Cervo 2006; Ortolani et al. 2010). In our experiment, which simulated real usurpation contests between *P. dominulus* hosts and the social parasite *P. semenowi*, concealment of the pattern did not result in greater aggression from hosts, in terms of either fight duration or intensity. In addition, a nonsignificant interaction between treatment and the proportion of hosts with clypeal marks showed that this response to the paint treatment was not dependent on hosts' clypeal patterns. Our results therefore suggest that *P. semenowi* clypeal patterns are not used in rival assessment during nest usurpation, either as status badges or amplifiers. The relatively small sample sizes in our study, necessitated by logistical considerations (i.e. the relative rarity of parasites in our population), might suggest that we cannot put too much faith in the negative results we have obtained. The effect size (Cohen's *d*) that we obtained was 0.24 with 95% confidence interval = −0.56–1.05 (note that this is on a log scale). Thus, for our analysis to detect a significant influence of the manipulation on fight duration, the effect size would need to be large (i.e. >1.05 standard deviations; similar effect sizes would also be necessary to detect a significant effect of the manipulation on fight intensity). However, other experiments using our Spanish population and employing larger sample sizes have also found no evidence that hosts react to rival clypeal patterns, this time during interactions with conspecifics (Green & Field 2011). Below, we discuss the difference in results between this study and that of Ortolani et al. (2010) in terms of the context dependence of receiver behaviour and the costs and benefits of rival assessment during usurpation contests (see Limitations on Rival Assessment).

Although parasite clypeal patterns play no role in usurpation contests, host clypeal patterns do influence fight dynamics: initial fights were significantly more intense and also tended to be longer in trials where a greater proportion of defending hosts had clypeal patterns. One explanation for this is that hosts with clypeal patterns have higher RHP and are better able to resist the invading parasite, investing energy in prolonged and high-intensity defence behaviours (Tibbetts & Dale 2004; Tibbetts & Shorter 2009), although we again note that other experiments on this population have found no evidence that clypeal patterns communicate this information to conspecifics (Green & Field 2011). A second explanation is that parasites are more motivated to attack nests of patterned hosts because such colonies are more attractive to the parasite, leading to longer and more intense fights. Previous work has shown that *Polistes* social parasites preferentially target larger nests with mature brood (Cervo & Turillazzi 1996; Shreeves et al. 2003). If host clypeal patterns reflect aspects of quality associated with greater colony size and productivity (e.g. survival, fecundity), then parasites able to assess host clypeal patterns, or traits correlated with patterning, might be expected to target high-quality hosts preferentially. Further research into the characteristics of host colonies targeted by the parasite is needed to determine which host traits are favoured by *P. semenowi*, as well as how these traits are assessed by the parasite during host selection.

The Importance of Body Size

Our analysis revealed the importance of opponent size on outcome of parasite usurpation attempts. Larger parasites were more likely to usurp nests successfully, while larger hosts were more successful in defending nests. Body size has often been highlighted as a potential determinant of RHP in *Polistes* wasps (e.g.

Turillazzi & Pardi 1977; Cervo et al. 2008). In particular, previous studies have indicated that body size influences both intraspecific (Tibbetts & Shorter 2009) and interspecific (Ortolani & Cervo 2010) usurpation contests. Ortolani & Cervo (2010) examined geographical variation in *P. dominulus* body size in relation to parasitism by a second social parasite, *P. sulcifer*. They found that larger hosts were more active in fighting a usurping parasite off the nest, and were less likely to be parasitized (Ortolani & Cervo 2010). Furthermore, the occurrence of larger hosts in populations experiencing high rates of parasitism led them to suggest that larger host body size may be the result of a parasite–host arms race, in which large body size is selected as a defence against parasite invasion (Ortolani & Cervo 2010). Our result suggests that a similar relationship may be found between *P. dominulus* size and *P. semenowi* density; however, more data on host size and parasitism rates from different areas are needed to test this hypothesis.

Our finding that size influences the outcome of usurpation contests raises the possibility that information about opponent size is used in decision making during competitive interactions (Arnott & Elwood 2009). To investigate whether size-based assessment occurs during usurpation contests, we analysed the relationship between duration and intensity of the first fight, as well as the total number and duration of fights within the observation period, and the size of winners and losers (as judged by usurpation success/failure). Looking within the first fight, we found that neither duration nor intensity was significantly predicted by the size of winners or losers. Furthermore, within the whole observation period, neither total fight duration nor the total number of fights was significantly predicted by either loser or winner size. Again, however, we note the relatively small sample sizes available in our study. Calculation of effect sizes indicates that moderate to large effects of size on fight measures could be detected with our sample size. For example, the size of the effect of loser size on contest duration (partial correlation coefficient, r) is -0.1 with 95% confidence interval $= -0.48–0.32$ (on a log scale), and the other effects were of similar sizes.

The absence of a positive correlation between loser size and measures of fight duration and/or intensity in particular argues against assessment by rivals during usurpation. A common prediction of all models of assessment is that contest duration and/or intensity should increase with increasing loser RHP (Arnott & Elwood 2009). This is true for strategies of self-assessment, where the decision to withdraw is taken when some cost threshold, determined by individual RHP, is exceeded (Taylor & Elwood 2003). In the case of mutual assessment, a positive relationship between loser RHP and duration and/or intensity is also expected, given that the decision to withdraw versus escalate is based on RHP asymmetry between contestants, which is most easily perceived when differences in RHP are large (Taylor & Elwood 2003). The absence of a positive relationship between loser size and duration or intensity in this study would therefore appear to rule out assessment during usurpation contests. Thus, while larger body size confers greater RHP, there is no evidence that size assessment is used to minimize fight costs during usurpation attempts.

Limitations on Rival Assessment

The ability to use information about opponent RHP to make tactical decisions during fights is often considered advantageous as it allows individuals to avoid the costs (e.g. injury, depletion of energy reserves) of escalated conflict. Given the benefits of assessment, our finding that wasps do not use information about rival RHP is somewhat surprising. A possible explanation for the apparent lack of assessment is that both hosts and parasite are highly motivated to fight on account of the high value of the contested resource. From the hosts' perspective, usurpation of a colony by a social parasite represents a potentially fatal assault on host fitness. Upon usurpation, the parasite destroys younger brood, preserving older brood as a workforce to rear its offspring (Cervo 2006). Combined with high reproductive skew in favour of the parasite (J. P. Green & J. Field, unpublished data), this often results in a dramatic reduction in host fitness following parasitism. Although it has been shown that *Polistes* foundresses can build new nests following nest predation (Strassmann et al. 1988), the extent to which this is a viable option for parasitized hosts is unknown. Usurpation by social parasites occurs at a relatively late stage in the season (i.e. just prior to worker emergence); opportunities for renesting may therefore be time limited. However, the potential for renesting is likely to influence perceived nest value during host–parasite contests and therefore merits further study, particularly as there is evidence that hosts do occasionally abandon nests following successful usurpation by parasites (E. Almond & J. Field, unpublished data).

From the perspective of the parasite, which is dependent on a host workforce for offspring production, successful usurpation is critical to parasite fitness. Furthermore, parasites enjoy only a brief window in which to attack, in the late pre-emergence period of the host nest cycle (Cervo 2006), which would be expected to limit the number of usurpation attempts a parasite can make, whether on the same nest or on different nests. No direct evidence for multiple usurpation attempts by *P. semenowi* in the wild is available at present, and would require both tracking of individual parasites and detection of all usurpation attempts, which are sometimes very brief (J. P. Green, personal observations).

In the case of usurpation contests, therefore, the fitness payoff associated with successfully usurping or successfully defending the nest may in fact exceed any costs associated with escalated fighting (Enquist & Leimar 1990), thereby negating any benefit of rival assessment. Furthermore, given the enhanced weaponry of *Polistes* social parasites (Cervo 2006), any respect shown for RHP asymmetries during usurpation fights would often, if not always, result in acceptance of the parasite by the host colony, and the fitness costs associated with parasitism. In the face of these 'divisive' asymmetries (Grafen 1987), the optimal strategy may be to persevere irrespective of asymmetries in RHP until the costs of injuries and depletion of energy reserves force retreat (Grafen 1987). Support for this scenario comes from observations (this study) of serious injuries sustained to both hosts and parasites during trials, including the loss of legs and damage to wings. Although such injuries impose significant costs, escalated fighting of the kind we observed may still be favoured if such costs are outweighed by the cost of losing the nest (Enquist & Leimar 1990; Elias et al. 2010).

High resource value may also explain why we found no evidence of rival assessment based on clypeal patterns. The use of signals or cues of RHP is argued to facilitate assessment prior to fighting, thereby minimizing costs of conflict (Maynard Smith & Harper 2003). However, such signals may have limited value in contexts where resource value is high (Maynard Smith & Harper 1988; Tibbetts 2008). As discussed, nest usurpation may be one context in which the value of the resource actually exceeds the cost of fighting; status signals may therefore be of limited importance in such contests. In the experiments by Ortolani et al. (2010), which demonstrated an effect of parasite clypeal patterns on host aggression, receiver responses were not tested in the context of nest usurpation. In such a context, we have found that parasite clypeal patterns do not modulate host aggressive behaviour. In a separate observational study of intraspecific nest usurpation in *P. dominulus*, usurpation success was predicted by the relative clypeal patterns of the intruder and resident (Tibbetts & Shorter

2009). However, signal manipulation experiments testing whether patterns alone determined contest outcome were not performed. If, in real usurpation attempts, the motivation for intruders (conspecifics or social parasites) to attack and for hosts to defend is high, then selection may favour escalation over information gathering that allows tactical retreat based on opponent assessment (Grafen 1987; Enquist & Leimar 1990; Moore et al. 2008).

This study aimed to investigate potential assessment rules guiding interspecific contests between a usurping social parasite and its hosts. We found no evidence that parasite clypeal patterns function to reduce host aggression during contests. Larger parasites were more successful in usurping nests, and larger hosts more successful in defence, but assessment based on size does not appear to occur during contests. We focused on size as a determinant of RHP in this study; future work that investigates assessment based on other RHP determinants would provide a clearer picture of assessment during *Polistes* host–social parasite contests. Studies that explored the physiological basis of energetic costs during usurpation fights (Weiner et al. 2009) may be particular valuable in this regard.

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