The elusive paradox: owner–intruder roles, strategies, and outcomes in parasitoid contests

Tom Bentley, Tristan T. Hull, Ian C.W. Hardy, and Marlène Goubault

The School of Biosciences, University of Nottingham, Sutton Bonington Campus, Loughborough, Leicestershire LE12 5RD, UK and Institut de Recherche sur la Biologie de l’Insecte, IRBI UMR CNRS 6035, Université François Rabelais, 37200 Tours, France

Models of dyadic contests for indivisible resources have predicted that the owner–intruder role distinction can suffice as a cue for evolutionarily stable resolution. This outcome may be “common sense” (prior owners retain the resource) or counterintuitively “paradoxical” (the intruder takes over), but the most recent models predict paradoxes to be an infrequent result, and there are also very few candidate examples provided by empirical study. Possible paradoxical outcomes were recently reported from the parasitoid wasp Goniozus legneri in which adult females compete directly for hosts. Here we provide further investigation, taking into account influences of contest ability (body size) and the value of the host to each contestant (correlated with the developmental stage of the owner’s brood). We additionally evaluate contest strategies in terms of respect for ownership as evidenced by attack behavior during contests. Goniozus legneri shows weak, and thus only partial, respect for role asymmetries: such mixed strategies are predicted by recent models that assume population-level feedback on resource value parameters. Contest outcomes are influenced by asymmetries in resource value and body size and are generally common sense. Instances of paradoxical contests remain predictably elusive. Key words: antibourgeois strategy, Goniozus legneri, maternal investment, paradoxical strategy, partial respect, resource value asymmetry. [Behav Ecol 20:296–304 (2009)]

Empirical evidence from many animal species indicates that owners (prior residents) are usually advantaged over intruders during contests for resources such as territories, food, or mates (reviewed by Kokko et al. 2006). Some of the earliest game theoretic models in behavioral ecology were developed to understand contest outcomes in terms of a range of contestants’ properties, including owner–intruder role asymmetries (e.g., Maynard Smith and Parker 1976; Hammerstein 1981; Maynard Smith 1982; Leimar and Enquist 1984). Two strategies, termed “bourgeois” and “antibourgeois,” were added to the original Hawk–Dove model of Maynard Smith and Price (1973): individuals adopting the bourgeois strategy behave aggressively only when they are the owner of the resource, whereas those adopting the antibourgeois strategy behave aggressively when in the owner role (Maynard Smith and Parker 1976). It is predicted that ownership asymmetry is sufficient to resolve contests, whether in the presence or absence of other types of asymmetries, such as differences in fighting ability or the value of the resource to each contestant; this is because costly activities such as injurious fighting are avoided to the benefit of both parties (Maynard Smith and Parker 1976). Further, both bourgeois and antibourgeois strategies can be evolutionarily stable when the value of the contested resource is less than the cost of fighting. Because the antibourgeois strategy appears counterevolutionary, it has been termed “paradoxical,” whereas the bourgeois strategy is known as “common sense” (Maynard Smith and Parker 1976; Maynard Smith 1982; Kokko forthcoming). The initial prediction that paradoxical strategies can be evolutionarily stable fuelled further debate and theoretical investigations (e.g., Grafen 1987; Maynard-Gibbons 1992; Maynard-Gibbons and Adams 1998; Kokko et al. 2006) predicting that paradoxes might be expected to be less frequent than commonsense strategies (Mesterton-Gibbons 1992; Kokko et al. 2006).

Although paradoxes remain theoretically possible, there is a dearth of empirical demonstration: candidate examples are rare. Apparent paradoxes in the social spider Oecobius civitas (Burgess 1976) have not received sufficiently detailed attention (Mesterton-Gibbons and Adams 1998); reported paradoxes in the butterfly Heliconius sara (Hernández and Benson 1998) turned out to be due to misinterpretation of incorrect terminological usage (Field and Hardy 2000; Kemp 2000), whereas in the goldeneye fish, Hiodon alosoides, paradoxical outcomes appear genuine, in that intruders tend to win, but are potentially explained by confounding effects of asymmetries in contest ability and/or resource value (Fernet and Smith 1976). Recently, it was reported (from a study focusing on chemical release behavior) that intruders, rather than owners, were advantaged during contests for paralyzed hosts between females of the parasitoid wasp Goniozus legneri (Goubault et al. 2006), and the same, apparently paradoxical, effect was found in independently collected data from a simple experimental design (Appendix 1). Paradoxical outcomes in G. legneri might be a particular comundrum because the conditions predicted to lead to their evolutionary stability (high background mortality of owners, low mortality of “floating intruders,” high frequency of discovery of resources by intruders, and high costs of fighting; Kokko et al. 2006) all seem unlikely. This paper therefore provides a reinvestigation of contests in this species. Because owner–intruder differences may also be associated with differences in resource value or fighting ability (Fernet and Smith 1976; Grafen 1987; Stokkebo and Hardy 2000; Kemp and Wiklund 2004; Kokko et al. 2006; Kokko forthcoming), we used more detailed experiments to assess whether paradoxical owner–intruder contest outcomes would be consistently obtained when further asymmetries were present.

Kokko et al. (2006) pointed out that discrepancies between theoretical predictions and empirical observations may be due
to models predicting contestants’ strategies, whereas empirical studies usually focus on contest outcomes. Although outcomes are influenced by the strategies adopted by contestants, they do not always reflect their behaviors. For instance, owner victory does not necessarily indicate respect for ownership as intruders can be predicted to fight (no respect) even when they have a low probability of winning (“desperado effect,” Grafen 1987; Kokko forthcoming). We therefore investigated whether owners and intruders respect ownership as evidenced by their behaviors during contests and the influences of asymmetries in fighting ability and resource value on these.

**Goniozus legneri biology and contest behavior**

*Goniozus legneri* Gordh (Hymenoptera: Bethylidae) females attack lepidopteran larvae that tunnel into tissues of crops such as pistachio nuts, almonds, and apples (Steffan et al. 2001; Zaviezo et al. 2007). They paralyze each host by stinging and lay eggs onto its surface approximately 24 h later (larger clutches are laid onto larger hosts; with range =5–20 and mean of =9 eggs; Hardy et al. 1998; Goubault and Hardy 2007). Females typically defend their host against conspecific intruders, which leads to classic owner–intruder contests with outcomes influenced by asymmetries in body size (which can be viewed as equivalent to fighting ability) as well as ownership status (Goubault et al. 2006; Table 1). Possible additional effects of asymmetries in resource value are likely, as they have been found in the congener *Goniozus nephantidis* (e.g., Humphries et al. 2006; Goubault et al. 2007; Table 1) but have not previously been evaluated in *G. legneri*. Similarly, intruder females that win against brood-guarding owners may be expected to commit ovicide and larvicide, as observed in *G. nephantidis* (Hardy and Blackburn 1991; Goubault et al. 2007), and *G. legneri* mothers may thus be expected to attenuate their maternal investment (host-guarding behavior) to the developmental stage reached by their brood (resource value), provided that this influences the probability of their offspring surviving the presence of an intruder (Goubault et al. 2007). We therefore investigated the time invested in brood guarding by unchallenged owners (mothers), the survival of offspring at different developmental stages in the presence of owners and intruders (owner’s payoff from winning owners), use of acquired hosts by intruders (intruder’s payoff from winning), as well as the influence of ownership, female size, and resource value asymmetries on contest outcomes and agonistic behavior.

**MATERIALS AND METHODS**

**Rearing procedure**

*Goniozus legneri* were reared on larvae of the factitious host *Corcyra cephalonica* (Stainton) (Lepidoptera: Pyralidae). Cultures and experiments were carried out in a climate room (27 °C, 12:12 light:dark) with relative humidity maintained by evaporation from a water bath. The parasitoid strain was obtained from a commercial insectary in the USA, and both host and parasitoid strains were the same as used in several previous studies (e.g., Goubault et al. 2006; Goubault and Hardy 2007). All culturing procedures followed those previously described for the congener *G. nephantidis* by Stokkebo and Hardy (2000).

**Maternal investment of unchallenged owners**

We investigated the time *G. legneri* mothers invest in brood guarding when they are unchallenged by conspecific intruders and free to leave their brood following methods developed for *G. nephantidis* by Goubault et al. (2007). Twenty newly emerged females of known weight (to an accuracy of 0.01 mg) were individually provided with a 30- to 40-ng host (mean = 34.44, standard deviation = 2.29). Once females had paralyzed their host (usually within 24 h), they were transferred with it into a 1-chamber plastic block covered by a transparent lid, which was placed into a sealed 1-L transparent plastic container. The owner–intruder setup was a 1-chamber block: females could therefore freely exit (and reenter) the chamber but not the larger container (Hardy et al. 2008).

**Table 1**

<table>
<thead>
<tr>
<th>Species</th>
<th>Study</th>
<th>Type of contest&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Ownership effect</th>
<th>Body size effect</th>
<th>Resource value correlates explored&lt;sup&gt;b&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Goniozus nephantidis</em></td>
<td>Petersen and</td>
<td>I-O</td>
<td>+</td>
<td>+</td>
<td>Egg load, NE; host size NE</td>
</tr>
<tr>
<td></td>
<td>Hardy 1996</td>
<td>O-O</td>
<td></td>
<td></td>
<td>Egg load, E; host size NE</td>
</tr>
<tr>
<td></td>
<td>Stokkebo and</td>
<td>I-O</td>
<td>+</td>
<td>0&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Host size, NE; intruder age, E</td>
</tr>
<tr>
<td></td>
<td>Hardy 2000</td>
<td>O-O</td>
<td></td>
<td></td>
<td>Host size, E; clutch size, NE</td>
</tr>
<tr>
<td></td>
<td>Humphries et al.</td>
<td>I-O</td>
<td>+</td>
<td></td>
<td>Brood stage, E&lt;sup&gt;d&lt;/sup&gt;; Host size, NE</td>
</tr>
<tr>
<td></td>
<td>Goubault et al.</td>
<td>O-O</td>
<td></td>
<td>0&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Brood stage, E; Host size, E; Clutch size, NE</td>
</tr>
<tr>
<td></td>
<td>2007</td>
<td>O-O</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Goniozus legneri</em></td>
<td>Goubault et al.</td>
<td>I-O</td>
<td>+</td>
<td>0&lt;sup&gt;c&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2008&lt;sup&gt;e&lt;/sup&gt;</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>This study (Appendix 1)</td>
<td>I-O</td>
<td>+</td>
<td></td>
<td>Brood stage, NE</td>
</tr>
<tr>
<td></td>
<td>This study</td>
<td>I-O</td>
<td>+</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> I-O, Intruder–owner contest; O-O, owner–owner contest.

<sup>b</sup> E, effect on contest outcome detected; NE, no effect detected.

<sup>c</sup> Body size differences were minimized in this experiment.

<sup>d</sup> Additional evidence is presented in Hardy and Blackburn (1991).

<sup>e</sup> Deuteration also affected outcomes in *G. legneri* but not *G. nephantidis*, see also Goubault and Hardy (2007).

<sup>f</sup> Interpretation based on visual inspection.
[1999] provide illustration of similar apparatus used to assess Goniozus dispersal.

The location of the females was monitored every 12 h, without disturbing the females (i.e., without moving or opening the containers), until they died. Females’ locations were classified as "in the chamber with the host," "in the opening of the plastic block," or "outside of the block" (i.e., within the larger container). In addition, the developmental stage reached by any offspring was noted when visible with the naked eye.

**Contestant properties, contest outcomes, and agonistic behavior**

To investigate contestant’s agonistic behaviors and maternal brood-guarding success during contests in relation to the developmental stage reached by their offspring, 105 contests were set up each between an intruder female and an owner guarding a host. On emergence from the pupal cocoon as adults, all females were marked with a dot of water-based acrylic paint (either red or yellow) on the dorsal surface of the thorax. Females designated as intruders were not given a host, whereas females designated as owners were provided with a 30- to 40-mg host larva. At the time of the contest (see below), the owner’s host was either unparasitized (hosts were paralyzed but no eggs had been laid on them, N = 31) or bore the owner’s offspring that had reached one of the following developmental stages: eggs (N = 26), young larvae (N = 21), or old larvae (N = 27). ”Young” larvae are those that have very recently hatched and started to feed (i.e., first and second instars), whereas “old” larvae are considerably larger, have consumed much of the host, and are close to detaching themselves from the remains of the host to pupate.

Contests were staged between nonsibling females of similar age and marked with a different paint color, using the previously developed “contest chamber” consisting of a 3-chamber plastic block covered by a transparent lid (Petersen and Hardy 1996; Goubault et al. 2000). The chambers were connected by a slot but initially isolated by barriers sliding in the slot. Owner females were introduced, with their host (bearing a known number of offspring), in the central chamber, whereas intruders were placed in a lateral chamber. After a settlement time of 30 min, the barriers separating the chambers were withdrawn, allowing the females to move freely through all chambers and the slot. Contests lasted 90 min and were filmed with a video camera placed above the central chamber. At the end of each replicate, the contest outcome was noted: the female in close vicinity of the host was considered as the winner and the losing female was no longer in the central chamber. At the end time for some replicates, contesting females were both in the central chamber or both in the lateral chambers; in these cases, contest outcome was classified as a draw.

At the end time of all replicates, both females were then weighed (to an accuracy of 0.01 mg) and dissected to assess their egg load (i.e., number of mature eggs present in their abdomen; Stokkebo and Hardy 2000). On subsequently viewing the videos, we noted the frequencies of agonistic behaviors (i.e., biting, attacking with stinger, or fighting by grappling; Goubault et al. 2006) displayed by owners and intruders during the observation period.

**Offspring survival in presence of intruders and intruder host use**

We compared the proportion of offspring reaching adulthood when in presence of the mother or another female (=intruder), which indicates the payoff to the owner of winning. Females were individually placed in a vial with a 30- to 40-mg host until the host was paralyzed only (no eggs laid) or on its surface bore eggs, young larvae, or old larvae. The hosts were then removed from the vials to count, under a dissecting microscope, the number of offspring present on the host and then either replaced with the mother or transferred to a vial containing a different adult female. Sample sizes usually ranged between 20 and 26 replicates (Tables 2 and 3).

When hosts bore eggs at the time of the transfer, eggs were individually marked red with eosin stain (Hardy and Blackburn 1991) to distinguish eggs laid before from those laid after host transfer. Numbers of eggs, larvae, cocoons, and adult emergents were checked daily to assess offspring survival. Offspring produced by intruders represent their payoffs from acquiring the owner’s host.

**Statistical analyses**

Data were analyzed using generalized linear modeling with Genstat statistical package (Version 8, VSN International, Hemel Hempstead, UK). We used (semi-)parametric analyses in which the assumed distribution of residuals was matched to the data, and we followed backward stepwise procedures and aggregation of factor levels to obtain the parsimonious “minimal adequate model” by model simplification (Crawley 1993; Quinn and Keough 2002; Wilson and Hardy 2002). Exploratory variables that were highly mutually correlated were not included in a same model to avoid interpretational problems due to collinearity (Grafen and Hails 2002; Quinn and Keough 2002). Egg load (correlated with female weight) and brood size (correlated with host weight) were therefore not included in the main analyses (see Results). Cohort-survival analyses (Crawley 1993) were used to explore the effects of female weight and host weight on the time mothers were first observed away from their brood (i.e., outside the observation block). The influences of females’, host’s, and brood’s properties on contest outcomes and the likelihood of agonistic behavior were assessed using logistic analyses (Hardy and Field 1998; Wilson and Hardy 2002; Goubault et al. 2006). Log-linear analyses (with correction for overdispersion; Crawley 1993) were used to explore relationships between

<table>
<thead>
<tr>
<th>Table 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percentage of offspring surviving to adulthood according to whether the mother or an intruder female was present</td>
</tr>
<tr>
<td>Mother’s brood</td>
</tr>
<tr>
<td>---</td>
</tr>
<tr>
<td>Absent (paralyzed host)</td>
</tr>
<tr>
<td>Eggs</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>Young larvae</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>Old larvae</td>
</tr>
<tr>
<td></td>
</tr>
</tbody>
</table>
Table 3
Intruder’s clutch size and offspring survivorship in relation to the stage of the brood on the owner’s host

<table>
<thead>
<tr>
<th>Owner’s brood stage</th>
<th>Intruder’s mean clutch size (N)</th>
<th>Mean % survival of intruder’s eggs to adulthood (N)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Absent (paralyzed host)</td>
<td>10.1 (20)</td>
<td>83.8 (20)</td>
</tr>
<tr>
<td>Eggs</td>
<td>8.0 (26)</td>
<td>60.8 (25)</td>
</tr>
<tr>
<td>Young larvae</td>
<td>1.4 (20)</td>
<td>32.1 (5)</td>
</tr>
<tr>
<td>Old larvae</td>
<td>0.0 (20)</td>
<td>— (0)</td>
</tr>
</tbody>
</table>

\[ F_{3,83} = 80.86, \quad F_{2,49} = 1.77, \quad P = 0.18^d \]

\[ a-c \] Different letters indicate a significant clutch size difference between brood stage categories.
\[ d \] Log-linear analysis corrected for overdispersion.
\[ e \] Logistic analysis corrected for overdispersion.

**RESULTS**

**Maternal investment of unchallenged owners**

Females tended to stay in the close vicinity of their hosts for 3–5 days (Figure 1). Once their eggs had hatched, mothers started leaving the observation block and most of them stopped attending their brood when offspring larvae began to pupate (i.e., after 6–7 days; Figure 1). The cumulative rate at which mothers were first observed out of the block was time dependent and increasing (i.e., a Weibull cohort-survival model with a rate and shape parameter fitted the data better than an exponential model with a rate parameter only: \( G_1 = 26.58, \quad P < 0.001 \)). The rate of leaving the block was influenced by neither female weight (\( G_1 = 0.35, \quad P > 0.05 \)) nor the initial weight of the host (\( G_1 = 0.56, \quad P > 0.05 \)).

**Contestant properties**

Egg load was correlated with both female weight (log-linear analysis, \( F_{1,195} = 54.08, \quad P < 0.001 \)) and female status (i.e., intruder or owner of paralyzed host or host bearing eggs, young larvae, or old larvae; \( F_{4,195} = 28.52, \quad P < 0.001 \)). The interaction between these 2 explanatory variables was also significant (\( F_{4,195} = 3.80, \quad P = 0.005 \); egg load generally increased with female weight except for females with old larvae for which the egg load slightly decreased with female size (Figure 2).

The number of offspring developing on owners’ hosts increased with host weight (log-linear analysis, \( F_{1,70} = 4.51, \quad P = 0.037 \)) but was independent of their developmental stage (i.e., eggs, young larvae, or old larvae; \( F_{3,70} = 2.30, \quad P = 0.11 \)).

**Contest outcomes**

Not all contests were clearly resolved at the end of the 90-min experiments: there was no clear winner in about one-third of the contests (37/105 summed across the 4 treatments). Although the probability of a contest having a clear winner was unaffected by intruder–owner weight difference (logistic analysis, \( G_1 = 0.01, \quad P = 0.94 \)), it decreased as offspring developed (\( G_3 = 19.94, \quad P < 0.001 ; \text{Figure 3} \)). The probability of having a winner was similar and high when owners guarded either paralyzed hosts or hosts bearing eggs (\( G_1 = 0.03, \quad P = 0.86 ; \text{Figure 3} \)) but was significantly lower when offspring were young larvae (\( G_1 = 12.64, \quad P < 0.001 ; \text{Figure 3} \)) and lower again when they were at the old larval stage (\( G_1 = 12.11, \quad P < 0.001 ; \text{Figure 3} \)). There was no significant interaction between size difference and developmental stage (\( G_3 = 0.70, \quad P = 0.55 \)).

Using the 68 replicates with a clear winner, we explored the effect of the difference in contest size (intruder weight minus owner weight), brood stage, and host weight on contest outcome. Outcomes were defined as a binary response: 1 = intruder won and 0 = intruder lost (Petersen and Hardy 1996).
The probability of an intruder winning was affected by the difference in contestant weights (logistic analysis, $G_1 = 31.61, P < 0.001$; Figure 4), with larger individuals tending to win. The probability of an intruder winning was, however, unaffected by the developmental stage of the owner’s brood ($G_0 = 0.37, P = 0.78$; Figure 4), host weight ($G_1 = 2.39, P = 0.12$), or the interactions between these 3 variables.

To investigate the importance of ownership status, we redefined contest outcome in terms of the color of the winning female: $1 =$ red wasp won and $0 =$ red wasp lost (for explanation, see Petersen and Hardy 1996) having first established that color was unrelated to contest outcome (red wasps won 34 of 68 contests; 2-tailed binomial test: $P = 1.00$). Using the color of the winner as the response variable, logistic analysis showed that both ownership status and contestant weight difference influenced outcome and interacted significantly ($G_1 = 4.56, P = 0.03$): owners were advantaged even when slightly smaller than intruders. Outcomes defined by contestant mark color were not influenced by the stage of the owner’s brood ($G_1 = 2.55, P = 0.054$).

**Agonistic behavior**

The occurrence of agonistic behavior exhibited by owners was uninfluenced by the owner–intruder weight difference (logistic analysis, $G_1 = 1.91, P = 0.17$) but was affected by both host weight and brood stage: owners were more likely to defend larger hosts ($G_1 = 8.11, P = 0.004$) and those that had not yet reached the “old larvae” stage ($G_1 = 10.18, P = 0.02$); there was no difference in the intensity of owners’ defense of hosts between the remaining categories of paralyzed, with eggs, or with young larvae, $G_2 = 0.78, P = 0.46$; Figure 5).

For intruders, exhibition of aggressive behavior was unrelated to host weight (logistic analysis, $G_1 = 1.91, P = 0.17$) and difference in female size ($G_1 = 1.60, P = 0.21$) but was affected by the stage of development of the owner’s brood ($G_1 = 24.06, P < 0.001$): intruders were more likely to interact aggressively with owners that were defending younger broods (i.e., paralyzed hosts and hosts bearing eggs or young larvae; there was no significant difference in terms of intruder aggression between these 3 host classes: $G_2 = 1.58, P = 0.21$; Figure 5).

**Offspring survival in presence of intruders**

The survival of offspring could be considerably reduced by the presence of a nonmother female “intruder” (Table 2). When broods of eggs were exposed to intruders, intruders reduced egg-to-larva survivorship (logistic analysis corrected for overdispersion, $F_{1,47} = 1.66, P < 0.001$) by eating, in 22 of 26 cases, the entire clutch of owner’s eggs. If eggs survived the intruder’s presence and developed into larvae, their subsequent survival to the cocoon (prepupal and pupal) stage ($F_{1,26} = 0.93, P = 0.35$) and their cocoon-to-adult survivorship ($F_{1,24} = 1.55, P = 0.23$) was unaffected by intruders. None of these interstage survivals were affected by the weight of the host ($F_{1,47} = 0.22, P = 0.64; F_{1,26} = 0.02, P = 0.89$; and $F_{1,24} = 0.01, P = 0.94$, respectively) nor was the overall egg-to-adult survival ($F_{1,47} = 0.02, P = 0.90$).

When broods of young larvae were exposed to intruders (when intruders had been absent before eggs had hatched), the probability of completing development was reduced (Table 2). Broods of young larvae were partially destroyed (i.e., the proportion of young larvae reaching pupation was reduced; logistic analysis corrected for overdispersion, $F_{1,38} = 9.71, P = 0.004$), but the subsequent cocoon-to-adult survivorship
was unaffected by the presence of intruders ($F_{1,36} = 3.87, P = 0.06$). Host weight did not influence the survival of young larvae between subsequent developmental stages (young larva to cocoon: $F_{1,38} = 0.20, P = 0.66$; cocoon to adult: $F_{1,36} = 2.16, P = 0.15$; young larva to adult overall survival: $F_{1,58} = 0.60, P = 0.44$). When broods of already old larvae were exposed to intruders the probability of completing development was unaffected (Table 2) but was positively correlated to the initial weight of host ($F_{1,38} = 5.58, P = 0.02$). Overall, these results indicate owners’ payoffs from winning decrease as their broods develop, due to the decreasingly detrimental actions of successful intruders.

**Intruder host use**

When presented with hosts already bearing a brood, at least some intruders accepted the host for oviposition, except in the case when the presented hosts bore old larvae (Table 3). The number of eggs laid per host was unrelated to host weight (log-linear analysis, $F_{1,35} = 0.66, P = 0.42$) but was related to the developmental stage reached by the owner’s brood (Table 3). When presented with hosts already bearing eggs, intruders removed the eggs (see above) and laid clutches of similar size as on paralyzed hosts (log-linear analysis, $F_{1,35} = 3.13, P = 0.08$). These clutches were, however, smaller than those of the initial mothers (log-linear analysis, $F_{1,51} = 12.55, P < 0.001$). Intruders laid fewer eggs on hosts bearing young larvae, after only partially destroying the brood. The survival of intruders’ eggs to adulthood was not significantly affected by the stage reached by owner’s brood prior to intruder oviposition (Table 3); however, there were only 5 cases in which intruders laid eggs on hosts already bearing young larvae, and in these, mortality was common (suggesting type II error due to low sample size). Overall, these results indicate intruders’ payoffs from winning decrease as the owner’s brood develops, due to depletion in host quality.

**DISCUSSION**

As already shown in *Goniozus* species (Table 1), we found that *G. legneri* female–female contest resolution is influenced by asymmetries in contest ability (body size) and resource value: larger females and females placing a higher value on possessing the contested host are more likely to win. However, we found no evidence for an advantage associated with being an intruder, which contrasts with both other studies of *G. legneri* contests (Goubault et al. 2006 and Appendix 1 of this paper). In fact, owners were more likely to win contests. We discuss the effect of brood stage on contest outcomes, the ownership advantage in contest resolution and behavior, and the lack of consistency in the effect of factors influencing contest outcomes, especially as concerns owner and intruder asymmetries.

**Effect of brood stage on contests**

In terms of resolution, contests were influenced by the developmental stage reached by the owner’s brood: resolution was more likely when broods were younger (>90% of contests had a clear winner when the contested host was paralyzed or bearing eggs, compared with <60% when offspring were young larvae and ∼10% for old larvae). Contest behavior was also influenced by brood stage: mothers behaved more aggressively when defending younger broods, which may equate to taking greater risks (loser fatality has been observed in *G. nephantidis* but is rare [Humphries et al. 2006] and is not known in *G. legneri*). Both results are compatible with the expectation that parental investment in offspring protection is influenced by both the reproductive value and the vulnerability of the offspring, both of which may change during development (e.g., Goertzen and Doutt 1975; Koskela et al. 2000; Goubault et al. 2007), as females adjust their behavior according to the offspring’s increasing probability of survival (younger broods are more vulnerable to infanticide) and the decreasing value to the intruder of winning, in much the same way as observed in *G. nephantidis* (Goubault et al. 2007).

Despite the reduction in mortality risk from conspecific infanticide as offspring develop, unchallenged *G. legneri* females stayed for about 5–6 days with their offspring, until these were about to leave the remains of the host and pupate (contrast, e.g., with *G. indicus* in which the mother usually remains only until the eggs hatch; Takasu and Overholt 1998). This prolonged brood-guarding behavior could potentially be a protection against the detrimental actions of other species, similar to what has been suggested or shown in other *Goniozus* species (Doutt 1973; Hardy and Blackburn 1991).

**Ownership advantage and respect**

In contrast to previous observations in *G. legneri* (Goubault et al. 2006; Appendix 1), owners were advantaged during contests: they were more likely to win even against slightly larger intruders. This effect of owner–intruder asymmetry on contest...
outcomes was unaffected by the stage reached by the owner’s brood, in contrast to observations in *G. nephantidis* in which the effect of ownership decreases as offspring develop, apparently due to a decreasing risk of conspecific infanticide (Goubault et al. 2007). However, in the current study, the sample size of contests with a clear winner was small (*n* = 3) when owner’s offspring were at the old larval stage, which makes statistical detection of effects difficult (and in this instance, the effect was only marginally nonsignificant, *P* = 0.054, and note that probability estimates generated from logistic analyses are approximate rather than exact; Crawley 1993).

Although the probability of winning was unaffected by host weight, owners were observed to attune their defense behaviors to host value assessed in terms of both host size and brood stage. Owners were more likely to initiate agonistic behaviors (i.e., bite, attack with stinger, and fight) when defending bigger hosts and hosts bearing offspring more vulnerable to conspecific infanticide (i.e., paralyzed hosts and hosts bearing eggs and young larvae). Intruders also adapted their aggressiveness to host value: they were more likely to attack owners defending hosts that offered higher survival chances to their own potential offspring (i.e., paralyzed hosts, hosts bearing owners’ eggs, and young larvae). The probability of intruder attack was, however, uninfluenced by host weight. A possible explanation is that the short period of time intruders spent close to the host gave them little opportunity to assess its size (see also Humphries et al. 2006), which may be less obvious to intruders than the stage of the owner’s brood.

Thus, considering owners’ and intruders’ behavioral strategies rather than ultimate contest outcomes, *G. legneri* females did not show a complete respect for ownership, with more than 60% of intruders attacking owners of good-quality hosts. This is in accordance with the prediction of Kokko et al. (2006) that partial respect for ownership status can be evolutionarily stable when feedbacks between population dynamics and individual behavior are considered.

### Contest outcome inconsistencies

In this study, we found that *G. legneri* owners were advantaged during contests; this contrasts with prior data (Goubault et al. 2006). To explore the overall evidence for ownership effects in *G. legneri*, we combined the data collected by Goubault et al. (2006) and this study (from both the main body and Appendix 1). We first carried out logistic analysis with the response variable defined as whether or not the intruder won the contest and fitted the difference in contestant weight, the origin of the data (fitted as a 3-level factor), and their interaction as explanatory variables. Both main effects and the interaction influenced contest outcome significantly (weight difference: *G*₁ = 19.69, *P* < 0.001; origin: *G*₂ = 9.24, *P* < 0.001; interaction: *G*₃ = 5.62, *P* < 0.004; Figure 6). Although Figure 6 illustrates the differences in ownership effects found between the 3 studies, these are not formally assessed. Following Petersen and Hardy (1996), we thus redefined contest outcome in terms of whether the red-marked female won and reran the analysis fitting the red wasp’s ownership status as an explanatory variable (for all data combined, the color of the mark did not affect contest outcome; binomial test: *P* = 0.55). Ownership status and weight difference influenced contest outcome significantly, with owners and larger contestants being advantaged (ownership: *G*₁ = 9.03, *P* < 0.003; weight: *G*₁ = 9.84, *P* < 0.002) as did data origin via an interaction with ownership (*G*₂ = 8.22, *P* < 0.001).

These sets of results are thus inconsistent with respect to the effect of ownership asymmetry on contest outcome but consistent with respect to the effect of body size asymmetry. All results (Table 1) were obtained using essentially the same apparatus and strains of organisms and greatly overlapping combinations of coauthors: although we cannot entirely exclude interobserver issues (Ruxton and Colegrave 2003), these do not provide a ready explanation. The results of Goubault et al. (2006) were obtained in a laboratory with locally maintained and relatively dry environmental conditions rather than in a relatively humid climate room (all new data reported in this paper), but the inconsistent results for ownership advantage cut across this distinction. We do, however, suggest that *Goniozus* behavior might be quite sensitive to relative humidity, in terms of influencing the probability of agonistic encounters occurring (Goubault M, personal observation) and the outcomes of those that do. The clear intruder advantage reported by Goubault et al. (2006) is potentially explained by owners, prior to contests, having experienced higher humidity due to host transpiration (weight loss of paralyzed hosts is typically around 5 mg day⁻¹; Hardy ICW, unpublished data) than intruders: intruders could have consequently lowered life expectancies and have thus placed an increased value on possession of the host resource.

Despite a degree of internal inconsistency, results from *G. legneri* are generally commensurate with results from the congeneric *G. nephantidis* (Table 1). Different studies on *G. nephantidis* have similarly reported largely but not entirely consistent effects on contest outcomes (Table 1 and see Stokkebo and Hardy 2000). Similar patterns of inconsistency have been obtained in other series of studies of invertebrate contests; for instance, Kemp and Wiklund (2004) concluded that neither ownership nor thermally correlated differences in fighting ability are used to settle contests in the speckled wood butterfly, *Pararge aegeria*. This runs counter to well-known prior conclusions (Davies 1978; Stutt and Willmer 1998) which Kemp and Wiklund (2004) argue can be accounted for by the experimental approaches used and also suggest that prior experience of contests and the intrinsic aggressive properties of individual contestants might explain outcomes. Prior experience of contests has been experimentally excluded from the studies of *Goniozus* listed in Table 1, but variation in contestants’ “personalities” is possible and has been found in at least one invertebrate species in which contests are well studied, the hermit crab *Pagurus bernhardus* (Briffa and Dallaway 2007; Briffa and Sneddon 2007; Briffa et al. 2008).

![Figure 6](https://example.com/figure6.png)

**Figure 6**  Intruder takeover probability according to the difference in contestant weight and the origin of data. Data points are displaced vertically to show the numbers of observations.
Conclusions

Considering contest strategies, *G. legneri* females play neither bourgeois nor antibourgeois; the general readiness of both owners and intruders to escalate via attack indicates a weak or partial respect for role asymmetries and that “hawk” (Maynard Smith and Price 1973) or “daring” (Kokko et al. 2006) would be more, but not perfectly, fitting descriptions. Such partial respect (mixed strategy) is not predicted by models that consider role asymmetries and assume fixed resource values and contest costs but is often found to be evolutionarily stable by more refined models that include population-level feedback on resource values (Kokko et al. 2006; Kokko forthcoming).

Considering contest outcomes, Kokko et al. (2006) tabulate 99 studies (on 97 species) of animal contests: 20 of these show no ownership effect, 77 show commonsense outcomes, and only one (on the goldeneye, *H. aloiaoides*; Fernt and Smith 1976) is listed as showing a paradoxical outcome. If topping up the evidence to a neat 100, we would be more confident, despite initial findings, to place *G. legneri* among the commonsense majority. New empirical examples of paradoxical outcomes might be expected from theory (Mesterton-Gibbons 1992; Kokko et al. 2006) to be possible but rare: they remain predictably elusive.

FUNDING

Biotechnology and Biological Sciences Research Council, UK (grant BB/C504778/1).

APPENDIX 1

Twenty 90-min contests were staged between *G. legneri* intruder females and owners defending paralyzed hosts (30- to 40-mg *C. cephalonica* larvae). Females in contest dyads were aged 2–4 days, mated, not siblings, and marked with different colors (red and yellow). After each contest, females were weighed to an accuracy of 0.01 mg. The probability of intruder takeover was influenced by the intruder–owner difference in weight (simple logistic regression, with outcome defined as 1 = intruder won and 0 = intruder lost; $G_1 = 20.10, P < 0.001$; Figure 6). On Figure 6, the curve showing the estimated probability of intruder takeover is displaced to the left, indicating that there is an advantage to being an intruder in addition to the size-related advantage shown by the slope of the fitted line.

The influence of ownership status on contest outcome can be formally assessed by redefining outcome in terms of the color of the winning female (Petersen and Hardy 1996) but only when contest outcome is unrelated to color. Here, red-marked females won more contests than yellow females (2-sided binomial test: $P = 0.04$), which contrasts with results of numerous prior studies on *Goniozus* contests, all of which have indicated a neutral effect (Petersen and Hardy 1996; Stokkebo and Hardy 2000; Humphries et al. 2008; Goubault et al. 2006, 2007; plus the main part of the current study). These data thus provide only graphical evidence for the intruder advantage but are qualitatively consistent with the statistically based result of Goubault et al. (2006).

We thank Tim Batchelor and Marie Decuigniere for commonsense discussion and Julietta Marquez for antibourgeois technical assistance. We have strong, but still only partial, respect for the helpful comments of 2 anonymous referees.

REFERENCES


REFERENCES

Biotechnology and Biological Sciences Research Council, UK (grant BB/C504778/1).

APPENDIX 1

Twenty 90-min contests were staged between *G. legneri* intruder females and owners defending paralyzed hosts (30- to 40-mg *C. cephalonica* larvae). Females in contest dyads were aged 2–4 days, mated, not siblings, and marked with different colors (red and yellow). After each contest, females were weighed to an accuracy of 0.01 mg. The probability of intruder takeover was influenced by the intruder–owner difference in weight (simple logistic regression, with outcome defined as 1 = intruder won and 0 = intruder lost; $G_1 = 20.10, P < 0.001$; Figure 6). On Figure 6, the curve showing the estimated probability of intruder takeover is displaced to the left, indicating that there is an advantage to being an intruder in addition to the size-related advantage shown by the slope of the fitted line.

The influence of ownership status on contest outcome can be formally assessed by redefining outcome in terms of the color of the winning female (Petersen and Hardy 1996) but only when contest outcome is unrelated to color. Here, red-marked females won more contests than yellow females (2-sided binomial test: $P = 0.04$), which contrasts with results of numerous prior studies on *Goniozus* contests, all of which have indicated a neutral effect (Petersen and Hardy 1996; Stokkebo and Hardy 2000; Humphries et al. 2008; Goubault et al. 2006, 2007; plus the main part of the current study). These data thus provide only graphical evidence for the intruder advantage but are qualitatively consistent with the statistically based result of Goubault et al. (2006).

We thank Tim Batchelor and Marie Decuigniere for commonsense discussion and Julietta Marquez for antibourgeois technical assistance. We have strong, but still only partial, respect for the helpful comments of 2 anonymous referees.

REFERENCES
