



Agonistic interactions between nymphs of *Lycorma delicatula* (Hemiptera: Fulgoridae)

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ABSTRACT

The nymphs of *Lycorma delicatula* typically aggregate on tree branches for feeding. We studied agonistic interactions between nymphs in the field and investigated the effects of prior residence and body size on contest outcome. Resident nymphs maintained positions on tree branches and engaged in feeding, whereas intruding nymphs moved along tree branches. When an intruder approached, the resident typically raised its front legs as a threat posture. The intruder would either move away or palpate the resident, and the resident often lowered its body when palpated. The intruder would then attempt to shake the resident back and forth, with the number of attempts varying from one to several. The resident either maintained its position or fled. After a contest, the winner was determined to be the one occupying the contested position on the branch. The resident nymphs won 84.2% of the agonistic encounters, and the nymphs with larger body size won 63.2% of the agonistic encounters. Logistic regression analysis revealed that prior residence was a significant factor for the contest outcome, but body size was not. We discuss the hypotheses for the dominance of the residents in agonistic interactions between nymphs of *L. delicatula*.

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Introduction

Evolutionary game theory has revolutionized our approach to animal contests, especially in addressing questions about contest outcomes, contest durations, and why animal contests are often settled by ritualized or stereotyped displays (Maynard Smith and Parker, 1973; Parker, 1974; Maynard Smith, 1982; Riechert, 1998). Of particular interest is the asymmetric contest in which contestants are not identical in terms of the choice of strategies (i.e., territory owners and intruders), prospective payoffs, and its typical outcome in which resource owners are victorious in agonistic contests (Kokko et al., 2006). Three hypotheses are generally put forward to explain the dominance of resource owners in agonistic interactions (Krebs and Davies, 1993): the resource holding potential (RHP) hypothesis, the resource value hypothesis, and the uncorrelated asymmetry hypothesis.

The RHP hypothesis states that resource owners and non-owners differ in RHP, and the asymmetry in RHP determines the outcome of asymmetric contests. RHP is a combination of characteristics such as body size, strength, and weaponry (Parker, 1974). For example, the asymmetry in body size, which is typically measured as an estimate of

RHP, is often correlated with dominance and territory ownership and is the determinant of asymmetric contests (Han and Jablonski, 2010). The resource value hypothesis suggests that owners value the resource more than intruders do (Krebs, 1982; Johnson and Forser, 2002). Resource value refers to the variation among individuals in the value of the contested resource. A resident possesses knowledge about its territory, which includes the value of its resources (Krebs, 1982). Consequently, residents are more likely to expend energy in defense of their territories (Davies, 1981; Beletsky and Orians, 1987; Stamps, 1987; Beletsky and Orians, 1989; Hatchwell and Davies, 1992). Conversely, intruders are less likely to fight over a resource of unknown quality. Another hypothesis based on evolutionary game theory is an arbitrary asymmetry of ownership (Maynard Smith and Parker, 1976; Maynard Smith, 1982). The use of ownership for contest settlement is a simple convention which individuals might follow to avoid potentially injurious combats. Because the decision convention is not correlated with RHP or resource value, it is often referred to as the uncorrelated asymmetry hypothesis (Kemp and Wiklund, 2004).

L. delicatula nymphs aggregate on branches of the tree of heaven (*Ailanthus altissima*), sometimes in huge numbers (Lee et al., 2009). They feed on juices of the host plant by inserting stylets into the stems. Some nymphs stay in one location and feed for quite a long time. These resident nymphs frequently encounter other nymphs who are passing along the tree branches. Such an encounter often results in an agonistic interaction between the resident and the intruder. The

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agonistic interactions appear to occur more frequently in higher-density aggregations. After an agonistic interaction, the victorious individual stays on the feeding site, and the defeated individual leaves. Here, we studied the agonistic encounters between *Lycorma delicatula* nymphs to determine the effects of prior residence and body size on contest outcome.

Materials and methods

Study species and study population

Occurrence of *L. delicatula* in the Republic of Korea has been the source of confusion for much of the last eight decades. The first report of its occurrence was made by Doi (1932a), but he promptly disputed his own finding (Doi, 1932b). Due to lack of collection since then, it was concluded that *L. delicatula* did not occur in Korea (Kwon and Hur, 2001). However, this species was sighted in the western areas of Korea in 2006 (Han et al., 2008). It may have been introduced into Korea from China where it is widespread. Since then, *L. delicatula* has increased its range each year (Lee et al., 2010). The aggregation of *L. delicatula* nymphs on the branches of the tree of heaven in urban areas causes nuisance to city dwellers and the aggregation on grapevines causes economic damage to grapes. Efforts to control the populations of *L. delicatula* using biological agents and non-chemical methods are currently underway.

For this study, nymphs of *L. delicatula* were observed and collected in the urban surroundings of Suwon (37° 14'22"N, 127° 0' 25"E), the Republic of Korea, in July, 2009. In this area, nymphs aggregated for feeding on branches of the tree of heaven. Field observations were made on rainless days between July 22 and July 30, 2009. Time of the day for field observations was between 10:30 am and 3:00 pm, local time. Observation was made only on the fourth stage nymphs of *L. delicatula*, which was determined by the unique red coloration appearing only in this stage, to standardize the age effect on the agonistic interactions (Hyman et al., 2004; Krebs, 1971).

Agonistic interactions

Tree branches of terminal 50 cm to the tip were observed for agonistic interactions. On the branches, resident nymphs were stationary at established feeding sites where they had pierced through the bark to suck plant juices. The intruder nymphs roamed up and down the branch seeking feeding sites or challenging the residents. Before recording agonistic interactions, we observed the residents for at least 30 min to confirm territory ownership. We identified the residents as individuals that had inserted their stylets to suck plant juices and stayed there for a 30 min period.

We recorded interactions only between pairs of nymphs. We avoided interactions among three or more individuals to isolate variables affecting the outcomes of the agonistic interactions. We monitored the branches for 30 min periods for all observable agonistic interactions between nymphs. Non-agonistic behaviors such as simple movements were ignored. We observed a total of 38 agonistic interactions and video recorded 26 of these using a Sony camcorder (model #: HDR-XR500; Tokyo, Japan). We recorded the type of agonistic interaction, the duration of the interaction, and which nymph won or lost the combat. After a contest, the nymph occupying the contested site was determined to be the winner. Agonistic encounters were considered complete when nymphs stopped interacting for 5 min, at which point we collected each individual and separately stored it in alcohol for morphological measurement. In the laboratory we used a caliper to measure each nymph's right front femur length, thorax length, and head length to the nearest 0.01 mm. Using custom software, we scored every behavior (Table 1) while watching each video.

Table 1

Agonistic behaviors between nymphs of the lantern fly *L. delicatula*. The letter in parentheses is the abbreviation for the behavior.

Behavior	Description
Pause (P)	Immobile for 10 s or longer
Pause briefly (PB)	Immobile for less than 10 s
Feed (F)	Proboscis pierces tree bark
Move (M)	Nymph moves more than its body length during an agonistic interaction
Approach (A)	Nymph approaches its opponent to within 1 cm range
Threat posture (TP)	Raising of front leg(s)
Body contact (BC)	Nymph contacts the body of its opponent with at least one body part
Mount (MT)	Climbs up onto opponent
Palpate (PL)	Examines opponent with continuous touching
Shake (S)	Moves the opponent's body with short, quick, irregular vibratory movements
Crouch (CR)	Lowers body down on a branch
Chase (C)	Runs after the opponent
Withdraw (W)	Moves away from opponent's attack

Statistical analysis

We performed binary logistic regression to determine the factors important for the contest outcome in the agonistic encounters between the nymphs of *L. delicatula*. The predictor variables of the logistic regression were body size and prior residence. To estimate the body size, we subjected head length, thorax length, and hind femur length to principal component analysis using the varimax rotation method with Kaiser normalization.

We used the first-order Markov chain analyses (Gottman and Roy, 1990) to test for nonrandom temporal association between behaviors in agonistic interactions in *L. delicatula* nymphs. We constructed a 13 × 13 transition matrix for residents and intruders by tabulating all instances in which one behavioral pattern led to another (Chen et al., 2002). We computed an expected frequency for a particular transition of two behaviors by dividing the number of that particular transition by the total number of all transitions starting with the first behavior of the two, and then we used likelihood ratio tests to determine the significance of the transition matrix (Bakerman and Gottman, 1997). We used SPSS 12.0 (SPSS Inc., Chicago, IL, U.S.A.) for all statistical tests.

Results

Ethogram

When potential intruders approached, residents typically raised their front legs as a threat display (Fig. 1A). Throughout our observations, the majority of potential intruders avoided contact with the residents when the threat posture was displayed. Occasionally, however, a nonresident initiated an interaction by palpating the resident with its front legs, despite the threat posture by the resident individual (Fig. 1B). After palpation, the intruder usually mounted the resident (Fig. 1C), except for some cases in which the intruder departed after palpation. When mounted, a resident typically lowered its body to a more stable position (Fig. 1D). The intruder put its front legs on the resident's thorax immediately before attempting to shake it (Fig. 1E), and the number of attempts varied from once to several times. The residents either maintained its position or fled. When a resident maintained its position despite a series of body shakes, the intruder eventually gave up. Rarely, a resident initiated an interaction by kicking the intruder, and in all such observations, the intruder fled. Each interaction ended as soon as either the resident fled or the intruder gave up (Fig. 1F). The interactions resulted in no visible injuries to the nymphs.

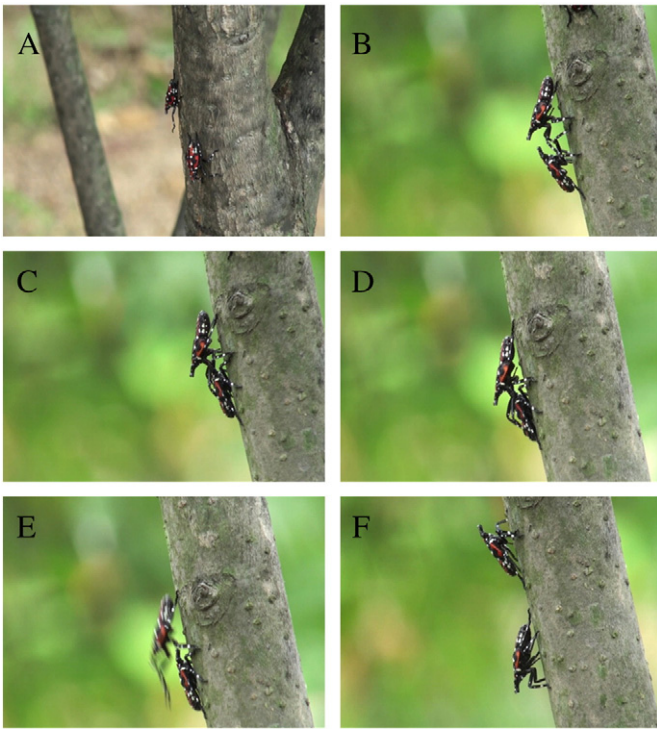


Fig. 1. Agonistic interactions in nymphs of *L. delicatula* nymphs. (A) A resident (above) displays threat posture to an intruder (below). (B) The intruder (above) palpates its opponent (below). (C) The intruder mounts the resident on the bottom of the branch. (D) The resident lowers its body. (E) The intruder shakes the resident with his front legs. (F) The resident (above) has successfully defended its position and the intruder departs.

Morphological characteristics

Head length of the residents ($n = 38$) was 3.930 ± 0.232 mm (mean \pm SD), and that of the intruders ($n = 38$) was 3.890 ± 0.205 mm (Fig. 2). Thorax length of the residents was 3.290 ± 0.170 mm, and that of the intruders was 3.232 ± 0.163 mm. Hind femur length of the residents was 4.820 ± 0.329 mm, and that of the intruders was 4.720 ± 0.325 mm. There was no statistical difference in any morphological character (head length: paired-samples t -test, $t = -0.840$, $df = 38$, $P = 0.406$, 2-tailed; thorax length: $t = -1.624$, $df = 38$, $P = 0.113$; hind femur length: $t = -1.601$, $df = 38$, $P = 0.118$) between the residents and the intruders. For further statistical analyses, we pooled morphological characters of all individuals including both the residents and the intruders. Due to strong correlation coefficients (Table 2), a principal component analysis was conducted for three morphological characters. Only the first component of this analysis (eigenvalue = 2.50) had an eigenvalue greater than one; it explained 83.2% of the variation. Subsequently, we used the first component as an estimate of the body size in the fourth instars of *L. delicatula*.

Agonistic interactions

The analyses of the first-order Markov-chain transitions revealed that the temporal association between the behavioral patterns was nonrandom for the intruders (likelihood ratio test: $\Lambda = 273.2$, $df = 64$, $P < 0.001$), but was random for the residents ($\Lambda = 59.1$, $df = 63$, $P = 0.616$). The Markov-chain diagrams showed that the behaviors exhibited during the agonistic interactions were markedly different in the residents and the intruders (Fig. 3). Three behaviors, feeding, threat posture, and crouching, occurred only in the residents (Fig. 3A), whereas approaching, palpating, and mounting occurred only in the intruders (Fig. 3B). The residents fed on branches before the onset of an agonistic interaction. When an intruder approached, a resident

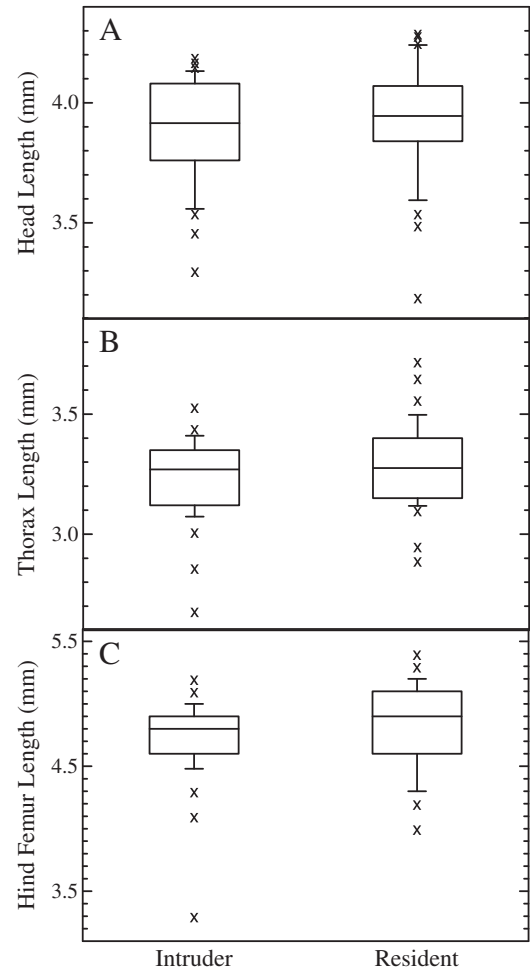


Fig. 2. Morphological characters of the intruders and the residents of the *L. delicatula* nymphs ($n = 76$). Box plots show distributions of (A) head length, (B) thorax length, and (C) hind femur length. Top, middle, and bottom lines of the boxes indicate 75th percentile, median, and 25th percentile, respectively. The upper and lower whiskers indicate 90th and 10th percentiles, respectively. X denotes an outlier.

typically performed one of three behaviors: threat posture, shaking, and crouching. A resident displayed threat posture or crouching until the intruder withdrew. Among 38 cases, we observed five cases in which the residents shook the intruders and successfully defended their feeding positions. There appeared to be no significant relationship between the residents' shaking behavior and the body size differences of the residents and the intruders.

When an intruder did not withdraw after receiving threat posture or shaking, it made body contact with the resident (Fig. 3B). It then either directly mounted the resident or palpated the resident, followed by movement or mounting. After mounting, the intruder paused briefly or shook the resident. Shaking and pausing frequently alternated with each other. The intruder moved away if the resident defended its position or paused if the resident withdrew from the intruder's attack. This sequence of escalated aggression involving shaking occurred in 14 out of the 26 cases. In the rest of the cases,

Table 2

Pearson correlation coefficients among three morphological characters in nymphs of *L. delicatula*. The first number in a cell is the correlation coefficient between the pair of characters, and the second number is the significance value of 2-tailed t test ($n = 76$).

	Head length	Hind femur length
Thorax length	0.758, <0.001	0.711, <0.001
Hind femur length	0.779, <0.001	

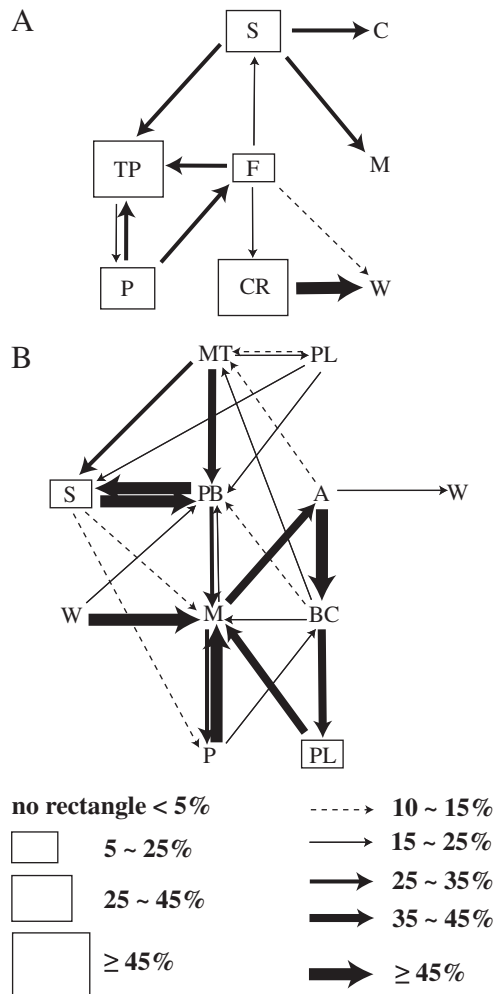


Fig. 3. Markov-chain diagrams for (A) resident nymphs (total number of events, $n = 53$) and (B) intruder nymphs (total number of events, $n = 216$) of *L. delicatula*. A rectangle denotes that the same behavior is repeated, and an arrow is a transition from one behavior to the next, with the point showing directionality and the line thickness representing frequency.

palpating was typically followed by movement. Then, the intruder sometimes approached to the resident again. In most cases, the intruder terminated the agonistic interaction by moving away.

Overall, the residents won 32 out of 38 observed agonistic interactions, and the intruders won the rest. The nymphs with bigger body size won 24 out of 38 agonistic interactions; the nymphs with smaller body size won the rest. The residents that were smaller in body size than the intruders won 11 out of 14 agonistic interactions. The result of the logistic regression revealed that residence was the only significant factor for contest outcome; body size was not significant (Table 3).

Discussion

In the nymphs of *L. delicatula*, prior residence was the most important factor influencing the outcome of agonistic contests. Because body size was not significant, the resource holding potential

Table 3
Result of logistic regression for contest outcome. Predictor variables were prior residence and body size ($n = 76$).

	df	Estimate	S. E.	Wald χ^2	P
Intercept	1	-1.68	0.45	13.88	0.0002
Prior residence	1	3.34	0.64	27.12	<0.0001
Body size	1	0.44	0.35	1.55	0.2134

(RHP) hypothesis is not supported in the territorial contests between *L. delicatula* nymphs. Although not measured in this study, there may be other RHP factors that determine the contest outcome. These include age (Choe, 1994; Kemp, 2000; Hyman et al., 2004; Jang et al., 2008), body weight (Barlow et al., 1986; Hagelin, 2002; Jennings et al., 2004), and weaponry (Sneddon et al., 1997; Judge and Bonanno, 2008). We cannot identify any trait that might be used as a weapon in the agonistic interactions in *L. delicatula* nymphs. However, age asymmetry is a possible factor for determining the contest outcomes, because the duration of the fourth instars is about two weeks (An, H.-G., personal observation). Body weight was not controlled for the agonistic interactions in this study and may be a factor for determining the contest outcome of the *L. delicatula* nymphs.

In black-winged damselflies, males may engage in prolonged aerial chases to determine the ownership of mating territories on streams, and asymmetry in fat reserves determines who wins territorial conflicts (Marden and Waage, 1990). Because resident *L. delicatula* nymphs typically fed on branches before encountering intruders, the residents and the intruders might differ in nutritional status, which could affect the determination of territorial ownership (Martínez-Lendeck et al., 2007).

Evidence for the uncorrelated asymmetry hypothesis, in which territory ownership is used as an arbitrary convention for conflict resolution, is seldom reported (Alcock, 2005). There is not enough information to assess whether our result supports this hypothesis. However, our result is largely consistent with the predictions of the resource value hypothesis, which would posit that branch positions would be of higher value to residents than to intruders of the *L. delicatula* nymphs. In the removal-replacement experiments with the European robin, *Erithacus rubecula* (Tobias, 1997), and in the great tit, *Parus major* (Krebs, 1982), dominance in territorial contests between newcomers and original owners is related to how long the newcomers have been in residence. As the time of occupation after the replacement increases, the newcomers probably gain an increasing knowledge of the acquired territory's value. Resident *L. delicatula* nymphs were likely to be more aware of the value of the branches on which they were feeding than were the intruders in this study (Stamps, 1987). If the resource value hypothesis accounts for how territorial contests in the nymphs of *L. delicatula* are resolved, then the nymphs that had recently established residency at their feeding sites may be more likely to be displaced by the intruders than are the residents that have been in their current sites longer.

The agonistic interactions in *L. delicatula* nymphs can be analyzed in the context of evolutionary game theory. In a war of attrition game, each player must decide at each instant whether to concede or wait and continue to compete (Maynard Smith, 1974). This basic model was extended by adding asymmetries, such as resource value or cost of fighting (Maynard Smith and Parker, 1976; Parker and Rubenstein, 1981). For example, the value of a resource is different for residents and intruders, because residents have a prior knowledge of the resource and its neighbors. The cost accrued during a contest may also be different between contestants in an asymmetric war of attrition game. Good fighters may accrue costs at a slower rate than poor fighters. The evolutionarily stable outcome of this asymmetric war of attrition game is that a contestant with the greatest benefit to cost ratio is victorious (Krebs and Davies, 1993).

Clearly, a feeding site should be more valuable to a resident nymph than to an intruder, because the resident probably knows the quality of the site (Magellan and Kaiser, 2010). Thus, the intruder should retreat in this case. It also appears that the intruder nymph invests a greater amount of energy during a territorial contest because the intruder typically shakes a resident's body when engaging in an agonistic interaction, while the resident in most cases simply crouches. In other words, the intruders seem to have a higher cost than the residents when engaging in aggressive interactions. Thus, the resident should be favored.

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