ORIGINAL ARTICLE

Janne S. Kotiaho · Rauno V. Alatalo
Johanna Mappes · Silja Parri

Honesty of agonistic signalling and effects of size and motivation asymmetry in contests

Abstract Game theoretical models predict that the main function of fighting behaviour is to assess the relative fighting ability of opponents. The sequential assessment game has often been used to investigate contests, while honest signalling theory has received much less attention. With the wolf spider *Hygrolycosa rubrofasciata* we investigated whether male agonistic signalling can reveal honest information about fighting ability, and how size and motivation asymmetries affect male fighting behaviour. We also determined whether male–male competition affects the courtship behaviour of the males. We found that agonistic drumming activity is an honest indicator of male fighting ability, and that relative size asymmetry and motivation to fight both contribute to the fighting ability. We also found that male–male competition decreases the courtship drumming rate of subdominant males, suggesting that male–male competition limits the opportunities for female choice. We conclude that sequential assessment and honest signalling may both be used in settling contests, and that they may be used simultaneously.

Key words Female choice · Fighting success · Honest signalling · *Hygrolycosa rubrofasciata* · Sequential assessment · Sexual selection

J.S. Kotiaho · R.V. Alatalo · J. Mappes · S. Parri
Department of Biological and Environmental Science,
Konnevesi Research Station, University of Jyväskylä, Finland

J.S. Kotiaho (✉)
Department of Zoology, University of Western Australia,
Nedlands, WA-6907, Australia
e-mail: jkotiaho@cyllene.uwa.edu.au
Tel.: +61-8-93801773; Fax: +61-8-93801029

Introduction

Fights between males are often used to settle disputes over a resource that has some fitness value (reviewed by Huntingford and Turner 1987; Andersson 1994). According to game theoretical models (Maynard Smith 1982; Enquist and Leimar 1987; Enquist et al. 1990), the assessment of relative fighting ability and motivation to fight are vital for settling the dispute. In the most advanced game theoretical model, the sequential assessment game (Enquist and Leimar 1983; Leimar and Enquist 1984; Enquist and Leimar 1987; Enquist et al. 1990), a fight is assumed to consist of a series of costly assessment rounds, and a dispute is settled when one opponent has gained reliable information about the other opponent's superior fighting ability and withdraws. This model is based on the assumption that individuals with high fighting ability accrue costs at a slower rate than individuals with low fighting ability (Enquist et al. 1990). This is in contrast to honest signalling, or handicap, theory (Zahavi 1975, 1977; Nur and Hasson 1984; Pomiankowski 1987; Grafen 1990a,b; Iwasa et al. 1991; Johnstone and Grafen 1992), the framework of which can be applied to agonistic signalling. Honest signalling is based on the assumptions that: (1) signalling is dependent on the quality of the individual; (2) signalling is costly, reducing the fitness of the signaller; and (3) for good quality individuals, absolute costs of signalling are higher than for poor quality individuals, but the costs are more than compensated for by the consequences of signalling on the outcome of the fight (Grafen 1990a; Johnstone and Grafen 1992).

There are several asymmetries that individuals may be assessing during a sequential assessment game (see e.g. Parker 1974; Maynard Smith and Parker 1976; Parker 1984; Enquist and Leimar 1987; Enquist et al. 1990). Two that are most likely to be important are the fighting ability, or resource holding potential (Parker 1974; Maynard Smith and Parker 1976), and the motivation to fight (Enquist and Leimar 1987). A common measure of fighting ability is size asymmetry between the opponents, and frequently the larger opponent has the advantage (e.g. Riechert 1982; Austad 1983; Turner and Huntingford 1986; Elgar and Fahey 1996; Pavey and Fielder 1996; Hack 1997a; Kotiaho et al. 1997). However, there are cases when relative body size does not predict the outcome of a fight. There is evidence that, in such cases,

asymmetry in fighting motivation, motivation that is affected by the opponent's subjective evaluation of the prospective fitness benefits, may settle the disputes (reviewed in Enquist and Leimar 1987).

In contrast, there is little empirical evidence for honest signalling in animal fights. There are only a handful of studies demonstrating that behaviour reveals the probable winner of a fight during that fight (Riechert 1978; Turner and Huntingford 1986; Franck and Ribowski 1989; Hack 1997a), and there is no evidence that behaviour can predict the winner of a contest before that contest is actually resolved. However, if opponents are signalling honestly about their fighting ability or motivation to fight, we could expect to find cases where a fight is settled before it has escalated much at all.

The most valuable resource males often fight for is mating partners (e.g. Huntingford and Turner 1987), and in sexual selection male size is often positively related to male mating success (Andersson 1994). If male–male competition is the only determinant of male mating success, we may expect that asymmetry in fighting ability between the opponents is more important than if there are other factors involved. For example, if females are choosy, selecting on a trait other than male size, the importance of size may diminish. It is very likely that the two mechanisms of sexual selection, male–male competition and female choice, both have an effect on the evolution of sexually selected traits (see e.g. Berglund et al. 1996; Forsgren 1997; Candolin 1999). Therefore, to better understand the importance of fighting asymmetries on the evolution of sexually selected traits, empirical studies trying to assess the relative importance of both mechanisms simultaneously are needed.

In this paper we present the results of two successive experiments on the wolf spider *Hygrolycosa rubrofasciata*, in which we studied the honesty of male agonistic signalling and the effects of size and motivation asymmetry on the outcome of fights. In the first experiment, we determined: (1) if male agonistic signalling reveals honest information on male fighting ability; and (2) how size asymmetry between males is related to the relative fighting ability when both opponents' motivation to fight is increased by introducing a valuable resource. In the second experiment, we determined: (1) how males of different relative fighting ability change their fighting behaviour after the motivation of one of the opponents is increased by introduction of a valuable resource; and (2) whether male–male interaction has an effect on their courtship behaviour. The most valuable resource males may be fighting for is likely to be females and, therefore, the resource we used was the receptive virgin female.

Methods

The spider

Hygrolycosa rubrofasciata (Ohlert 1865) is a ground-dwelling wolf spider (Lycosidae) inhabiting moist meadow and bog habitats. Males court females by drumming dry leaves with their abdomen. Courtship drumming is clearly audible to the human ear and it is a crucial component in mate choice; females prefer males with high a drumming rate (Kotiaho et al. 1996; Parri et al. 1997; Kotiaho et al. 1998a). When a female is willing to copulate she responds immediately after a single male courtship drumming by vibrating her body. It is easy to see when, and with which male, the female is willing to mate. During the mating season males are actively searching for receptive females, and while searching engage in agonistic encounters with each other. In these encounters males use a different type of drumming signal. This agonistic drumming is also clearly audible to the human ear, but it is shorter and more intense than courtship drumming. There is no possibility of confusing the two signals. Males use agonistic drumming in male–male interactions and we have not observed it in any other context. In an earlier, less controlled study, concentrating only on males with small size asymmetry, we found that body size may be of some importance in male–male fights when size asymmetry gets bigger (Kotiaho et al. 1997).

Individuals for this study were collected from a bog at Sipoo in southern Finland (60°16'N and 25°14'E) before the mating season in late April and early May 1995. Before the experiments, males were weighed to the nearest 0.1 mg and marked individually by placing a small dot of paint on the dorsal surface of their abdomen. We used the body mass of the males as a measure of their size because the body mass of *H. rubrofasciata* males is highly repeatable in laboratory and field conditions (82–99%) (Kotiaho et al. 1996, 1999), and because body mass is highly correlated with other more accepted size measures for spiders such as prosoma width and length ($r=0.84$, $n=94$, $P<0.001$ and $r=0.90$, $n=94$, $P<0.001$, respectively) (unpublished results).

Honesty of agonistic signalling and fighting ability (experiment 1)

We arranged pair-wise encounters over a valuable resource (a receptive female) between males of five size asymmetry classes. Asymmetry classes were <10, 10–20, 20–30, 30–40, and >40% difference in body mass. To each class we addressed ten pairs of randomly chosen males and each male was used only once. Altogether we had 50 pairs in this first experiment. In this set up males differed only by their size, and either of the males would gain in terms of fitness if he was able to repel the other. Encounters in round plastic cups were observed (diameter of 10 cm). In the cups we placed four dry birch leaves so that the leaves did not overlap. The female was placed under the arena in a smaller plastic cup separated from the male arena by fine mesh net so that the female was in close contact with both males. Males were released simultaneously from opposite sides of the arena with small test tubes. At the time of the release there was a plastic fence in the middle of the arena to prevent males from accidental encounter. The fence was removed 1–2 s after the release, when males were settled. Each encounter was observed for 15 min, during which time the agonistic drumming rate, courtship drumming rate, and outcomes of fights were recorded. To ascertain that the males were showing their real fighting ability, and that the fighting success was not a consequence of some other non-stable factor, we repeated the above procedure with 11 previously used pairs the following day.

Effects of size and motivation asymmetry (experiment 2)

In this second experiment we used two groups of males: those with less than 10% and those with more than 30% size asymmetry. These size asymmetry classes were chosen because we wanted as clear a difference between asymmetry classes as possible to attain the maximum power of the experiment. This experiment consisted of three successive phases. First, a pair of randomly chosen males (not used in the previous experiment) were placed in the aforedescribed arena and observed for 5 min without a female. If males did not establish clear dominance during these 5 min the experiment was terminated and the males were not used again. However, in most cases dominance was clear and we continued to the second phase.

In the second phase, both males were moved from the encounter arena to a new arena. One male was moved to an arena where there were four dry birch leaves and a receptive female as a resource to increase the males' motivation to fight. The other male was moved to a similar arena without the female. The courtship drumming rate of the males and the behaviour of the female were recorded. Prior to the experiment, the females were tested with playbacks of male courtship drumming to ensure that they were receptive. We observed the trial until the female responded or if the female did not respond within 15 min the trial was terminated.

The third phase was to introduce males to each other again and repeat the procedure of phase one. If no clear dominance was established during the 5 min, we continued to observe the males for up to 15 min, after which the trial was terminated.

The male to whom the resource was introduced, to increase his motivation, was randomly chosen so that in both size asymmetry classes the larger subordinate and the smaller subordinate were introduced to the resource 12 times. The larger dominant and smaller dominant male were introduced to the resource eight times. In the more than 30% size asymmetry class the smaller male was often not dominant and, thus, the sample sizes differed among size asymmetry classes (see frequencies in Fig. 2 for exact sample sizes). Altogether we had 67 pairs that completed all three phases of the experiment. Each male was used only once.

Statistical tests

Non-parametric statistics were used to test the effects of the factors on the variables. First values of the variables were ranked and then sum squares (SS) and mean squares (MS) were estimated as in parametric two-way analysis of variance (ANOVA). The test value H (SS_{SOURCE}/MS_{TOTAL}) follows asymptotically the chi-square distribution with df_{SOURCE}. Details of analyses are described by Zar (1984). All reported probabilities are two-tailed.

Results

Fighting behaviour

Fighting behaviour of *H. rubrofasciata* consisted of two clearly separable phases. The first phase was agonistic drumming. During this phase males may be several centimetres apart. Usually males engaged in agonistic drumming after another males' courtship drumming. This first phase was long, lasting several seconds or even minutes. After the agonistic drumming phase, the fight sometimes escalated to actual contact fighting. In this second phase fighting was very intense but short, lasting only up to 1–2 s. We did not observe serious injuries to the males (see also Kotiaho et al. 1997).

Honesty of agonistic signalling and fighting ability (experiment 1)

Honesty of agonistic signalling

Seventeen of the 50 encounters (34%) did not escalate to the contact fighting phase, and the fight was settled without direct contact. Of those fights where contact fighting did occur, in 61% (20/33) there was only one contact fight, and more than two contact fights occurred only in 4% (2/50) of all trials. The median time for engaging in a contact fight was 115 s from the beginning of the trial (1st and 3rd quartile: 62.5 and 240.5 s respectively).

Before the first contact fight, size asymmetry was not related to the difference in agonistic drumming rate between the opponents ($r_s=-0.17$, $n=50$, $P=0.250$). Because these two variables were not related, we performed a logistic regression with size asymmetry and difference in agonistic drumming rate as independent variables, and the occurrence of a fight (0/1) as a dependent variable. The occurrence of fight was not explained by the size asymmetry, but the difference in agonistic drumming rate had a significant effect: when the difference was great, there was no fight [whole model $\chi^2_2=7.33$, $P=0.026$; size asymmetry $\beta=-0.01\pm0.03$ (SE), Wald=0.05, P=0.827; difference in agonistic drumming rate (ln transformed) $\beta=-1.46\pm0.58$ (SE), Wald=6.32, $P=0.012$]. There was no correlation between the time before the first fight and size asymmetry, or between the time before the first fight and the difference in agonistic drumming rate ($r_s=0.14$, $n=33$, $P>0.4$, and $r_s=0.26$, $n=33$, $P=0.138$, respectively).

In those trials where a contact fight occurred, there was a significant difference in agonistic drumming rate, before the first contact fight, between the males who won and those who lost that combat (Wilcoxon rank test $T=-28$, $n=17$, $P=0.022$). However, there was no difference in agonistic drumming rate between smaller and larger males of the pair (Wilcoxon rank test $T=49$, $n=17$, $P>0.2$). After the first contact fight, 97% of the winners but only 30% of the losers engaged in further agonistic drumming ($\chi^2_{1,Yates\ corrected}=28.88$, $P<0.001$). In those cases where the males who lost did engage in agonistic drumming, they still had significantly lower agonistic drumming rates than the winners (Wilcoxon rank test $T=9$, $n=33$, $P<0.001$).

However, if the agonistic drumming rate of the winner of the first contact fight was equal to or less than the first quartile (25%) of the agonistic drumming rate of all winners, the loser more often engaged in agonistic drumming than losers after the combats where the agonistic drumming rate of the winner was higher (Mann–Whitney rank test $z=2.14$, $n_{1,2}=8.25$, $P=0.032$). For the winners, size asymmetry was negatively related to the agonistic drumming rate after the first fight, but this was not the case for the losers of the fight ($r_s=-0.377$, $n=33$, $P=0.030$, and $r_s=-0.077$, $n=33$, $P>0.6$ respectively).

Fighting ability

Males with small size asymmetry had similar fighting abilities. However, when the size asymmetry between males increased, the fighting ability of the larger male was greater and when size asymmetry was more than 40% the larger male always won (Fig. 1). When we repeated the procedure with 11 previously tested pairs on successive days the outcome of the repeated trial was the same as earlier in 10 cases out of the 11. This indicates that the fighting ability of the males is repeatable and thus the outcome of a single encounter is reliable.
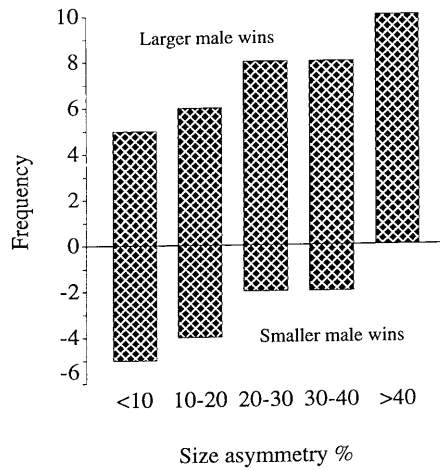
Fig. 1 Frequency of males winning and losing the encounter in relation to the size asymmetry. There are ten cases in each asymmetry class, tested with unweighted logistic regression using size asymmetry as a continuous variable. Probability of larger male winning: $\chi^2_1=8.44$, $P=0.004$; $\beta=0.077\pm0.029$ (SE)

Fig. 2 Changes in dominance after the introduction of the resource in different size symmetry classes (<10% and >30%). (*LS* larger subordinate, *SS* smaller subordinate, *LD* larger dominant, *SD* smaller dominant)

## Effects of size and motivation asymmetry (experiment 2)

Dominance

When the resource was introduced to one of the males it clearly affected the dominance of the males (Fig. 2). Overall, when the resource was introduced to a subordinate male, the dominance changed more often than if the resource was introduced to dominant males ($\chi^2_{1,\text{Yates corrected}}=30.9$, $P<0.001$). However, whether the male to whom the resource was introduced was smaller or larger did not affect the change of dominance when tested across all data ($\chi^2_{1,\text{Yates corrected}}=0.03$, $P=0.863$).

Within the smaller size asymmetry class (<10% asymmetry), the probability of the dominance turnover was high when the resource was introduced to the subordinate males ($\chi^2_{1,\text{Yates corrected}}=23.4$, $P<0.001$). However, when the resource was introduced to the dominant males there were no changes in dominance (Fig. 2). Similarly, the size of the male introduced to the resource did not have any effect on the change of dominance ($\chi^2_{1,\text{Yates corrected}}=0.00$, $P=1.0$). Thus, the only factor influencing dominance turnover was the introduction of the resource and, thus, the motivation to fight.

Within the larger size asymmetry class (>30% asymmetry) the pattern was slightly different (Fig. 2). When the resource was introduced to the subordinate males the dominance still changed ($\chi^2_{1,\text{Yates corrected}}=9.32$, $P=0.002$), but size asymmetry also had an effect. When the resource was introduced to the larger subordinate, the dominance changed (Fisher's exact test $P<0.005$), but it did not change when the resource was introduced to the smaller subordinate (Fisher's exact test, $P=0.217$). When the resource was introduced to the dominant males dominance did not change (Fig. 2).

The only difference between the asymmetry classes was when the resource was introduced to smaller subor-
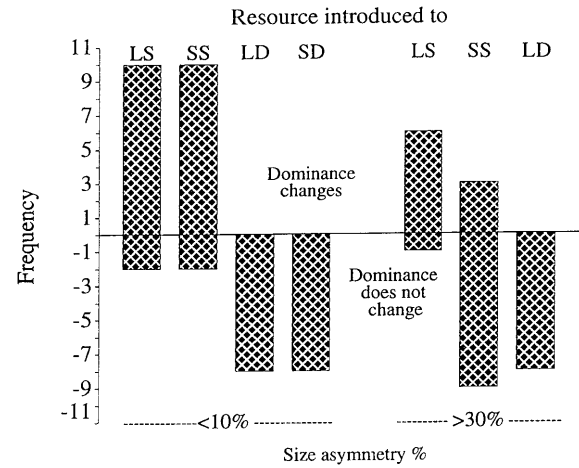
Table 1 The effect of introduction to the female, size difference, asymmetry class and the interactions on courtship drumming rate and agonistic drumming rate

Factor	Independent variables in phase 3			
	Courtship		Agonistic	
	H*	P	H*	P
a. Introduced to female	59.84	0.000	39.67	0.000
b. Size difference	2.13	0.144	6.26	0.012
c. Asymmetry class	0.21	0.647	0.50	0.480
Variable in phase 1†	5.04	0.025	0.38	0.538
a by b††	0.01	0.920	0.18	0.671
a by c††	0.08	0.777	6.36	0.012
b by c††	0.91	0.340	3.91	0.048
a by b by c††	1.59	0.207	0.51	0.475

* H is the test value for the effect of factors on ranked values of variables (see details for variance analyses in Methods)
† Variable value in phase 1 was used as a covariate in the model
†† Interaction terms

dinates: in the larger asymmetry class the dominance did not change as often as in the smaller asymmetry class (Fisher's exact test, $P=0.012$).

Courtship drumming

Introduction to the female affected the males' courtship drumming rate (Table 1). Males that were introduced to the female increased their courtship drumming rate (Wilcoxon signed rank test $z=6.86$, $n=66$, $P<0.001$) and maintained the rate at the increased level when returning to the original fighting arena (Wilcoxon signed rank test $z=0.74$, $n=66$, $P=0.463$) (Fig. 3). Similarly, males that were not introduced to the female, but were moved to an empty arena, increased their courtship drumming rate
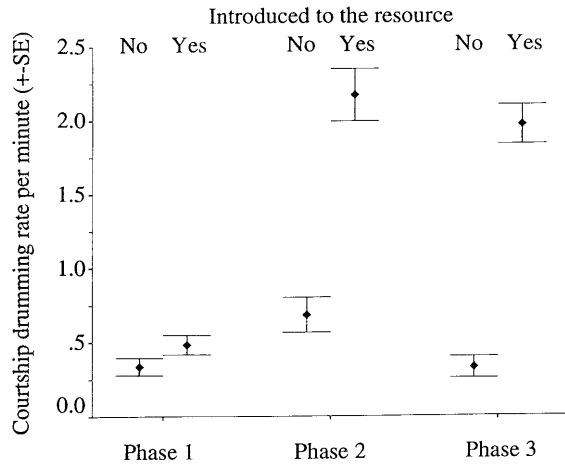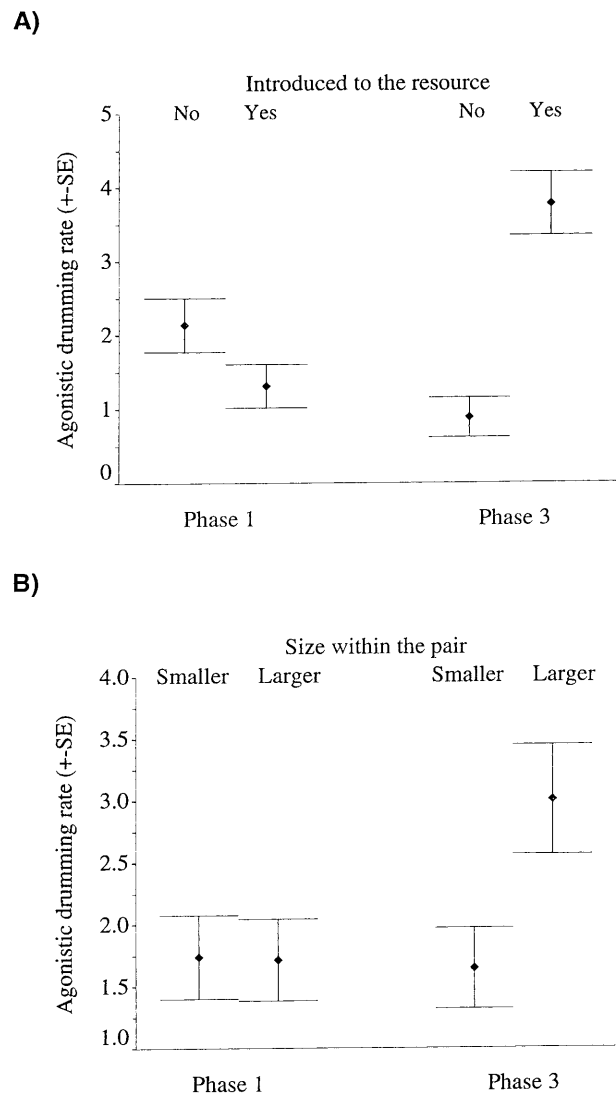
Fig. 3 Courtship drumming rate per one minute (mean±SE) separately for males introduced and males not introduced to the resource in each phase of the experiment. (For details of different phases see Methods)

A)

B)

Fig. 4. A Agonistic drumming rate per minute (mean±SE) separately for males introduced and males not introduced to the resource in phases 1 and 3. **B** Agonistic drumming rate per minute (mean±SE) separately for smaller and larger males within the pair in phases 1 and 3. (For details of different phases see Methods)

(Wilcoxon signed rank test $z=3.06$, $n=52$, $P=0.002$). However, these males increased their courtship drumming rate significantly less than males introduced to the female (difference in the increase, Mann–Whitney two-sample rank sum test $z=6.51$, $n_{1,2}=66.66$, $P<0.001$), and did not maintain their increased drumming rate when returned to the original fighting arena, but significantly decreased it (Wilcoxon signed rank test $z=3.63$. $n=47$, $P<0.001$) (Fig. 3). The covariant in the model, courtship drumming rate in phase 1 (Table 1), was also significant indicating that there was a relationship in courtship drumming rate between phases 1 and 3.

Agonistic drumming

Introduction to the female also influenced male agonistic drumming rate (Table 1). Males that were introduced to the female increased their agonistic drumming rate while males not introduced to the female decreased their rate (Wilcoxon signed rank test $z=4.45$, $n=64$, $P<<0.001$ and $z=-3.50$, $n=46$, $P<0.001$, respectively) (Fig. 4A). The size asymmetry within the pair also had an effect on agonistic drumming rate (Table 1, Fig. 4B). Larger males increased their agonistic drumming rate while smaller males did not change their rate (Wilcoxon signed rank test $z=2.19$, $n=57$, $P=0.028$ and $z=0.43$, $n=53$, $P=0.671$ respectively) (Fig. 4B).

There were also interaction effects on the agonistic drumming rate (Table 1). In the smaller size asymmetry class, males introduced to the resource had a much higher agonistic drumming rate than males not introduced to the resource, but in the larger size asymmetry class the difference was very slight (Fig. 5A). Also the size asymmetry within the pair had a differential effect in smaller and larger size asymmetry classes: in the former the size asymmetry within the pair seemed to have no effect, but

in the latter larger males performed more agonistic drumming (Fig. 5B).

Discussion

Honesty of agonistic drumming and assessment of fighting ability

In game theoretical models of fighting behaviour, assessment of relative fighting ability is assumed to be the most important activity (e.g. Maynard Smith 1982; Enquist and Leimar 1987; Enquist et al. 1990). One of the major predictions of sequential assessment game is that, as the asymmetry between opponents decreases, the costs of the contest increase (Parker and Rubenstein

A)
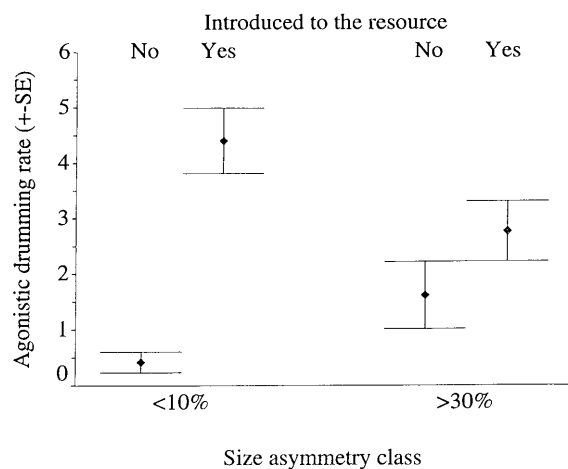
B)
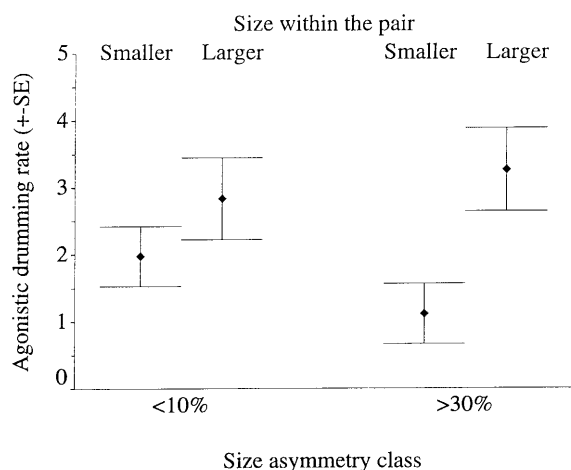
Fig. 5. A Agonistic drumming rate per minute (mean±SE) separately for males introduced and males not introduced to the resource in both smaller and larger asymmetry class. **B** Agonistic drumming rate per minute (mean±SE) separately for smaller and larger males within the pair in both smaller and larger size asymmetry classes

1981; Enquist and Leimar 1983; Enquist et al. 1990). It is further predicted that the costs increase more quickly for opponents that have a lower fighting ability (Enquist et al. 1990).

The fighting behaviour of *H. rubrofasciata* males seems to fulfil the first prediction. The fighting begins with agonistic drumming and only then escalates to actual contact fighting. It is likely that the cost of agonistic drumming, although potentially substantial (see below), is less than the cost of contact fighting. Contact fighting was not observed to cause serious injury to the opponents but, nevertheless, it is likely to pose a risk of serious injury.

The second prediction is more complicated. As pointed out by Hack (1997a,b), the cost of injury may often be lower for the opponent with greater fighting ability as

predicted by the sequential assessment models, but other costs, such as energetic costs, may well not be. When the fighting costs are greater for the opponent with the higher fighting ability, there is disagreement with the predictions of the sequential assessment models (Enquist et al. 1990; Hack 1997a). However, honest signalling theory (e.g. Zahavi 1977; Grafen 1990a; Johnstone and Grafen 1992) is based on the assumption that the costs are greater for better quality individuals, but that the prospective fitness benefits more than compensate for these costs. Fighting behaviour has rarely been analysed from the perspective of honest signalling theory (see Hack 1997a).

In *H. rubrofasciata*, fights started with agonistic drumming. Our results show that even before the contact fight, the winner of that fight had a significantly higher agonistic drumming rate than the loser of that fight. In a previous study, we showed that during courtship drumming the energy consumption is over 22 times higher than that at rest and over four times higher than energy consumption during active walking (Kotiaho et al. 1998b). Because the production of courtship drumming and agonistic drumming are essentially homologous, it is very likely that agonistic drumming is, energetically, as equally expensive as courtship drumming. Therefore, it is plausible that the costs of early fighting are greater for males with a higher fighting ability, contrasting with the sequential assessment hypothesis, but agreeing with the honest signalling hypothesis.

There is another line of evidence suggesting that agonistic drumming in *H. rubrofasciata* males may indeed be honest signalling. Overall, 34% of the fights were settled prior to escalation into a contact fight, and whether fights were settled prior to such escalation was explained by the difference in agonistic drumming rate between the opponents. In those trials that did not escalate to contact fighting, the difference in agonistic drumming rate between the opponents was significantly greater than in those trials that did escalate to contact fighting. This suggests that agonistic drumming rate may be an honest indicator of fighting ability. When there is a large difference in agonistic drumming rate, the dispute is settled with information based on this signal, without a contact fight. If the signal was not reliable we should not expect this to happen.

Surprisingly, size asymmetry did not explain the occurrence of a contact fight. There was also no correlation between the size asymmetry of the pair and the difference in their agonistic drumming rate prior to the first contact fight. Furthermore, there was no difference in the agonistic drumming rate prior to the first contact fight between smaller and larger males of the pair. These three results strongly suggest that agonistic drumming activity is not an indicator of body size. Given the homology to courtship drumming, and the high energy expenditure of courtship drumming, it is then more likely that the agonistic drumming rate indicates a higher fighting ability through greater energy reserves. Indirect support for the theory that agonistic drumming rate is not an indica-

tor of size again comes from prior results with courtship drumming: there is strong evidence that courtship drumming rate is not related to body size (Kotiaho et al. 1996, 1999).

In spite of the fact that the probability of males engaging in the contact fight was independent of size asymmetry, the probability of winning the fight was strongly affected by the size asymmetry. There was also a negative correlation between size asymmetry and agonistic drumming rate after the contact fight for the winners of the fight, but no such relationship for the losers. This indicates that when the size asymmetry between the opponents was small, the winner was reinforcing his dominance by maintaining a higher agonistic drumming activity. However, when the size asymmetry was large, there was no need for such putatively energetically costly reinforcement. The reinforcement function of the agonistic drumming after a fight is further supported by our other results. Even after a contact fight, and thus reliable assessment of the size asymmetry and fighting ability, some males that lost the fight still engaged in agonistic drumming. This happened significantly more often if the winner of the fight had a relatively low agonistic drumming rate after the fight. Thus, if the winner did not reinforce his dominance after the fight, he ran the risk of further disputes and reassessment of his fighting ability.

Fighting ability and motivation

When we introduced a resource to one of the opponents in the second experiment, the importance of size asymmetry diminished. In the small size asymmetry class (<10%), in most of the cases (20/24) dominance changed in favour of the male to whom the resource was introduced. This indicates that if the size asymmetry is not great, motivation to fight easily overrides its importance. Recalling that the dominance changed only once out of 11 repeated encounters, it seems that the change of dominance was indeed caused by the introduction of the resource, and thus increased motivation to fight. Similarly, in the high size asymmetry class (>30%) the introduction of the resource had an effect on the fighting motivation. However, in this class the effect of size asymmetry was not completely overridden but it also had an effect; if the male introduced to the resource was smaller the dominance changed only 3 times out of 12 (25.0%) but if the male introduced to the resource was larger the dominance changed 7 times out of 8 (87.5%). Thus, when size asymmetry is large, both resource value and size asymmetry are important in determining the outcome of the fight. These findings are similar to those of several other studies on the effects of size asymmetry and resource value on the outcome of fights (e.g. Riechert 1978, 1982; Austad 1983; Hack 1997a) see also (Enquist and Leimar 1987; Huntingford and Turner 1987). However, it may be that this picture is oversimplified. In *H. rubrofasciata*, the agonistic drumming rate of each male in a pair was a good indicator of their dominance. When we looked at the effects of size, size asymmetry class, and resource introduction on the agonistic drumming rate of the males, it is evident that there are complicated interaction effects between these factors. The agonistic drumming activity is dependent very much on resource introduction, but whether the male is smaller or larger and whether the size difference between the males is small or large all have different and substantial effects on the agonistic drumming activity. Thus, it seems that, rather than being clear-cut, winning the fight is in fact a complicated result of several factors that have differential effects simultaneously.

Male–male competition, female choice and sexual selection

Often both mechanisms of sexual selection, male–male competition and female choice, affect the evolution of traits, but most studies have concentrated only on one of these mechanisms (Andersson 1994; but see Kodric-Brown 1996; Forsgren 1997; Candolin 1999). Investigating the relative importance of male–male competition and female choice has been emphasized before for traits that have a dual function (Berglund et al. 1996), but it is likely to be as important always when both mechanisms are working.

There is some empirical evidence that male–male competition has an influence on the traits that are important for female choice (e.g. Morris et al. 1995; Galeotti et al. 1997; Candolin 1999). However, there is only one study where the influence of such male–male-competition-mediated changes in sexual traits on female choice has been identified (Candolin 1999). In her elegant experiments with three-spined sticklebacks, Candolin (1999) showed how male–male competition reinforces male dominance by increasing the difference in their expression of red coloration. This increased difference in the expression of the red coloration, in turn, facilitated female choice for dominant males by eliminating the "wrong" choices that females made before males were allowed to interact.

In our experiment, the presence of a rival male had a negative effect on male courtship drumming rate. This was evident because the male that was not introduced to the resource increased his courtship drumming rate when alone in the control arena. Furthermore, after introducing the males together again, the male that was not introduced to the resource decreased his courtship drumming rate back to the lower level, while the male that was introduced to the resource maintained his courtship drumming rate at a high level. In *H. rubrofasciata*, females choose males based on their courtship drumming rate (Kotiaho et al. 1996; Parri et al. 1997; Kotiaho et al. 1998a), while the size of the males seems to be unimportant (Kotiaho et al. 1996). Courtship drumming rate, but not the size, is related to male viability (Kotiaho et al. 1996; Mappes et al. 1996; Kotiaho et al. 1999; Kotiaho

in preparation), and females mating with males with a high courtship drumming rate males gain indirect benefits through increased offspring survival, while again male size has no effect (Alatalo et al. 1998). Thus, provided that the dominance of a male is not related to his quality, i.e. quality that is of interest to females, the female choice may be hindered by male–male competition (see also Forsgren 1997).

Conclusions

Agonistic drumming rate in *H. rubrofasciata* is likely to be an honest signal of male fighting ability. The agonistic drumming rate does not seem to indicate male size, but is more likely to indicate high energy reserves. Males with a relatively higher fighting ability are likely to spend more energy during agonistic drumming, thus contrasting with an important assumption of sequential assessment game. On the other hand, a crucial assumption in honest signalling theory is that better quality males have higher costs.

It may be that sequential assessment and honest signalling are both used in settling disputes between males. During the initial assessment, the agonistic drumming phase, males may use honest signalling, but if this does not settle the dispute, the pair may escalate to sequential assessment of the fighting ability. This switch is more likely to happen when the agonistic drumming rate difference between opponents is small. In these cases, males do not rely on the information based on agonistic drumming rate difference alone, but require more information, which they obtain through sequential assessment. It may even be that agonistic drumming is itself a part of the sequential assessment game, but that it is based on different set of cost rules, namely the rules of honest signalling.

References

Alatalo RV, Kotiaho J, Mappes J, Parri S (1998) Mate choice for offspring performance: major benefits or minor costs? Proc R Soc Lond B 265:2297–2301

Andersson M (1994) Sexual selection. Princeton University Press, Princeton

Austad SN (1983) A game theoretical interpretation of male combat in the bowl and doily spider, *Fontinella pyramitela*. Anim Behav 31:59–73

Berglund A, Bisazza A, Pilastro A (1996) Armaments and ornaments: an evolutionary explanation of traits of dual utility. Biol J Linn Soc 58:385–399

Candolin U (1999) Male–male competition facilitates female choice in sticklebacks. Proc R Soc Lond B 266:785–789

Elgar MA, Fahey BF (1996) Sexual cannibalism, competition, and size dimorphism in the orb-weaving spider, *Nephila plumipes* Latreille (Araneae: Araneoidea). Behav Ecol 7:195–198

Enquist M, Leimar O (1983) Evolution of fighting behaviour: decision rules and assessment of relative strength. J Theor Biol 102:387–410

Enquist M, Leimar O (1987) Evolution of fighting behaviour: the effect of variation in resource value. J Theor Biol 127:187–205

Enquist M, Leimar O, Ljungberg T, Mallner Y, Segerdahl, N (1990) A test of the sequential assessment game: fighting in the cichlid fish *Nannacara anomola*. Anim Behav 40:1–14

Forsgren E (1997) Female sand gobies prefer good fathers over dominant males. Proc R Soc Lond B 264:1283–1286

Franck D, Ribowski A (1989) Escalating fights for rank-order position between male swordtails (*Xiphophorus helleri*): effects of prior rank-order experience and information transfer. Behav Ecol Sociobiol 24:133–143

Galeotti P, Saino N, Sacchi R, Møller AP (1997) Song correlates with social context, testosterone and body condition in male barn swallows. Anim Behav 53:687–700

Grafen A (1990a) Biological signals as handicaps. J Theor Biol 144:517–546

Grafen A (1990b) Sexual selection unhandicapped by the fisher process. J Theor Biol 144:473–516

Hack MA (1997a) Assessment strategies in the contests of male crickets, *Acheta domesticus* (L.). Anim Behav 53:733–747

Hack MA (1997b) The energetic costs of fighting in the house cricket, *Acheta domesticus* L. Behav Ecol 8:28–36

Huntingford F, Turner A (1987) Animal conflict. Chapman and Hall, New York

Iwasa Y, Pomiankowski A, Nee S (1991) The evolution of costly mate preferences II. The "handicap" principle. Evolution 45:1431–1442

Johnstone RA, Grafen A (1992) Error-prone signalling. Proc R Soc Lond B 248:229–233

Kodric-Brown A (1996) Role of male–male competition and female choice in the development of breeding coloration in pupfish (*Cyprinodon pecosensis*). Behav Ecol 7:431–437

Kotiaho J, Alatalo RV, Mappes J, Parri S (1996) Sexual selection in a wolf spider: male drumming activity, body size and viability. Evolution 50:1977–1981

Kotiaho J, Alatalo RV, Mappes J, Parri S (1997) Fighting success in relation to body mass and drumming activity in the male wolf spider *Hygrolycosa rubrofasciata*. Can J Zool 75:1532–1535

Kotiaho J, Alatalo RV, Mappes J, Parri S, Rivero A (1998a) Male mating success and risk of predation in a wolf spider: a balance between sexual and natural selection? J Anim Ecol 67:287–291

Kotiaho JS, Alatalo RV, Mappes J, Nielsen MG, Parri S, Rivero A (1998b) Energetic cost of size and sexual signalling in a wolf spider. Proc R Soc Lond B 265:2203–2209

Kotiaho JS, Alatalo RV, Mappes J, Parri S (1999) Sexual signalling and viability in a wolf spider (*Hygrolycosa rubrofasciata*): measurements under laboratory and field conditions. Behav Ecol Sociobiol 46:123–128

Leimar O, Enquist M (1984) Effects of asymmetries in owner-intruder conflicts. J Theor Biol 111:475–491

Mappes J, Alatalo RV, Kotiaho J, Parri S (1996) Viability costs of condition-dependent sexual male display in a drumming wolf spider. Proc R Soc Lond B 263:785–789

Maynard Smith J (1982) Evolution and the theory of games. Cambridge University Press, Cambridge, UK

Maynard Smith J, Parker GA (1976) The logic of asymmetric contests. Anim Behav 24:159–175

Morris MR, Mussel M, Ryan MJ (1995) Vertical bars on male *Xiphophorus multilineatus*: a signal that deters rival males and attracts females. Behav Ecol 4:274–279

Nur N, Hasson O (1984) Phenotypic plasticity and the handicap principle. J Theor Biol 110:275–297

Parker GA (1974) Assessment strategy and the evolution of fighting behaviour. J Theor Biol 47:223–243

Parker GA (1984) Evolutionarily stable strategies. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach. Blackwell Scientific, Oxford, pp 30–61

Parker GA, Rubenstein DI (1981) Role assessment, reserve strategy, and acquisition of information in asymmetric animal conflicts. Anim Behav 29:221–240

Parri S, Alatalo RV, Kotiaho J, Mappes J (1997) Female choice for male drumming in the wolf spider *Hygrolycosa rubrofasciata.* Anim Behav 53:305–312

Pavey CR, Fielder DR (1996) The influence of size differential on agonistic behaviour in the freshwater crayfish, *Cherax cuspidatus* (Decapoda: Parastacidae). J Zool 238:445–457

Pomiankowski A (1987) Sexual selection: the handicap principle does work – sometimes. Proc R Soc Lond B 231:123–145

Riechert SE (1978) Games spiders play: behavioural variability in territorial disputes. Behav Ecol Sociobiol 3:135–162

Riechert SE (1982) Spider interaction strategies: communication vs. coercion. In: Witt PN, Rovner JS (eds) Spider communication, mechanisms and ecological significance. Princeton University Press, Princeton, pp 281–315

Turner GF, Huntingford FA (1986) A problem for game theory analysis: assessment and intention in male mouthbreeder contests. Anim Behav 34:961–970

Zahavi A (1975) Mate selection – a selection for a handicap. J Theor Biol 53:205–214

Zahavi A (1977) The cost of honesty (further remarks on the handicap principle). J Theor Biol 67:603–605

Zar JH (1984) Biostatistical analysis. Prentice-Hall, New Jersey