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**Competitive aggression in male and female Japanese medaka (*Oryzias latipes*) in
relation to the operational sex resource ratio**

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A Thesis in
the Department of Biology

Presented in Partial Fulfillment of the Requirements

for a Degree of Master of Science at

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Abstract

Competitive aggression in male and female Japanese medaka (*Oryzias latipes*) in relation to the operational sex ratio

Lia Clark

Because of the fundamental asymmetry between the sexes, males typically compete for access to females. Hence, most studies on intra-sexual mating aggression have focused only on males, and have shown increasing aggression with increasing operational sex ratio (OSR). However, one study documented a “dome-shaped” relationship between aggression and OSR, presumably because aggression became ineffective at high competitor densities as predicted by resource defence theory. The few studies that have investigated female intra-sexual aggression have used only a narrow range of OSR. The purpose of my study was to investigate the patterns of both male and female mating aggression over a broad range of OSR. I also compared how females competed for two different resources, food and mates. Male and female aggression initially increasing with OSR, peaked and then levelled off. For a given value of OSR, however, the rate of male aggression was higher than female aggression. The rate of male aggression was consistent with a dome-shaped pattern, whereas the rate of female aggression did not decrease at high levels of OSR. In contrast, courtship rates for both males and females decreased with increasing OSR in a linear manner. The pattern of male and female intra-sexual aggression were broadly consistent with the predictions of resource defence theory.

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Introduction

Animals compete in two basic ways for resources. Interference competition is defined as one individual using aggression to deny others access to the resource, whereas exploitation competition involves individuals reducing the available pool of the resource via consumption (Keddy, 1989). A resource is economically defensible if it is energetically more profitable to compete via interference than via exploitation (Brown, 1964). Animals often use aggression when competing for mates, territories, nesting sites and food (Huntingford & Turner, 1987). By using aggression, dominant individuals have the potential to defend and monopolize a larger than average share of the resources (Grant & Kramer, 1992; Monaghan & Metcalfe, 1985). However, aggression is also costly in terms of energy, time, the risk of injury, and an increased predation risk (Brown, 1964). Time spent engaging in aggressive behaviour is time that cannot be spent on other activities, such as courtship of mates. For example, male eastern bluebirds, *Sialia mexicana*, that defend their nest the most aggressively have the lowest reproductive fitness, as they have less time for courting and parental care (Duckworth, 2006).

In most mating systems, males typically compete for access to females or the resources they require. Emlen & Oring (1977) introduced the concept of the operational sex ratio (OSR), defined here as the ratio of competitors of one sex to potentially receptive individuals of the opposite sex in a population at a given time. OSR can be used to predict the intensity of intra-sexual competition for mates, and which sex is non-limiting and therefore compete for access to the limiting sex. Not all individuals are

capable of mating at a given time, so the operational sex ratio is rarely equal to one. For example, the age at sexual maturity often differs between the sexes, leading to an imbalance in the OSR (Emlen & Oring, 1977).

When the male/female OSR is less than 1, males are predicted to court the abundant females and engage in little aggression (Jirotkul, 1999). As the OSR increases, however, the relative abundance of females decreases, so the rate of male aggression should increase (Kvarnemo & Ahnesjo, 1996), while the rate of male courtship should decrease (Grant et al., 1995). At extremely high values of OSR, resource defence theory predicts that aggression will no longer be effective because of the high costs of chasing multiple intruders and males should switch to scramble competition (Grant, 1993). Hence, OSR theory predicts an increase in aggression with increasing OSR (Kvarnemo & Ahnesjo, 1996), whereas, resource defence theory predicts a dome-shaped relationship (Grant et al., 2000).

Two patterns of aggression in relation to OSR have been described in the literature, the linear increase and the “dome-shaped” pattern. The linear increase in aggression with increasing OSR has been verified in studies of sand gobies, *Pomatoschistus minutus* (Kvarnemo et al., 1995), lobsters, *Homarus gammarus* (Debusse et al., 1999) and guppies, *Poecilia reticulata* (Jirotkul, 1999). However, in all these studies the range of OSR used was relatively narrow (e.g. 0.4-3.0). In contrast, the only study to show a dome-shaped relationship was of male Japanese medaka, *Oryzias latipes*, over a broader range of OSR (from 0.2-8.0) (Grant et al., 2000). Hence, a broad range of observed values of OSR may be required to provide a crucial test of these two competing

patterns.

The OSR can also predict which sex should be more aggressive. At male/female OSRs greater than one, females will typically be the limiting sex, and males should be the more aggressive sex (Clutton-Brock & Parker, 1992). When OSR is much less than one, males will normally be the limiting sex, and females will be the more aggressive sex (Clutton-Brock & Parker, 1992). However, at OSRs near one, the sex with the higher potential rate of reproduction, typically males, should be non-limiting and therefore more aggressive (for a review, see Kvarnemo & Ahnesjö, 1996). For example, in “sex-reversed” species (e.g. *Syngnathus typhle*, *Nerophis ophidian* and *Julidochromis marlieri*), males invest more time/energy into the rearing of the young than the females and become the limiting sex for which females compete via active courtship (Berglund & Rosenqvist, 2003; Barlow & Lee, 2005).

Competitor-to-resource ratio (CRR), a more general formulation of the concept of OSR, is defined as the ratio of the total number of competitors to the total number of resources in a population at a given time (Grant et al., 2000). Like OSR, CRR can predict the intensity of competition for any resource, including mates. The CRR concept allows for the direct comparison of rates of aggression between sexes and between resource types (Grant et al. 2000; Grant & Foam, 2002). For example, the rate of intra-sexual aggression in Japanese medaka was similar whether males competed for food or for mates (Grant et al., 2000).

Because males are typically the more aggressive sex, female competitive aggression during mating has not received a great deal of attention (Clutton-Brock &

Parker, 1992). As in males, female intra-sexual aggression is predicted to increase with increasing female/male OSR and this has been verified in sand gobies (Kvarnemo et al., 1995), Japanese medaka (Grant et al., 2000; Grant & Foam, 2002) and lobsters (Debusse et al., 1999). To date, these are the only studies to examine simultaneously the aggressive and courtship behaviour of both males and females in response to changes in OSR.

Because they have elaborate courtship rituals and spawn daily, the Japanese medaka is an ideal species for testing the effects of OSR and CRR on reproductive and competitive behaviour. The medaka breeding system, typical of many fish species, involves external fertilization and no parental care. Females are capable of producing only one clutch per day and are selective when choosing a male, whereas male medaka can potentially spawn with as many as 20 different females in one day (Casey, 1993). This difference in the reproductive potential between the sexes is also thought to affect the patterns of aggression and courtship, as well as the OSR. I will explore the effect of the operational sex ratio on the behaviour of both male and female medaka.

Previous work on the medaka indicates that (1) males are more aggressive than females at similar values of OSR (Grant & Foam, 2002), and (2) the patterns of male aggression are similar regardless of whether males are competing for food or mates (Grant et al., 2000). Male intrasexual aggression initially increases with increasing OSR, peaks at an OSR of 2, and then decreases. While this “dome-shaped” curve had been shown for males there has been little work on female aggression. Hence, my thesis will focus on female aggression over a broad range of OSR (0.5-16). Specifically, I test the predictions that: 1) male-male aggression and 2) female-female aggression will exhibit a

dome-shaped relationship with respect to OSR; 3) female courtship will decrease as OSR increases; and 4) the pattern of female aggression will be similar when competing for food and mates.

Methods

Experimental subjects

Japanese medaka are small freshwater fish native to the streams and rice paddies of eastern Asia (Hiramatsu & Shikasho, 2004). They are sexually dimorphic and exhibit external fertilization. During the mating season, female medaka can spawn daily producing 10-50 eggs. The sticky egg masses remain attached to the female for a few hours until they become attached to vegetation as the female swims by. Males can spawn with up to 20 females per day (Casey, 1993), but the actual number per day depends on a variety of local conditions, such as OSR and population density. There is no parental care after the eggs drop off the female; eggs and young fry are often eaten by the adults, at least in aquaria (personal observation).

All 150 fish used in this study were purchased from a biological supply company at a 2 male: 3 female sex ratio. They were kept in two mixed stock tanks measuring 91.5 x 46 x 38 cm (LxWxH) and were fed a mixture of frozen brine shrimp and commercial flake food once per day. The fish were kept under a 13:11 (light-dark) regime, with the

lights coming on at 9:00am. The fish were held for approximately one month in the stock tanks before experimentation, to ensure that the egg laying cycle had commenced in the females. I used only sexually mature females for testing and assumed that all fish had previous breeding experience by the time experiments began. All experiments were conducted from mid-June to mid-September 2007 at Concordia University.

Experimental Design

Four experimental tanks, measuring 60 x 30 x 30cm (LxWxH), were covered with dark, opaque plastic wrap on three sides to prevent interactions between fish in adjacent tanks. The fourth side was left uncovered for filming purposes. Experimental tanks were also equipped with a feeding tube, 2.5 x 15 cm (diameter x length), attached to one of the back corners of the tanks, an air stone and gravel to a depth of 2cm (see Figure 1). Each trial lasted seven days and was divided into two parts: training (days 0-4) and filming (days 5-7). Female fish (in groups of 2, 4, 8, & 16) were placed in the experimental tanks on day 0. Females were then given four days for acclimatization and training. Training consisted of placing males into the experimental tanks each morning at 9:30am. The female/male OSR during the training period was always 2 (e.g. 8 females: 4 males), except for the group size of 16 which received only four males (to limit the total number of fish in the experimental tanks). Sixteen males were placed into a holding tank for use in the experiments each week. Each day, I removed the required number of males from the holding tanks for use in the trials. Males remained in the experimental tanks for one

hour or until all females had spawned, whichever came first; afterwards the males were removed and returned to the holding tank, separate from the stock tanks. Immediately following the removal of the males, females were fed five brine shrimp via the feeding tube and then 2 minutes later 20 brine shrimp. Fish in the experimental tanks were fed to satiation with brine shrimp and flake food, at least one hour after the introduction of the 20 shrimp.

Experimentation and videotaping took place on days 5-7. Females were exposed to three resource densities, in a repeated measures design, either 1, 2 or 4 males and 1, 2 or 4 brine shrimp/30 sec, on each of the three days of filming (randomly assigned). At 9:30am, approximately 30 minutes after the lights came on, the males were placed in the experimental tanks and fish behaviour was filmed for 30 minutes. After the videotaping of the mating trials in all tanks for the day, the males were removed. These treatments created a range of male/female OSRs (0.0625 to 2), female/male OSRs (0.5-16) and female/shrimp CRRs (0.5-16).

The tops of the experimental tanks were then covered with a piece of dark/opaque plastic, so the fish were not disturbed by the presence of the researcher standing behind the tanks. Brine shrimp were introduced into the tanks via the feeding tube every 30 seconds and videotaping lasted for 10 minutes. The total number of brine shrimp introduced into the experimental tanks varied and was determined by both the density of the resource being tested and the number of females in the experimental tank (see Table 1). The total shrimp introduced varied across treatments so that no tanks received more than 10 shrimp/fish during the feeding trials. After filming on day 7, all fish were

removed from the experimental tanks, weighed and returned to the stock tanks. Individual fish were re-used, but never in consecutive replicates. Males and females could potentially have been used up to five times over the course of my trials.

For each trial, all aggressive interactions in the first 5 minutes were scored; scoring began 1 minute after the males were introduced into the tank or when the first shrimp was introduced into the feeding tube. Courtship behaviour was also scored in the mating trials. The mating trials were more complex as interactions between males, between females, and between males and females were scored. I also noted whether males or females initiated the between-sex interactions. Mutual interactions, when neither sex initiated the interaction first (e.g. crossing and spawning), were also recorded. The types of behaviour that were scored are listed in Table 2. In the feeding trials, I only scored female intrasexual aggression.

All data were analysed using the statistical package SPSS version 12. All data were log₁₀-transformed to reduce heteroscedasticity and to ensure that the data were normally distributed. Male aggression and courtship data were analysed using 2-way ANOVAs (male group size x female group size). Female data (mating aggression, feeding aggression & courtship) were analysed using a 2-way repeated measures ANOVA (female group size x resource number x resource type). The Huynh-Feldt correction was used for all tests of within-subject effects, because the data were not completely spherical (Potvin et al., 1990). Rates of aggression and courtship with respect to OSR were compared using polynomial regressions, beginning first with the linear term, followed by the quadratic and cubic terms, although cubic terms were never

significant. Higher order terms were only included in the model if the partial r^2 value for that term was significant.

For the feeding trials, the total number of females engaged in competing for food under the feeding tube was recorded every 30 seconds. Females were considered to be actively feeding, and under the feeding tube, if they were in the water column within 5 body lengths directly under the tube. Females under the tube, but foraging in the gravel at the bottom of the tanks were not counted. The counts were done 15 seconds before/after shrimp were introduced into the feeding tube. The 10 counts per trial were averaged to give the average effective number of females feeding per trial, which was used to calculate the effective CRR for the trial.

Results

Description of Intra-Sexual Aggressive Behaviour

Both male and female medaka exhibited intra-sexual aggression when competing for mates (Table 2). When competing for females, males primarily butted and chased encroaching males in an attempt to keep intruders away (Figure 2a). Occasionally, two males would engage in extended bouts of chasing and butting near the top of the tank that lasted for more than a minute. During these bouts, the males did not engage in courtship.

Females also competed for mates primarily by butting and chasing (Figure 2c). In

contrast to males, females did not attempt to defend a mate, but rather chased females who were being courted or disrupted a spawning pair. When females did chase other females, they chased for only a few body lengths and then resumed whatever behaviour they had been engaged in prior to the interruption. Mutual butting was common when neither female withdrew from the approaching competitor. Females often butted other females who were being courted or followed by a male. One or several females would also butt a spawning pair in an apparent attempt to disrupt the spawning process. Females would also attempt to eat any eggs that were released by a spawning female.

When competing for food, females also engaged primarily in butting and chasing (Figure 2c). However, females used these two behaviour patterns differently when competing for mates vs. food. Feeding aggression was concentrated below the feeding tube and was directed at other females who approached the tube. Females vied for position below the tube prior to the arrival of a food item. Chases were short and fast, as the aggressor did not leave the vicinity of the feeding tube for long. Butting was more common when the females vied for the optimal position to capture the shrimp as it descended from the tube.

Rates of Intra-Sexual Aggression During Mating

The per capita rate of male-male aggression increased with increasing competitor number (Figure 3a; 2-Way ANOVA, $F_{1,72} = 21.28$, $P < 0.001$) and differed among female group sizes (2-Way ANOVA, $F_{3,72} = 25.78$, $P < 0.001$). Female aggression was lowest in

groups of two. Although there was a significant interaction between female group size and the number of males on the rate of male-male mating aggression (2-Way ANOVA, $F_{3,72} = 3.25$, $P = 0.027$), the magnitude of the interaction, as indicated by the F-ratio, was small in comparison to the size of the main effects. When plotted against OSR, male-male aggression initially increased with OSR and then levelled off (Figure 4), as indicated by the quadratic term in the equation, which was significant ($t = -3.995$, $df = 1$, $P < 0.001$) after the linear term was first entered into the model. According to the quadratic equation, male aggression was highest at a OSR of 1.17 ($r^2 = 0.510$, $P < 0.001$; Quadratic Equation: $\text{Log}_{10}\text{Agg} = -0.81 \text{Log}_{10}\text{OSR}^2 + 0.11\text{Log}_{10}\text{OSR} + 0.90$).

As expected, the per capita rates of female-female aggression decreased with increasing male number (see Figure 3b; 2-Way Repeated Measures ANOVA, $F_{2,70} = 4.69$, $P = 0.012$). Group sizes also differed significantly in aggression (2-Way Repeated Measures ANOVA, $F_{3,35} = 5.597$, $P = 0.003$). However, the rate of female aggression was lowest in group size two and increased with group size. While the effect of male number appeared greatest in group size two, there was no significant interaction between the effects of male number and female group size (2-Way Repeated Measures ANOVA, $F_{6,70} = 1.295$, $P = 0.271$). When plotted against OSR, female aggression initially increased with increasing OSR and then levelled off (Figure 4). The quadratic term in the equation was significant ($t = -2.20$, $df = 1$, $P = 0.030$) after the linear term was first entered in the model. According to the quadratic curve, female aggression peaked at a OSR of 10 ($r^2 = 0.208$, $n = 120$; Quadratic Equation: $\text{Log}_{10}\text{Agg} = -0.39 \text{Log}_{10}\text{OSR}^2 + 0.78\text{Log}_{10}\text{OSR} + 0.47$).

Rates of both male and female behaviour followed similar patterns: aggression initially increased with OSR and then levelled off (Figure 4). However, males were more aggressive than females and the peak in the female curve was shifted to the right compared to the male curve. Over the range of OSR in which the male and female data overlapped (i.e. 0.5-2.0), males were more aggressive than females (2-Way ANOVA, $F_{1,74} = 17.83$, $P < 0.001$).

Courtship

Both males and females displayed courtship behaviour, but there was a marked difference in the types of behaviour used (Figure 2b&d). Males actively courted females, often beginning by following a female until she ceased swimming. Males would then engage in circle dancing until attempting to spawn with the female (i.e. crossing; see Table 2). Circle dancing is an overt courtship display (Ona & Uematsu, 1957), which is used exclusively by males. Female courtship was much simpler. Females gently nudged or followed a male in what appeared to be an attempt to attract the attention of the male.

As expected, male courtship rate decreased as the number of competitors increased (Figure 5a; 2-Way ANOVA, $F_{2,107} = 41.74$, $P < 0.001$), and increased with female group size (2-Way ANOVA, $F_{3,107} = 12.67$, $P < 0.001$). There was no significant interaction between the number of males and the female group size on male courtship rate (2-Way ANOVA, $F_{6,107} = 0.171$, $P = 0.984$). When plotted against OSR, courtship rate

decreased with increasing OSR (Figure 6; linear regression: $r^2 = 0.437$, $n = 120$, $P < 0.001$).

Female courtship increased with increasing male number (Figure 5b; 2-Way Repeated Measures ANOVA, $F_{2,70} = 20.73$, $P < 0.001$), but decreased with competitor number (2-Way Repeated Measures ANOVA, $F_{3,35} = 28.85$, $P < 0.001$). There was no significant interaction between the number of males and the number of females on female courtship rate (2-Way Repeated Measures ANOVA, $F_{6,70} = 1.29$, $P = 0.276$). Female courtship rate also decreased with increasing OSR (Figure 6; linear regression: $r^2 = 0.550$, $n = 120$, $P < 0.001$).

The rate of female courtship decreased at a faster rate with increasing OSR than did male courtship rate, as indicated by the significant interaction between gender and OSR (Figure 6; ANCOVA, $F_{1,234} = 24.64$, $P < 0.001$). Over the narrow range of OSR in which the male and female data overlapped (i.e. 0.5-2) males courted at a higher rate than females (2-Way ANOVA, $F_{1,74} = 21.73$, $P < 0.001$).

Female-Female Aggression During Feeding Trials

Contrary to my expectation, the average per capita rate of female-female aggression did not differ significantly as the number of shrimp per 30 s increased (Figure 7; 2-Way Repeated Measures ANOVA, $F_{2,72} = 1.11$, $P = 0.328$). However, the rate of female aggression differed between group sizes (2-Way Repeated Measures ANOVA,

$F_{3,36} = 5.04$, $P = 0.005$), primarily because of the low rate of aggression in groups of two females. There was also no significant interaction between female group size and the number of shrimp (2-Way Repeated Measures ANOVA, $F_{6,72} = 0.81$, $P = 0.547$). Female-female aggression during feeding increased with increasing CRR (Figure 8a; $r^2 = 0.049$, $n = 120$, $P = 0.015$), but CRR explained relatively little of the variation in the rate of aggression. On average, only about half the total number of females in the tanks were actively feeding at one time (Figure 9). When plotted against the effective CRR, using the actual number of females feeding, the proportion of the variation in aggressive rate explained by CRR increased to 13.5% (Figure 8b; $r^2 = 0.135$, $n = 116$, $P < 0.001$).

To facilitate a comparison of the rates of female-female aggression when competing for mates versus food, I assumed a linear relationship between aggression and CRR. There was no significant interaction between the type of resource and CRR (Figure 10; ANCOVA, $F_{1,235} = 0.879$, $P = 0.349$). However, female-female aggression was higher when competing for food than for mates (ANCOVA, $F_{1,235} = 5.23$, $P = 0.023$).

Comparisons with Previous Work

Rates of aggression and courtship found in this study were compared to those of previous studies to see if consistent patterns emerged. In order to compare the data from this study to the previous ones, per capita rates of behaviour per 5 minutes were reformatted to per minute and then \log_{10} transformed.

Like previous studies, the data in this study were consistent with the prediction of a “dome-shaped” pattern (see Figure 11a). The peak in the dome occurred at an OSR of 1.17 in this study compared to 2 in Grant et al. (2000). The rates of aggression in my data were higher than those observed in Grant et al. (2000), perhaps because I considered and scored a wider range of interactions when observing mating aggression. When I considered only the subset of aggressive behaviours scored by Grant et al. (2000) (i.e. Chasing & Butting), the rates were more similar (Figure 11a). However, the rates of aggression in my study were considerably higher than the previous studies at OSRs less than 1.

As in previous studies, male courtship rate declined linearly with increasing OSR (Figure 11b). As with the rate of aggression, the rate of courtship in this study was higher than that of Grant et al. (2000), perhaps because I scored a greater variety of interactions. The rates of Circle Dancing only were lower than the rates from both previous studies, but again had the same pattern.

The dome-shaped pattern was not as clear in the female data as in the male data (Figure 12a). Similar to Grant & Foam (2002), rates of aggression initially increased with increasing OSR, but began to level off. Courtship rates in this study were higher than in Grant & Foam (2002), but showed a similar pattern of decreasing linearly with increasing OSR (see Figure 12b).

Discussion

When plotted against OSR, male behaviour in my study was broadly consistent with resource defence theory and the dome-shaped relationship described by Grant et al. (2000). Moreover the peak in aggression in my study was similar to their value of 2. Unfortunately my data are also consistent with the linear increase predicted by Kvarnemo & Ahnesjo (1996), because my highest level of OSR was only two. However, aggression in this study was consistent with the left-hand side of the expected dome-shape pattern, although the rates of aggression were higher in my data than in Grant et. al, (2000). This difference might be partially explained by differences in the total number of interactions scored as aggression; I included chasing, butting and interrupting, whereas Grant et al. (2000) included only chasing and butting.

As predicted, male courtship rate decreased as the OSR increased and in a manner consistent with previous studies in terms of rate per minute. When the OSR was well below 1, there was little to no aggression as males spent most of their time courting and attempting to spawn with abundant females. As the OSR approached 1, male-male competition increased as males increasingly encountered one another as they courted females. At an OSR of 2, animal contest theory provides a general insight into the nature of competition (Maynard Smith, 1982). The “hawk-dove” model predicts that “hawk”(i.e. aggressive behaviour) is an evolutionary stable strategy when

two individuals compete for a valuable resource (i.e. $OSR = 2$) (Maynard Smith, 1982). Hence, it was not surprising that aggression was highest at a OSR close to 2.

At OSRs greater than 2, male competition is predicted to decrease, as aggression becomes uneconomical. Males switch to scramble competition to maximize their reproductive fitness. Scramble competition in male medaka includes sneaking behaviour, when a male spawns with a female who is already in the process of spawning with another male. Sneaking requires minimal energetic costs, as courtship and aggression are virtually absent, and males can spawn up to 20 times in a day (Casey, 1993). Courtship rate also decreased with high values of OSR, as most males will sneak rather than court. The dome-shaped pattern in aggression reflects a trade-off between aggression and courtship behaviour.

Contrary to my expectation, the patterns of female behaviour found in my study did not conform to the dome-shaped pattern. Instead, the rate of female aggression increased, levelled out, but did not decrease at high values of OSR. As expected, males had higher rates of aggression than females at a given value of OSR. This finding is consistent with other studies on medaka (Grant & Foam, 2002) and sand gobies (Kvarnemo et. al., 1995). Unlike aggression, the rate of female courtship was as expected. Female courtship rate decreased with increasing OSR and was lower than male courtship rate at a similar value of OSR.

While OSR is a good predictor of the rate of male and female behaviour, OSR per se was not responsible for the observed patterns, as indicated by the lack of a significant interaction between male number and female group size. All patterns

observed could be explained by the number of males and the number of females. Nevertheless, OSR was a good predictor of the trends and rates of both male and female aggression and courtship.

When competing for mates, the peak of the female curve was at a higher value of OSR than the male curve. This difference is likely related to differences in how males and females compete for mates. Females primarily competed by interfering with a spawning pair. Because they do not attempt to defend a male, female interference behaviour may be effective even at high levels of OSR. In contrast, males attempted to defend access to a female, which became impossible at higher levels of OSR.

The difference in the patterns and rates of female aggression for the two resource types might be explained by the distribution of the resources in space and time. The food patch did not move, whereas mates are mobile. Hence, the food patch was smaller than the "mate patch" and was predictable in space. Both attributes likely made the food more economically defensible than the mates (Grant, 1993).

In the rich literature on male mating aggression, the dome-shape pattern of aggression has not been detected in many studies, whereas the linear increase is well documented (Kvarnemo & Ahnesjö, 1996). These results may be due to testing over a narrow range of OSR, which did not include values of OSR much greater than 2. Interestingly, the dome-shaped relationship was not apparent in my data on female intra-sexual aggression despite the broad range of OSR used. My results suggest that the rate of female intra-sexual aggression continues to increase at OSRs much greater

than 2. Further research is required to determine whether or not this is a general pattern.

My results suggest that the aggressive, competitive, and reproductive behaviour of females are just as interesting as in males. Just as the mate choice literature has evolved to include male choice behaviour, the mating competition literature needs to evolve to include the behaviour of females. Because comparisons between the sexes enrich our understanding of mating systems, further studies of the behaviour of both sexes are needed.

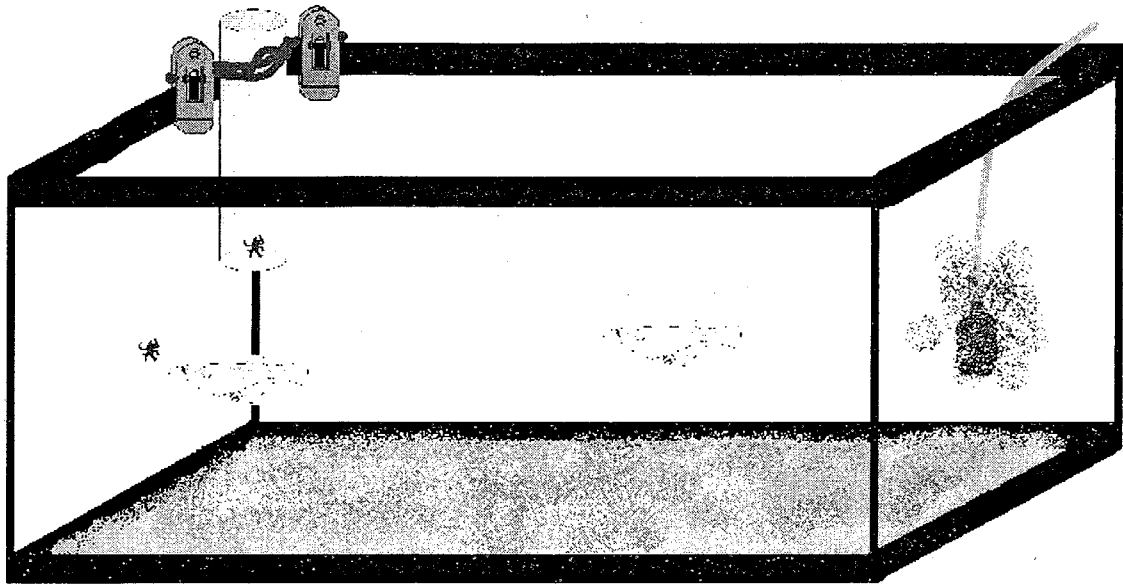


Figure 1. Experimental setup prior to and during filming for group sizes of 2, 4, 8 & 16 females.

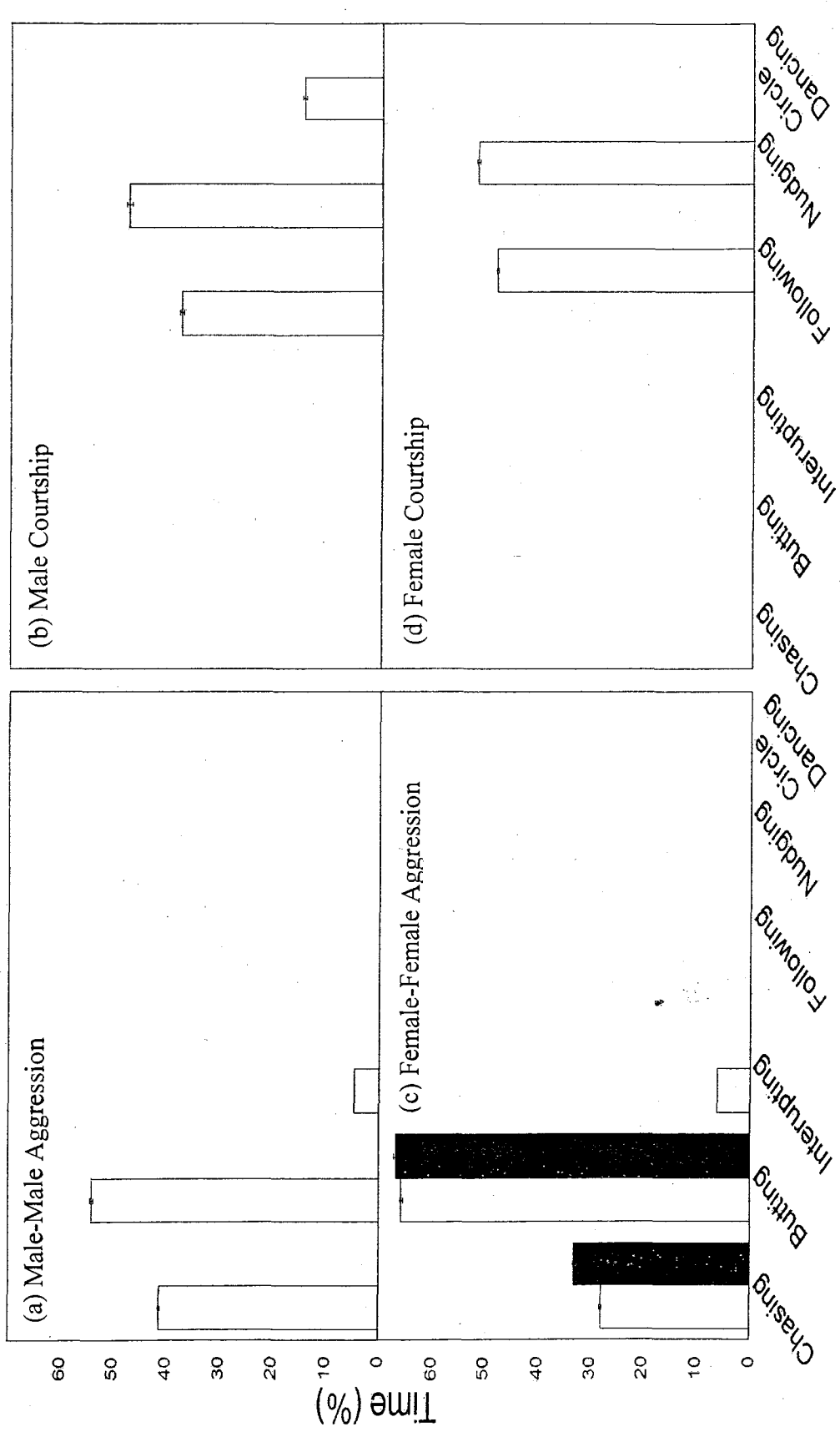


Figure 2. Mean (\pm SE, $n=10$) percent time spent on aggression and courtship during mating trials(■) and feeding trials(□): (a) male aggression - mating trials; (b) male courtship - mating trials; (c) female-female - mating trials and feeding trials; (d) female courtship - mating trials.

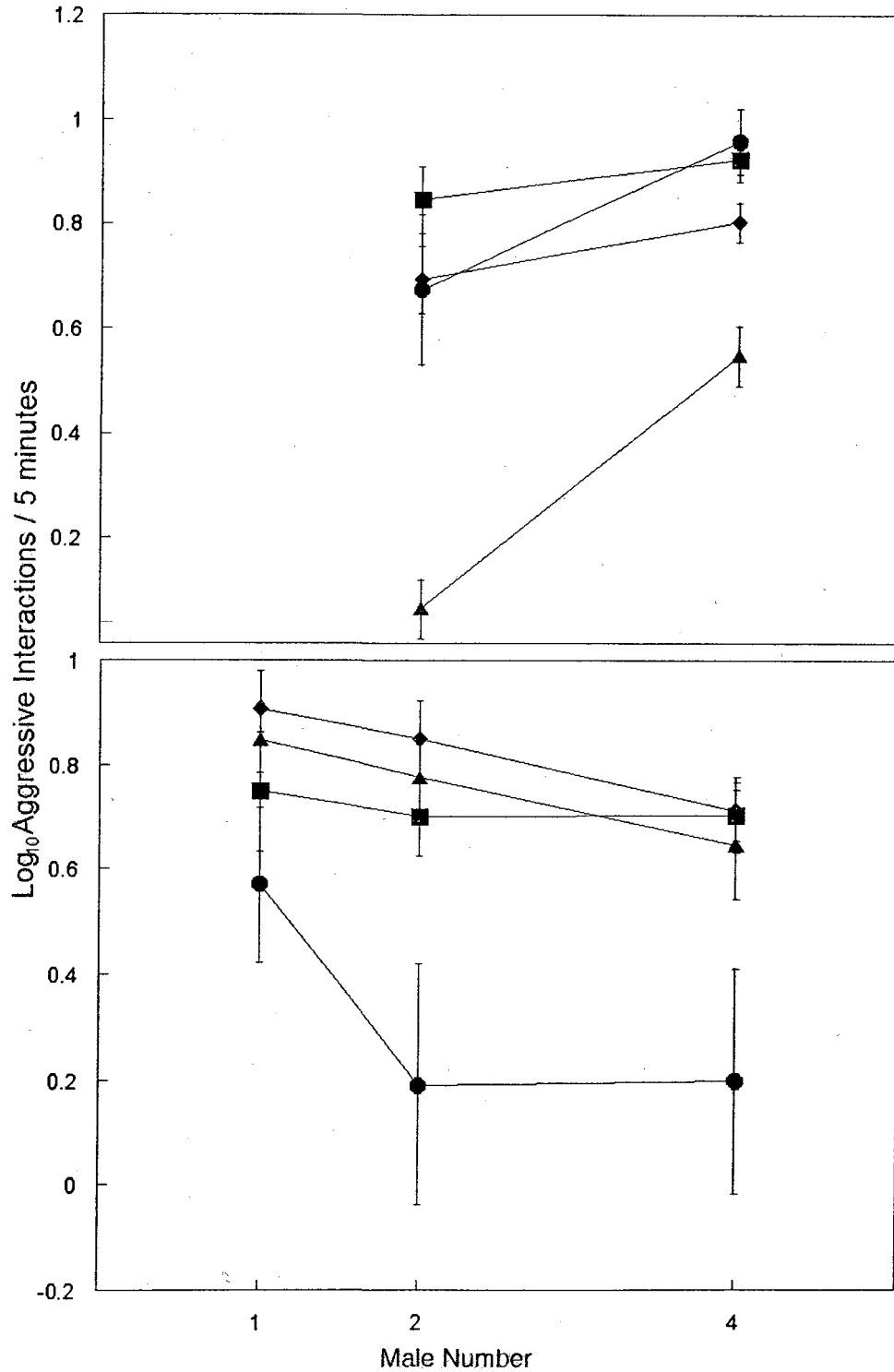


Figure 3. Mean (\pm SE, $n=10$) per capita rates of intra-sexual mating aggression by (a) males and (b) females in relation to the number of males in the tank and female group size: 2 (●), 4 (■), 8 (◆) and 16 (▲).

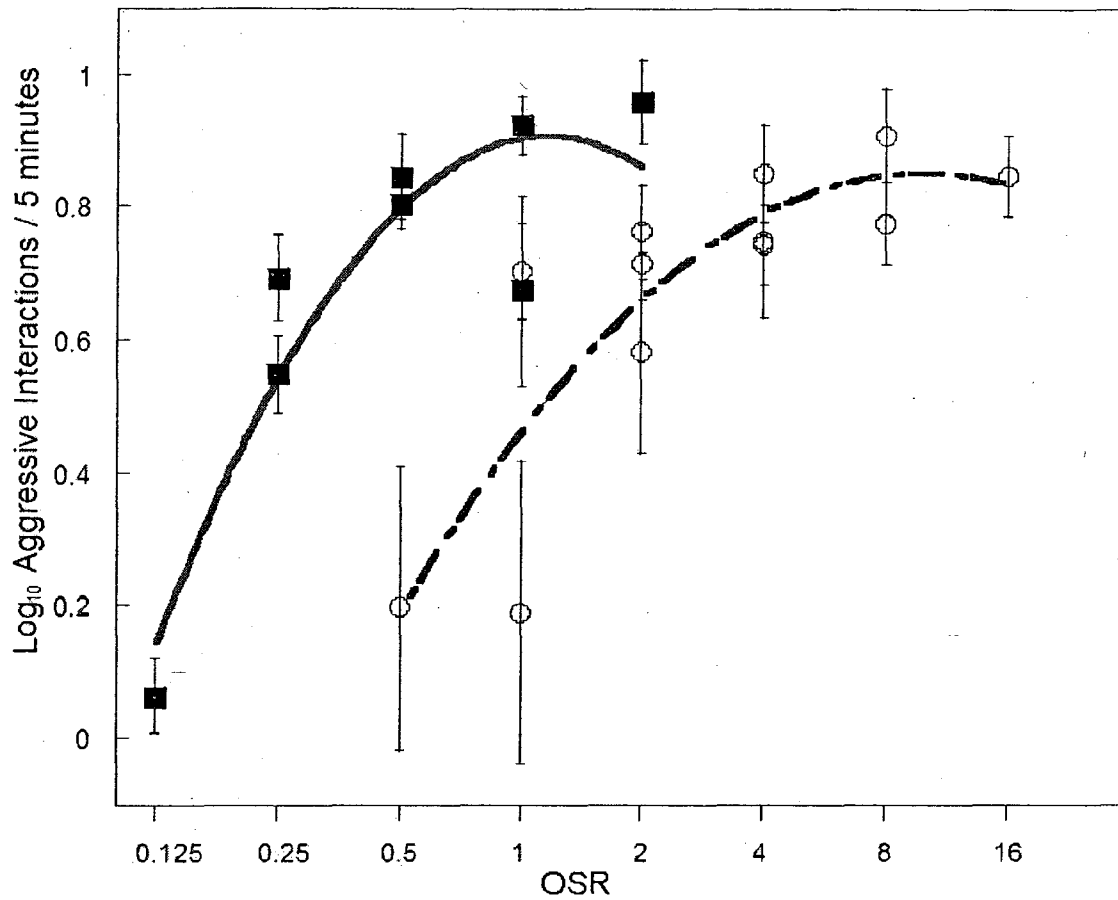


Figure 4. Mean (\pm SE, $n=10$) per capita rates of intra-sexual mating aggression by females (○) and males (■) in relation to the competitor-to-resource ratio (CRR) defined as the number of competitors / the number of the opposite sex. Note: both are on log scales.

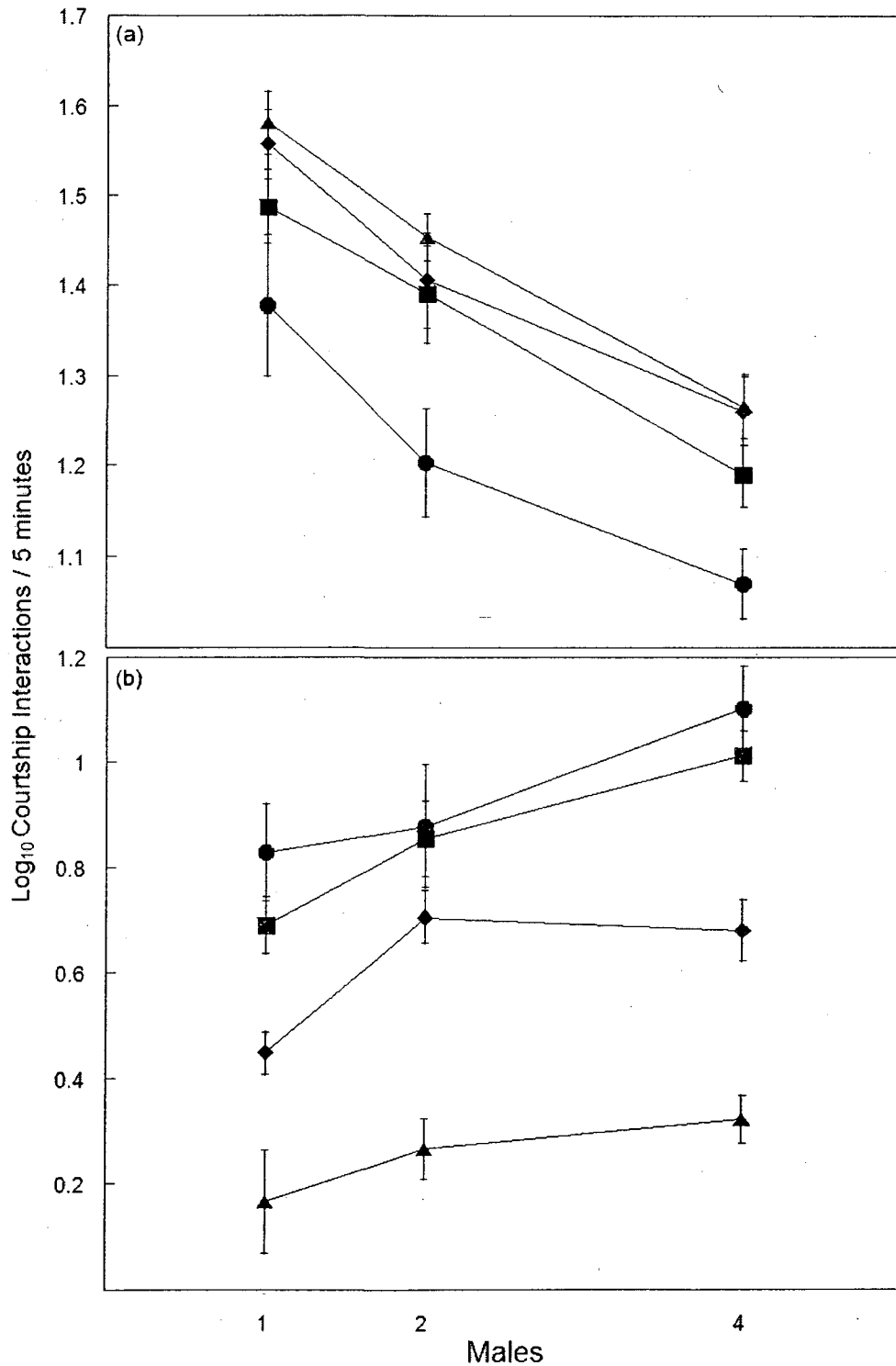


Figure 5. Mean (\pm SE, $n=10$) per capita rates of (a) male courtship and (b) female courtship in relation to the number of males in the tank and female group size: : 2 (●), 4 (■), 8 (◆) and 16 (▲).

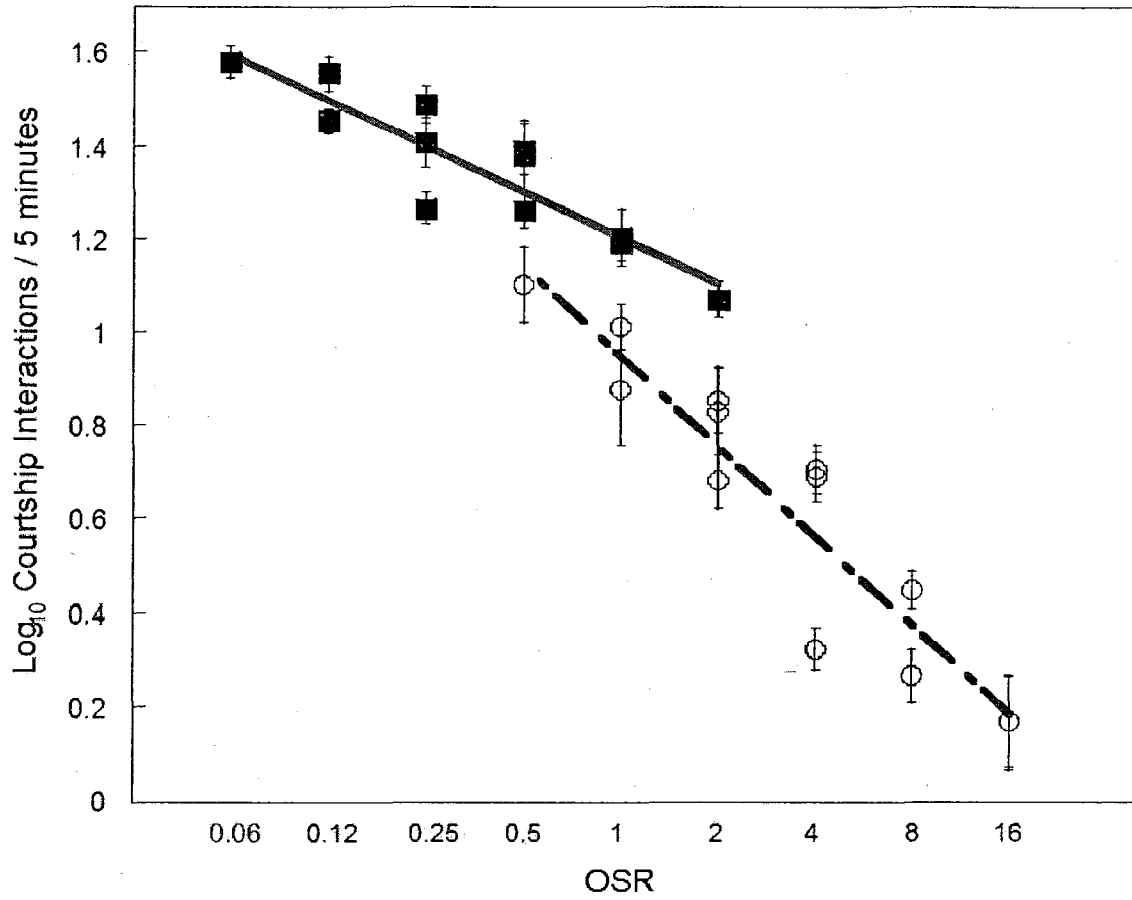


Figure 6. Mean (\pm SE, $n=10$) per capita rates of female courtship (\circ) and male courtship (\blacksquare) in relation to the competitor-to-resource ratio (CRR) defined as competitors/resources.

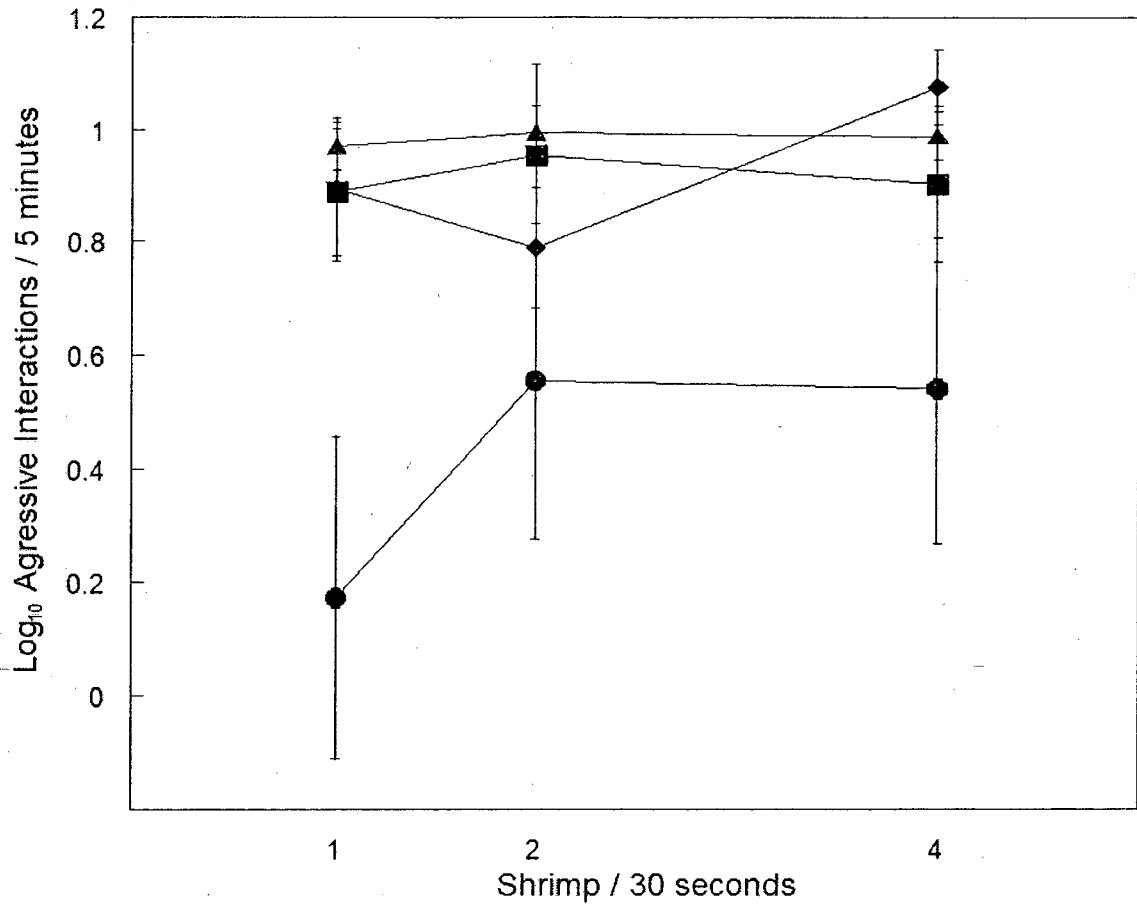


Figure 7. Mean (\pm SE, $n=10$) per capita rates of female feeding aggression in relation to the number of shrimp / 30 sec and female group size: 2 (●), 4 (■), 8 (◆) and 16 (▲).

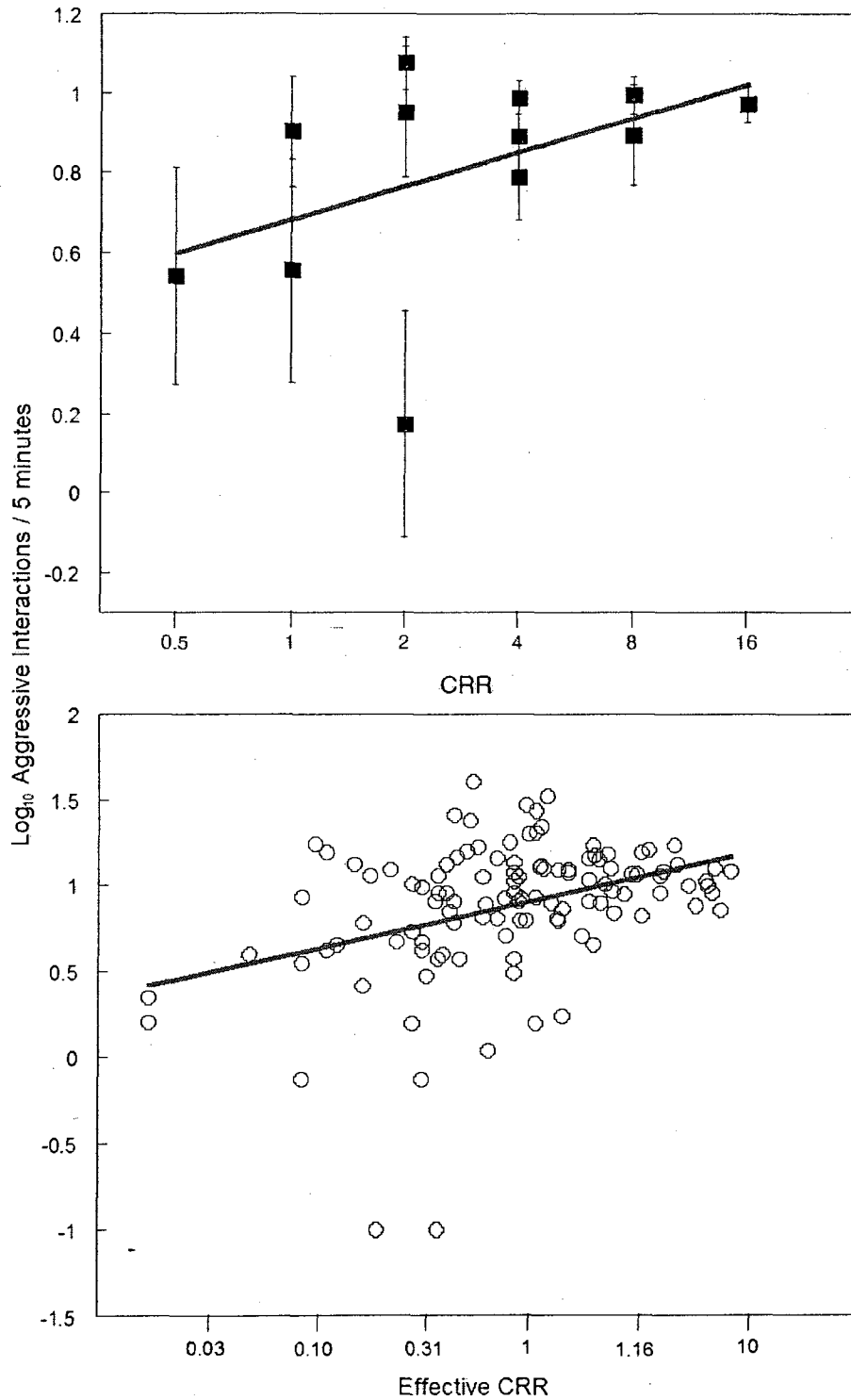


Figure 8. (a) Mean (\pm SE, $n=120$) per capita rates of female feeding aggression in relation to competitor-to-resource ratio (CRR) defined as competitors/resources. (b) Per capita rates of aggression ($n=116$) in relation to the effective CRR.

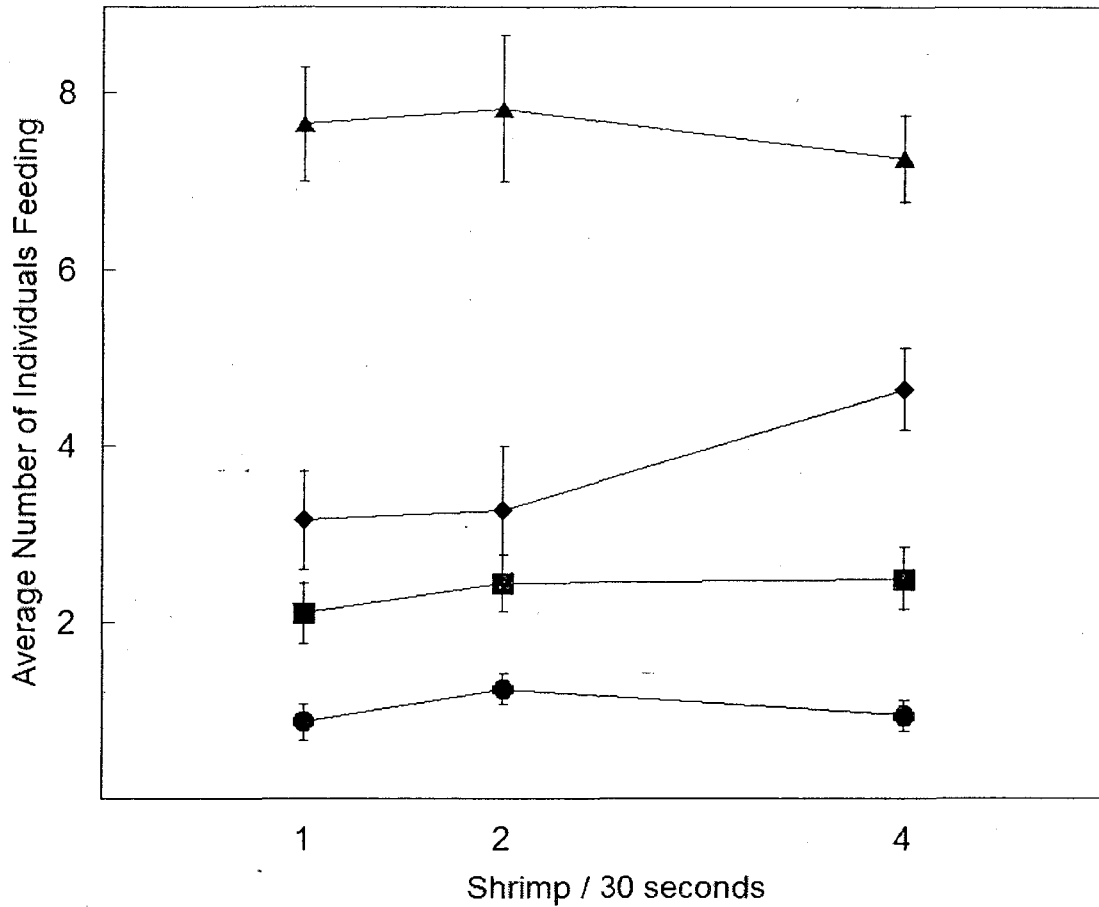


Figure 9. Mean (\pm SE, $n=10$) number of females that were actively feeding in each trial, defined as the average of the number feeding directly under the feeding tube in relation to the number of shrimp entering the tank every 30seconds and female group size: 2 (●), 4 (■), 8 (◆) and 16 (▲).

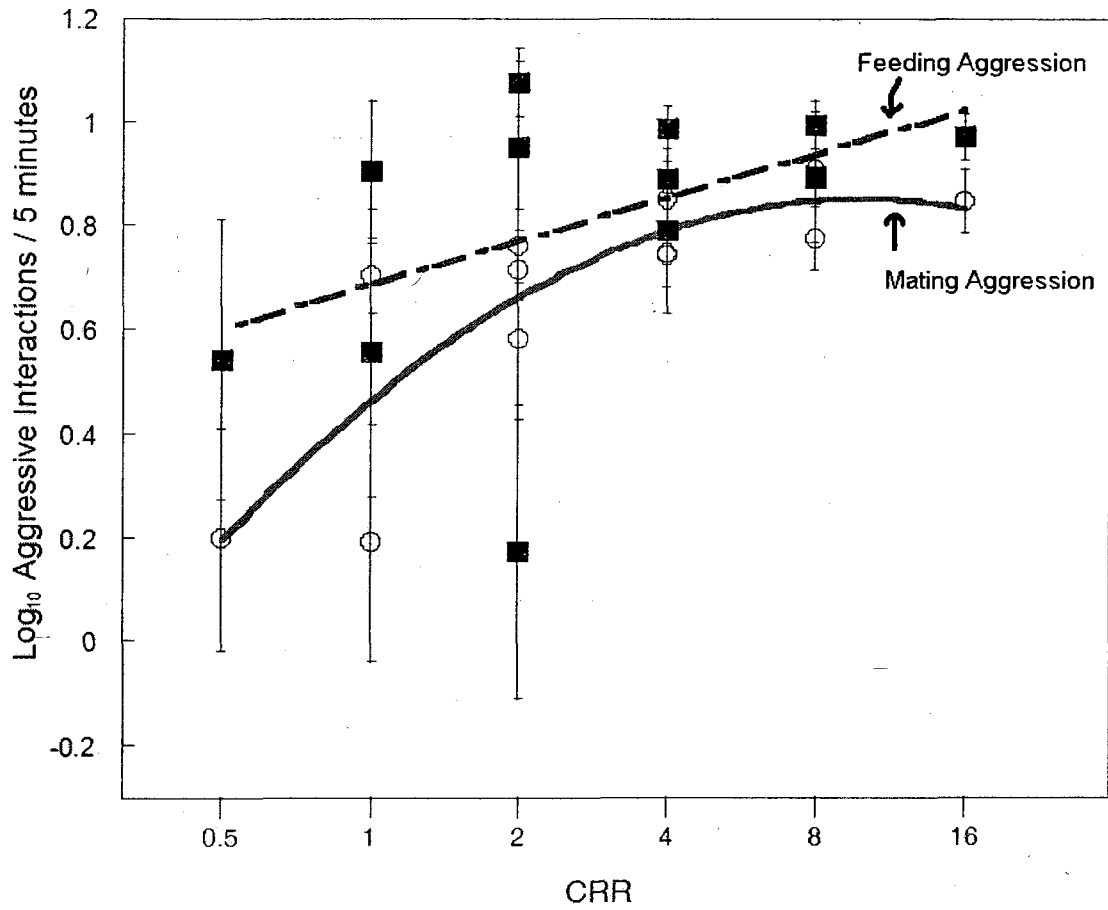


Figure 10. Mean (\pm SE, $n=10$) per capita rates of female mating aggression (○) and female feeding aggression (■) in relation to competitor-to-resource ratio (CRR) defined as competitors/resources.

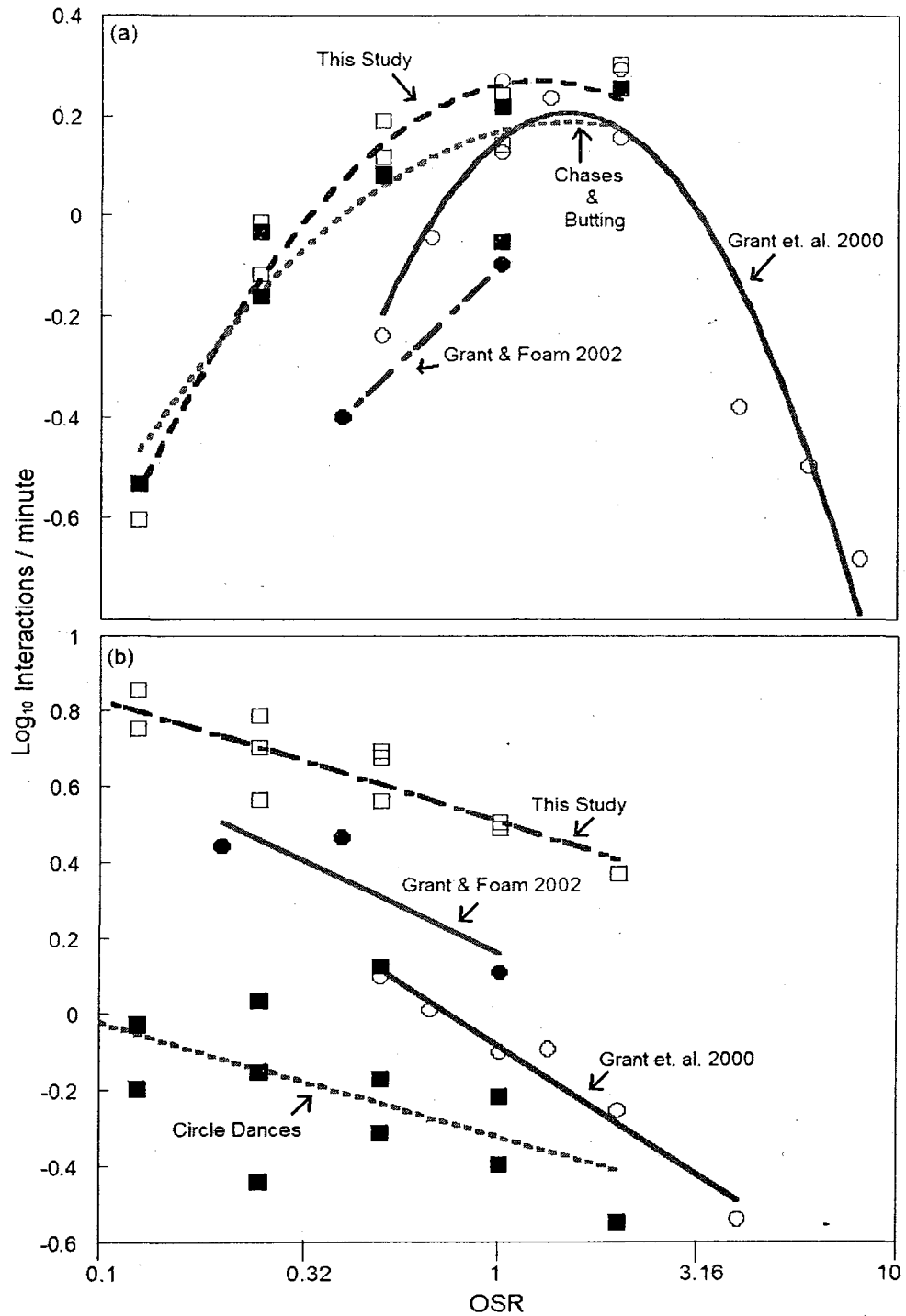


Figure 11. Mean per capita rates of (a) male mating aggression and (b) male courtship data from (●) Grant & Foam, 2002, (○) Grant et al., 2000, (□) total male interactions from this study and (■) subset of male interactions (chasing & butting only in (a) and circle dancing only in (b)) in relation to the log competitor-to-resource ratio (CRR) defined as competitors/mate.

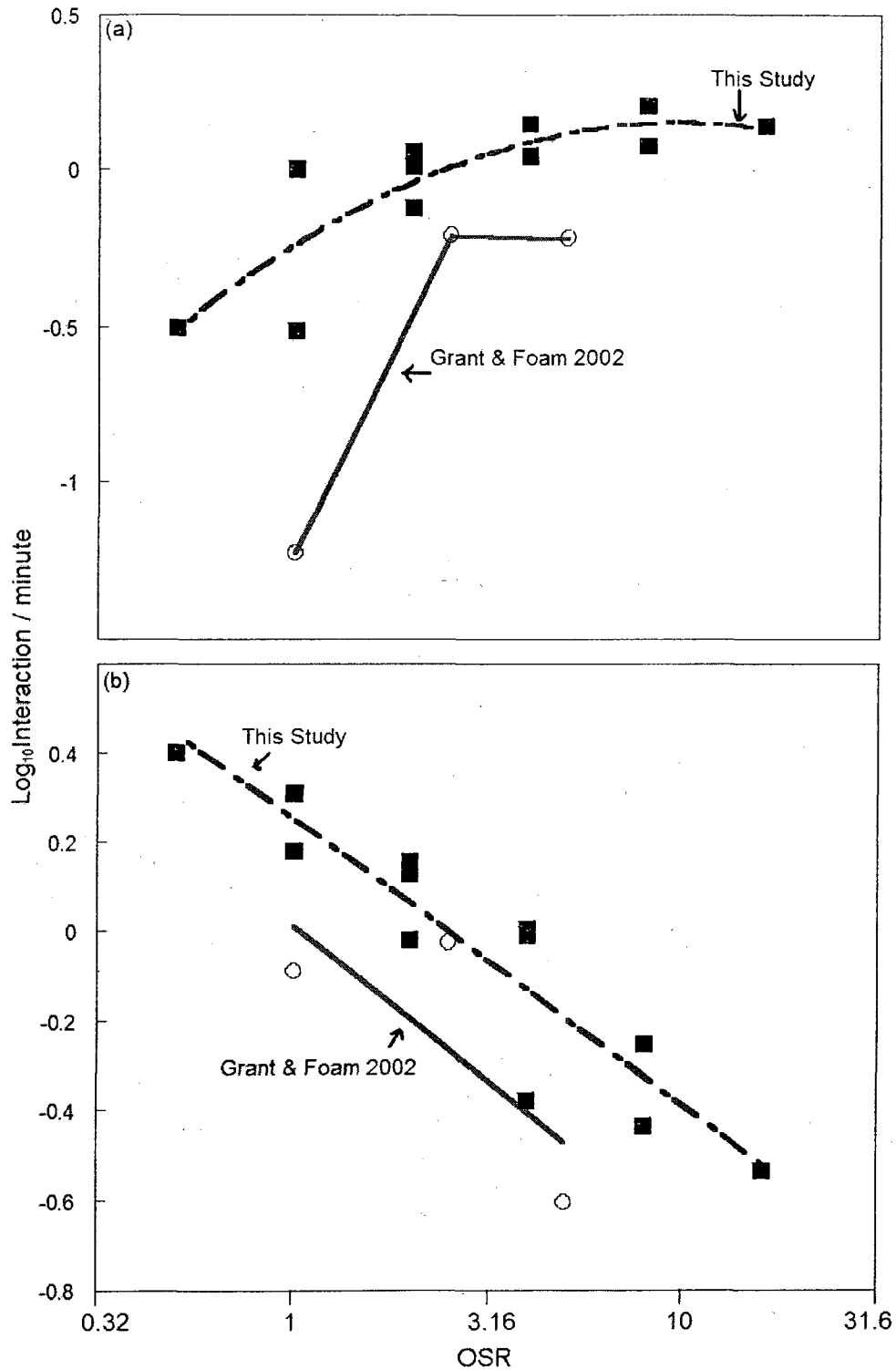


Figure 12. Mean per capita rates of (a) female mating aggression and (b) courtship for data from (○) Grant & Foam, 2002 and (■) total interactions from this study in relation to the log competitor-to-resource ratio (CRR) defined as competitors/resources.

Table 1. The number of males per trial, the number of shrimp per 30 sec, the total shrimp per trial and the duration of the feeding trial for each group size. Replicates were compared for each combination in a repeated measures design.

Female Group Size	Mates / Trial	Shrimp / 30 sec	Total Shrimp / Trial	Total Time (mins) ¹
2	1	1	20	9.5
	2	2	20	4.5
	4	4	20	2.5
4	1	1	20	9.5
	2	2	40	9.5
	4	4	40	4.5
8	1	1	20	9.5
	2	2	40	9.5
	4	4	80	9.5
16	1	1	20	9.5
	2	2	40	9.5
	4	4	80	9.5

¹ Total time shrimp were added to the experimental tank.

Table 2. Description of aggressive and courtship behaviour observed and scored for both males and females in this study.

Behaviour Type	Description	Context ¹ /References ²
Aggression		
Chasing	One fish swims rapidly towards and follows another fish. Distance varies from a few body lengths to across the tank multiple times.	MM & FF (3)
Butting	One fish swims rapidly towards another and makes contact with its head against the other.	MM & FF (2)
Interrupting	Fish butt or nudge at a mating pair in the crossed position (see below).	(5)
Courtship		
Following	One fish swims behind another of the opposite sex at the same speed and at a constant distance.	MF & FM (1)
Nudging	An individual makes gentle contact with a member of the opposite sex using their head, in what seems to be an attempt to gain the attention of the other individual.	MF & FM (4)
Circle Dancing	The male, from a position along side the female, swims in a quick circle directly	MF

in front of the female, and returns to its original position. Several can be done in succession (1)

succession

Mutual

The male floats up along side the female, curves his tail towards her and clasps her with his dorsal and anal fins. MF & FM (1)

Crossing

In the crossed position, both fish quiver and slowly sink towards the bottom head

first. Lasts from 30sec to a minute. Operational definition was a cross that lasted for more than 10sec. MF & FM (1)

¹ MM = Male-Male Aggression, FF = Female-Female Aggression, MF = Male Courtship, FM = Female Courtship

² (1) Ona & Uematsu 1957, (2) Baerends & Baerends-Van Roon 1950, (3) FitzGerld & Keenleyside 1978, (4) Keenleyside 1979, (5) Grant & Foam 2002

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