

The effects of sex ratio on sexual competition in the European lobster

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During the breeding season an individual's access to mates may be affected by operational sex ratios, causing strong variation in mating success. We manipulated adult sex ratios of the European lobster, *Homarus gammarus*, to test the predictions of models that relate sexual competition to (1) the sex ratio, (2) the time that an individual is not available to mate and (3) 'collateral investment', whereby two males contribute to a single clutch. The model predictions proved to be relatively insensitive to collateral investment. Male–male competition predominated in the male-biased but not in the female-biased sex ratio. This matches the predictions of one model that incorporates an extended period of female receptivity because the time that a male was unavailable to mate was small compared to the time spent by females in cohabitation and parental care. Although females increased their competitiveness when males were in the minority, male competition remained high. The insensitivity of male–male competition to sex ratios may be due to an upper limit to the costs that males can afford when there is a serious risk of injury, preventing males from increasing their aggression when females are in short supply.

The operational sex ratio (OSR: ratio of fertilizable females to sexually active males at a given time) is a principal factor influencing the intensity of sexual selection (Emlen & Oring 1977; Gwynne 1991; Clutton-Brock & Parker 1992; Vincent et al. 1994; Kvarnemo & Ahnesjö 1996; Reynolds 1996). The direction of bias of OSR is thought to be determined primarily by the potential rates of reproduction of each sex. These are defined as the maximum rate at which each sex could produce offspring if given unlimited access to members of the opposite sex, averaged over all individuals and conditions (Parker & Simmons 1996). Typically, males devote less time and energy than females to offspring production and therefore have a higher potential rate of reproduction. This skews the OSR towards a male bias, causing more variation between males in mating success, and selecting for males to compete more intensely for mates. Females may also compete for males if males vary in quality, although courtship role reversal, where females are the predominant competitors, occurs in only a few species, usually where male parental input is relatively higher (Gwynne &

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Simmons 1990; Gwynne 1991; Almada et al. 1995; Forsgren et al. 1996).

The overall adult sex ratio is a key factor affecting sexual competition (Kvarnemo et al. 1995; Parker & Simmons 1996). If the adult sex ratio is biased, potential rates of reproduction are not sufficient to predict the direction of sexual competition (Parker & Simmons 1996). The OSR can also be influenced by the distribution of individuals in time and space (Reynolds et al. 1986; Naylor et al. 1988; Gwynne et al. 1998), temperature (Ahnesjö 1995; Kvarnemo 1996) and precopulatory guarding of multiple mates (Manning 1980; Jormalainen et al. 1994). The latter is widespread in aquatic crustacea, and reduces the incidence of extrapair matings (Manning 1980; Ridley & Thompson 1985; Cowan & Atema 1990; Dunham & Hurshman 1991; Goshima et al. 1996). This slows down the males' potential rate of reproduction, despite their small direct contribution to offspring production.

In clawed lobsters, *Homarus* spp., pre- and postcopulatory mate guarding occurs, lasting 7–12 days per female in the American lobster, *H. americanus* (Atema 1986; Cowan & Atema 1990). Thus, unlike many other species with female care, male costs of reproduction include more than the production of spermatophores. The clawed lobsters are especially relevant to the study of OSRs because variation in sex ratios has been shown in wild populations. In the American lobster, size appears to be an important correlate of sex ratio, with higher proportions of females than males found among larger individuals in commercial catches (Templeman 1936; Skud & Perkins 1969). Sex ratio may also be influenced by exploitation rates in commercial fisheries (Skud 1969; Campbell 1992), salinity (Jury et al. 1994), water depth (Skud & Perkins 1969) and season (Cooper et al. 1975).

Male intrasexual competition has been shown clearly in the American lobster (Atema et al. 1979; Atema 1986; Cowan & Atema 1990). Males defend shelters from which they attract females and in which they perform pre- and postcopulatory mate guarding. Mate guarding occurs before, during and after the female moults, and the female leaves the shelter only after her exoskeleton has hardened, which can require at least 7 days. The hard exoskeleton then provides better protection, and females are less receptive or prone to the possibility of extrapair matings (Atema et al. 1979; Atema & Cobb 1980; Atema 1986; Atema & Voigt 1995). Despite this, extrapair fertilizations may be possible through intermoult matings (Waddy & Aiken 1991), although the ultimate fertilization success of these encounters is still unknown. Sperm are thought to be held for up to a year before fertilized eggs are extruded. The eggs are carried on the underside of the abdomen for a further 9–11 months until hatching (Atema & Voigt 1995).

Prolonged male mate guarding in the European lobster, *Homarus gammarus*, may reduce the male's potential reproductive rate, and therefore has implications for the intensity of sexual selection and associated changes in competitive behaviour. Hence, our aim was to investigate whether variation in the sex ratio of the European lobster influences sexual competition between and within the sexes and to relate our results to three simple models that incorporate potential rates of reproduction, adult sex ratio and the degree of collateral investment by males through multiple matings (Clutton-Brock & Parker 1992; Parker & Simmons 1996).

MODELS AND PREDICTIONS

Parker & Simmons (1996) devised a series of models to predict the direction of sexual competition, using three key components that control the intensity of sexual selection: the time that an individual is not available to mate ('time out'); the adult sex ratio; and the degree of 'collateral' input by each sex. A typical example of the latter is when a female mates with more than one male before producing her clutch. More generally, collateral input occurs when more than one member of either sex contributes 'time out' in a single reproductive event of the opposite sex (Parker & Simmons 1996).

For the case when females mate with only one male per reproductive cycle, Parker & Simmons (1996) used the earlier model of Clutton-Brock & Parker (1992) to express the direction of sexual competition as a function of the female reproductive cycle length, adult sex ratio and time out. They predicted that males would be the predominant competitors when

$T(M-1) - (G_{\rm m} - G_{\rm f}) > 0$

and similarly, females would be predominantly competitive when the left hand side of this equation is less than zero. Here, *T* represents the total time taken for a complete reproductive event to occur and *M* is the number of males per female. G_m and G_f represent the time out from mate acquisition by males and females, respectively, when individuals are not available to mate with other members of the opposite sex. This includes parental care, mate guarding, copulation and replenishing energy and somatic resources.

For collateral investment, Parker & Simmons (1996) expressed the male total time out to be $mG_{\rm m}$, where m males (m=2) invest an average time out of $G_{\rm m}$. Hence, males are predicted to be predominant competitors when

$$\Gamma(M-1) - (mG_{\rm m} - G_{\rm f}) > 0$$

and females are predominantly competitive when the left-hand side of this equation is less than zero.

Parameters for European lobster

We ran three key models to encompass uncertainty in details of the reproductive biology of European lobsters. The first assumed that the female reproductive cycle lasts 1 year, during which each female mates with only one male. Thus, T=365 days, composed of 304.2 days of parental care (aerating the developing eggs; Atema & Voigt 1995), and 4.4 days of permanent cohabiting and mating (G_f =308.6 days; Karnofsky & Price 1989). Males spend 30 min mating, but guard the female before and after the moult for 4.4 days (Karnofsky & Price 1989). As we assumed that females are soft shelled and vulnerable to attack for 4.4 days, we also assumed that males are vulnerable for the same period around their moult (4.4 days) and cannot acquire mates during that time. This gives an average time out from mate acquisition (G_m) of 8.8 days. M represents the adult sex ratios used in this study: a male-biased sex ratio (four males, two females, hence M=2) and a female-biased sex ratio (two males, four females, hence M=0.5).

The second model was identical to the first, but with a 2-year cycle, based on information for the closely related American lobster, for average-sized females (Waddy & Aiken 1986, 1991). Thus, T=730 days, again composed of 304.2 days of parental care and 4.4 days of permanent cohabitation and mating. In addition, females may retain eggs for up to 1 year before extrusion; we assumed that the average period lasts for 212.9 days (Caddy 1986), during which the female is unavailable for mating $(G_{\rm f}=521.5 \text{ days})$. As before, males spend 8.8 days out from mate acquisition ($G_{\rm m}=8.8$ days). Again, M is defined by the adult sex ratios used in this study (male biased: M=2; female biased: M=0.5).

The third model was identical to the second (T=730 days), but with the female having a much longer period of receptivity (again to a single male). As before, the female spends 308.6 days ($G_{\rm f}$) in total performing parental care and in permanent cohabitation and mating,

but she remains receptive to other males throughout the period when she is retaining unfertilized eggs internally (212.9 days). As with the previous models, M is defined by the adult sex ratios used in this study (male biased: M=2, female biased: M=0.5).

To account for the possibility of collateral investment, we also ran these models assuming that two males invest sequentially in a single clutch, as later observed in two replicates and for the American lobster in the wild (Nelson & Hedgecock 1977).

Parker & Simmons' (1996) model predicts the average sexual competition expected over a full breeding season, and hence would assume that all individuals are monitored constantly over that period. In our study, we observed each replicate for 9 days and these 9-day periods spanned 10 weeks of the total mating season which lasts from May to August (Branford 1978; Free 1994). We used parameter inputs in the model according to two ways in which lobsters might perceive their circumstances in each replicate with respect to the end of the season. First, since the sexes were separated before the experiment, they might perceive the start of the experiment as the start of their season. In this case, the parameters for female time out are as given above. We use this as our 'basic assumption' (Fig. 1a) to derive the main predictions listed below.

Alternatively, if lobsters are less flexible and operate on a seasonal clock, those individuals used in the later replicates could perceive less time remaining in the breeding season. This could affect their sexual behaviour if, for example, males are 'hard-wired' to expect fewer females to be receptive as the date progresses. To account for this possibility, we used a 'seasonal assumption' (Fig. 1b) in which the average female time out increased in proportion to the amount of time remaining in their natural breeding season compared with the date that the replicate was studied. Averaged over all replicates, 28% of the breeding season remained after the observation periods, indicating that 28% of females might on average be perceived to be available for mating at the time of observation. The adjusted female time out $(G_{f(adj)})$ from the original female time out (G_f) was derived using the equation:

$$G_{\rm f(adi)} = T - ((T - G_{\rm f}) \times 0.28)$$

where T is the total time taken for a complete female reproductive event to occur. The adjusted female time out was then incorporated into the original equation. We consider our results in relation to this 'seasonal assumption' in the Discussion.

We made four predictions, the first two of which arose directly from the basic (nonseasonally adjusted) assumption (Fig. 1a).

Prediction 1: males should be the predominant competitors in both male- and female-biased treatments over both 1- and 2-year cycles (models 1 and 2), unless females are receptive for long periods (model 3; Fig. 1a). Inclusion of collateral investment had a negligible effect on the models' predictions (not shown: see Discussion).

Prediction 2: although we expect males to be more competitive than females (prediction 1), we expected this



Figure 1. Predictions of the intensity of sexual competition $(T(M-1)-(mG_m-G_f))$ for values of M (number of males per female) for (a) the 'basic' model and (b) the 'seasonal' model, where T is the total female cycle time and G_m and G_f represent time that males and females are not available to mate, respectively. Positive values indicate predominant male competition and negative values indicate predominant female competition. Model 1 assumes a 1-year reproductive cycle where females mate with only one male $(m=1; \bullet)$. Model 2 represents a 2-year female reproductive cycle in which females mate with one male and are unreceptive during egg retention $(m=1; \circ)$. Model 3 represents a 2-year female reproductive cycle in which females mate with only one male but are receptive during egg retention $(m=1; \bigtriangleup)$. Numbers at the end of each line refer to the model number to which they relate.

difference to be highest in the male-biased treatment (all models; Fig. 1a).

Prediction 3: an increase in the numbers of one sex should correspond to an increase in its competitiveness. This did not follow from the models, because they predict only relative differences in the competitiveness of the sexes, not absolute differences. Nevertheless, we expected this from general sexual selection theory (Kvarnemo & Ahnesjö 1996).

Prediction 4: the period of courtship and pair bonding should be longer in male-biased than in female-biased conditions, because females can afford to be choosier (Johnstone et al. 1996) and males may gain more from monopolizing mates as a paternity assurance.

METHODS

We carried out the study from June to September 1996 at the Lowestoft Laboratory, Centre for Environment, Fisheries and Aquaculture Science (CEFAS), Suffolk, U.K. Lobsters used in the experiments were caught using baited traps between Skipsea (53°58.75'N, 0°11.80'W) and Withernsea (53°43.80'N, 0°02.35'E) on the east coast of England at a depth of 1–9 m. Lobsters were housed in tanks with continuously renewed natural sea water, either individually or in groups separated into sexes for logistical reasons. Although this difference was not ideal, those that were housed individually were moved to communal tanks for 4 days before the experiment to help standardize social experience, and all lobsters were then allocated randomly to the experimental tanks. Hence, any differences in social experience would have been random with respect to treatments. In addition, lobsters were left for 1–2 days to acclimatize in the experimental tanks before we started observations. Each lobster was fed with two fish (sprats, *Sprattus sprattus*) once each week throughout the experiment.

We conducted tests in four outdoor tanks $(3.8 \times 1.3 \text{ m})$ and 0.9 m high). These were grouped in a two-by-two tank block, each with a 10-cm thick layer of pea gravel and continuously renewed sea water. Temperature over the study period varied from 14.5 to 19.4°C with a salinity of 29–33‰. Each tank contained four clay ridge roof tiles which were used as shelters (length 30.9×26.5 cm and 12.5 cm deep). Light levels were manipulated using black polythene sheeting, under which two sets of eight 60-W and nine 15-W incandescent light bulbs were suspended. To measure light levels we used a quantum radiometer, which measures the light that is perceived by animal photoreceptors, known as photon irradiance (Endler 1990; Jones & Reynolds 1996). Three light levels were used to represent four periods within a 24-h cycle: 'day' lasting 13 h (3.5 µmol/m² per s), 'dawn' lasting 1 h $(0.3 \,\mu\text{mol/m}^2 \text{ per s})$, 'dusk' lasting 3 h $(0.3 \,\mu\text{mol/m}^2 \text{ per s})$ and 'night' lasting 7 h (<0.1 μ mol/m² per s). Karnofsky & Price (1989) showed that American lobsters are most active during dusk. Hence, the light regime provided an extended dusk period for observations and represented the natural photoperiodicity at this latitude. Treatments were alternately assigned to two tanks, enabling two replicates to be run simultaneously. Male-biased treatments (N=8) consisted of four males and two females, and female-biased treatments (N=8) contained two males and four females.

We selected reproductively mature lobsters belonging to the most common adult sizes in the wild (85.0-104.9 mm carapace length, CL). Maturity was verified by the fact that all females produced eggs at the end of the breeding season. For the more abundant sex in each treatment we selected two 'small' individuals (85.0-89.9 mm CL), one 'medium'-sized (90.0-94.9 mm CL) and one 'large' individual (95.0-104.9 mm CL) to mimic the greater abundance of smaller animals in wild populations. For the least abundant sex we used one small individual and one medium-sized individual. The mean sizes of males and females did not differ between treatments (one-way ANOVA: males: F_{1,62}=0.703, P=0.406; females: F_{1.62}=1.581, P=0.215). Lobsters were placed in experimental tanks 1-2 days before observations to allow them to settle, with the exception of replicate 2 where lobsters from both treatments remained in the experimental tanks for 16 days for logistical reasons. Removal of the results from this replicate made no difference to the overall mean frequency of interactions (Mann–Whitney *U* test: males: Z = -0.156, $N_1=32$, $N_2=28$, P=0.876; females: Z = -0.134, $N_1=32$, $N_2=28$, P=0.893) so the results were included in the final analysis. Observations of both male and female-biased treatments were carried out in parallel on days 1, 3, 5, 7 and 9 in each replicate, since we felt that 9 days was the minimum duration for lobsters to settle down, compete, court, cohabit and mate. Each tank was observed for 1.5 h in the dusk period, allowing 15 min of observation per individual lobster.

We recorded the duration and subsequent success of mating-related behaviour (reviewed by Atema & Cobb 1980). We defined competition between lobsters by eight aggressive behaviours and five avoidance behaviours (Scrivener 1971; Table 1). For the analyses, the competitive behaviour between individuals was classified into four categories: male winning against another male (male–male); male winning against a female (male–female); female winning against a male (female–male) and female winning against another female (female–female).

We needed to control for different expected frequencies of encounter according to the numbers of individuals in the tank. These were affected by two factors: sex ratio, which affected the probability of an individual encountering another of a particular sex, and the number of active individuals in the tank. Active individuals were those individuals that were receptive, and thus did not include females that were cohabiting with males or that had extruded eggs (six out of 48 females). We observed males competing with other males during cohabitation so we did not exclude them from the final analysis. If all four females in the female-biased treatment are receptive, the likelihood of a male encountering another male is less than in the male-biased treatment because the male will spend more time engaged in courtship or aggression with females. Indeed, this was our impression, based on our observations (Fig. 2a). Therefore, for each category of sexual encounters, we divided frequencies of behaviours per individual by the proportion of all active individuals of the relevant sex that could have been encountered (Fig. 2b). Thus, in the male-biased treatment, the proportion of males that another male could meet was three out of five, assuming that all individuals in the tank were active (Fig. 2b). If a male died, this proportion would then be two out of four. We also analysed the data correcting only for members of the relevant sex that could have interacted, without accounting for the total density of both sexes in each replicate. For the examples above, this would mean dividing the encounters per individual male by three and two, respectively; this correction made no difference to the results and these corrections are therefore not presented.

Ethical Note

The lobsters were bought from commercial fishermen who caught them as part of their normal trade, and so they were not taken from the wild for the purposes of the experiment. They were kept at higher densities than we believe they occur in the wild; however, the shelters were

Table	 Aggressive 	and avoida	ance behaviours	s recorded (fr	om Scrivener	1971
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Behaviour type	Aggressive behaviour	Description
Aggression	Meral spread	Body raised, abdomen extended, claws held up and extended towards opponent
	Approaching	Moving towards opponent with abdomen extended and claws held above bottom
	Pushing	Body raised high, abdomen extended, opponents pushed with claws
	Antennae whipping	Antennae swept back and forth horizontally lashing the opponent
	Boxing	Withdrawing claws followed by jabbing or punching the opponent: occurs during extended periods of pushing
	Rushing Scissoring	Running towards opponent, claws in meral spread position Claws rapidly brought together from meral spread position, usually striking opponent
	Rapid turning	Quick, 180° body rotation and immediate meral spread as
Avoidance	Backing	Retreating away backwards from opponent, tail fan folded and tucked under abdomen
	Abdomen flexing	Vigorous contraction of abdomen causing propulsion of the body upwards and backwards, raising the lobster off the bottom
	Jumping Running away Sideways	Rapid abdomen flex, claws maintained in meral spread position Turning from opponent and moving rapidly away Moving sideways away from opponent

evenly distributed throughout the tanks, enabling easy access to shelters from any part of the tank. At any one time, two-thirds of the lobsters had access to shelters, but some chose not to use them, and others used them only on a temporary basis, so invariably there were shelters available into which individuals could escape. During daily observations of replicates, the lobsters were monitored for signs of injury. The only problems noticed were four out of 96 individuals that lost claws, and subsequently died. However, two of these cases followed moulting and although claw loss is not a common occurrence in captivity, we have observed occasional similar problems with animals moulting when held in isolation. Indeed, claw loss is often seen in wild-caught lobsters. On one additional occasion, a lobster died without any apparent prior injury. The majority of encounters did not involve claw contact, but were stand-offs, during which individuals faced each other and appeared to assess one another, probably through chemical communication (Atema 1986). Even when claw contact occurred, it was often relatively low-level aggression such as claw pushing.

After the first three replicates had ended, the majority of the lobsters were returned to communal tanks at about the same densities as in the experimental tanks and the remainder were housed individually. The majority of the communally held lobsters were kept at this density for 12 days before 32 additional individual tanks were made available at the end of replicates 4 and 5. This provided 33% more space than before to keep holding tank densities as low as possible. The remaining lobsters from the first replicate were kept at the same density as in the experiment for about 1 month before being moved. All communally held lobsters were fed and monitored regularly for injuries by trained U.K. Home-Office licensed staff at the CEFAS Fisheries Laboratory, Lowestoft, Suffolk. Communal tanks were also checked daily for moulted individuals. When found, these individuals were removed and held individually until the exoskeleton had hardened. The lobsters remained in the tanks after the experiment for further behavioural study.

Statistical Analyses

Our corrected data were log transformed for normality, and pooled for each behavioural category and treatment. We used ANOVA to test differences between male-male and female-female encounter frequencies within sex bias treatments (predictions 1 and 2). In addition to using 'sex bias' and 'behaviour' as factors, we also included 'tank' as an additional factor. This approach was used because our design became nonorthogonal after we omitted replicates that contained more than two egg-carrying females over both treatments; that is, uneven numbers of sex bias treatments were allocated to each experimental tank, and thus the effect of tanks was included in the model. We used an ANOVA to test the significance of each of the factors 'sex bias', 'behaviour' and 'tank' and each of the two- and three-way interactions between the factors. We ran the ANOVA first with all factors and interactions included and then with the three-way interaction removed. For each ANOVA the χ^2 for goodness-of-fit was computed, and the difference between the values of χ^2 was used to test the significance of the factor or interaction being omitted. A nonsignificant value indicated that there was no evidence for the presence of the three-way interaction and therefore the interaction could be omitted from the model (Dobson 1990). This process was repeated with all other interactions and factors until



Figure 2. Intra- and intersexual competition between males (M) and females (F) in (\blacksquare) male-biased (N=8) and (\square) female-biased treatments (N=8), (a) before and (b) after being corrected for the probability of encounter (N=8). Values are mean encounters per individual calculated from five 15-min observation periods per individual. Asterisks indicate significant differences between male-biased and female-biased treatments, in the presence of other significant terms in the final model: *P<0.05; **P<0.01; ***P<0.001.

all nonsignificant terms had been excluded, thus producing the best-fitted model to our data, accounting for 65% of the variability of encounter frequency. The model for the frequency of encounters, corrected for the proportion of active animals of the relevant sex that an individual could meet is: behaviour+sex bias+behaviour*sex bias+behaviour*tank. To assess how the frequency of male-male and female-female encounters was affected by 'sex bias' we ran two further ANOVAs, one per sex bias treatment, using behaviour and tank as factors and excluding any nonsignificant factors or interactions.

We followed the same procedure for testing the effects of sex ratio manipulation on within- and between-sex encounter frequencies and durations (prediction 3). Encounter duration was measured as the time from which one individual began aggressive behaviour to when it, or the other lobster, had completed its avoidance behaviour, since the aggressor was not necessarily the winner of the encounter. Using ANOVAs, we rejected nonsignificant factors and interactions to produce best-fitting models to our data. These models accounted for 65 and 94% of the variation in our data for encounter frequencies and durations, respectively. The model for the frequency of encounters, corrected for the proportion of active animals of the relevant sex than an individual could meet is: behaviour+behaviour*sex bias+behaviour*tank. The final model for the duration of encounters is: tank+ behaviour*sex bias+behaviour*tank+sex bias*tank+ behaviour*sex bias+tank). To determine the effect of 'sex bias' and 'tank' on each category of sexual encounters, we ran four ANOVAs, one for each behaviour, using sex bias and tank as factors. As before, we excluded any nonsignificant factors or interactions from the final model.

We tested the effect of sex ratio on encounter intensity by fitting an ANOVA using a forward procedure, in which the simplest model was fitted to the data, and factors and interactions were added one at a time. A backwards procedure could not be used as the high variance in the data prevented convergence of the model. As with the backwards procedure, factors and interactions were excluded from the final ANOVA if they were nonsignificant. The final model accounted for 20% of variability in encounter intensity (encounter intensity: behaviour+sex bias). Although there was no overall significant effect of sex bias on behaviour, we nevertheless ran four ANOVAs, one per category of sexual behaviour, to compare the effect of sex bias on each of the four sexual encounters.

We used a Mann–Whitney *U* test to compare differences in courtship duration between sex ratio treatments. Statistical power (Bond 1996; Thomas & Juanes 1996) was measured as $1 - \beta$ where β is the probability of accepting a false null hypothesis.

RESULTS

Competition Within Sexes

Our first prediction was that males should be the predominant competitors in both male- and femalebiased treatments over both 1- and 2-year cycles (models 1 and 2), unless females are receptive for long periods (model 3; Fig. 1a). We found that male-male competition predominated only in the male-biased treatment (ANOVA: χ_1^2 =18.024, *P*=0.0001; Fig. 2b); male-male encounters were as frequent as those between females in the female-biased treatment (ANOVA: χ_1^2 =2.597, *P*=0.107; Fig. 2b). These analyses used 'behaviour' and 'tank' as factors, and excluded any nonsignificant factors or interactions.

As expected from prediction 2, there was a greater difference between same-sex encounters in male than in female-biased conditions. This can be seen by comparing the differences between the male-biased and femalebiased treatments (see statistics for prediction 1; Fig. 2b), suggesting that even a small manipulation in sex ratio may affect the degree to which each sex competes.

Contrary to prediction 3, there was no effect of sex ratio on the frequency of male–male encounters (ANOVA: $\chi_1^2=0.137$, *P*=0.711; Fig. 2b). However, the encounters tended to last longer in the male-biased treatment than

	Male-biased treatment	Female-biased treatment		Р
Encounter	$(\bar{X}\pm SE)$	$(\bar{X}\pm SE)$	χ^2_1	
Duration				
Male-male	40.6±11.8	36.1±3.6	2.745	0.098
Female–female	37.4±4.8	39.5±5.8	5.178	0.023
Male–female	42.5±8.2	39.1±2.9	0.036	NS
Female–male	39.7±18.1	68.4±29.1	1.889	NS
Intensity				
Male-male	0.29±0.08	0.68±0.12	10.715	0.001
Female–female	0.00 ± 0.00	0.23±0.08	1.315	NS
Male–female	0.28±0.07	0.29±0.10	0.239	NS
Female–male	$0.06 {\pm} 0.05$	0.14±0.09	0.210	NS

Table 2. Duration (s) and intensity (proportion of encounters that included claw contact) of competitive behaviours within and between sexes

in the female-biased treatment although not significantly so; but, surprisingly, they were more intense in the female-biased treatment (Table 2).

Females interacted with each other more frequently in the female-biased treatment than in the male-biased treatment, showing a clear effect of sex ratio on their behaviour (ANOVA: χ_1^2 =9.283, *P*=0.002; Fig. 2b). Indeed, encounters between females lasted significantly longer in female-biased conditions, indicating an increase in competitiveness; however, there was no effect of sex ratio on the intensity of the encounter (Table 2).

Our uncorrected data, which ignore probabilities of encounter (Fig. 2a), showed similar results to our corrected data (Fig. 2b); male-male encounters predominated over female-female competition only in the malebiased treatment (ANOVA: male-biased: χ_1^2 =21.161, *P*=0.0001; female-biased: χ_1^2 =0.220, *P*=0.639; Fig. 2a). Again, there was a greater difference between same-sex behaviours in the male-biased than in the female-biased conditions (see statistics for prediction 1; Fig. 2a). However, unlike the corrected data, there were significant effects of sex ratio on the frequency of within-sex encounters (prediction 3); the frequency of male-male encounters was significantly greater in the male-biased treatment whereas female-female competition was greater in the female-biased treatment (ANOVA: malemale: χ_1^2 =4.852, P=0.028; female-female: χ_1^2 =22.006, *P*=0.0001; Fig. 2a).

Competition Between Sexes

In those encounters in which the males were considered as winners (M–F; Fig. 2b), the frequency, duration and intensity of the encounter were not affected by sex ratio (ANOVA: χ_1^2 =0.161, *P*=0.688; Fig. 2b, Table 2). Sex ratio bias also had no effect on encounter frequency, duration or intensity of encounters in which females won over males (ANOVA: χ_1^2 =0.937, *P*=0.333; Fig. 2b, Table 2).

When we ignored probabilities of encounter, we found that unlike the corrected data, males won against females significantly more often in female-biased conditions (ANOVA: χ_1^2 =16.485, *P*=0.0001). Conversely, female wins

against males were more frequent in the male-biased treatment (ANOVA: χ_1^2 =7.448, *P*=0.006).

Mating Behaviour

Intense mating-related behaviour (advanced stages of courtship, cohabitation, mate guarding and mating) was recorded in 12 pairs of lobsters, six of which were in the male-biased treatment, and six in the female-biased treatment. The encounters lasted 1–9 days, with four resulting in successful mating, and one ending with an unsuccessful attempt. Multiple mating in which one female mated with two males sequentially was observed in two replicates. In both cases, the dominant male, that is, the male that won most encounters, mated with the female after the other male. In an additional replicate, a male mated with a female, which the dominant male then guarded. Mating between the latter pair was not observed.

Contrary to prediction 4, we found no difference in courtship duration between treatments, although the power of the test was low, owing to small sample size (Mann–Whitney *U* test: U=16.5, $N_1=N_2=6$, P=0.775, $1-\beta=0.1$).

DISCUSSION

The finding that competition between females was as frequent as between males in the female-biased treatment was most closely predicted by model 3, although all models predicted similar levels of male and female competitiveness. Model 3 assumed a 2-year female cycle and included an extended period of female receptivity during the egg retention stage. Collateral investment by males did not affect the models' predictions significantly, and the 'seasonal assumption' of receptivity performed less well than the assumption that the animals' perception of the reproductive season matched the start of the experiment.

Typically, contributions by multiple males per clutch will decrease the male potential reproductive rate if male time out increases (Simmons & Parker 1996). Here, the increase in male time out was small compared to the females' time out. It is still not known whether female European lobsters remain receptive during the period when they are retaining unfertilized eggs internally, but it is plausible that they could gain genetic benefits using this strategy. If last-sperm precedence occurs, as it does in many arthropods (Hemmi et al. 1993; Simmons & Siva-Jothy 1998), a long period of receptivity may improve the chances of mating with a genetically superior male. This strategy may be particularly important if females use stored sperm to fertilize more than one brood, as occurs in the American lobster (Waddy & Aiken 1991). Indeed, in the two cases of multiple mating observed, a dominant male that was interacting with a female 'allowed' another male to mate with her, before he mated with the female.

Our results supported the second prediction (made by all models), that the differences in same-sex encounter frequencies should be greater in the male-biased treatment than in female-biased conditions. This reflects the larger change in the intensity of mate competition when the population is biased towards the sex with the higher rate of reproduction. In a 2-year reproductive cycle (model 2) the discrepancy between intermale and interfemale competition would be larger than in a 1-year cycle (model 1).

The lack of increase in male-male aggression in malebiased conditions shown in our data corrected for probability of encounter does not support prediction 3, namely that an increase in the relative numbers of one sex would be correlated with an increase in competitiveness of that sex. This did hold for females. There are two likely explanations. First, if males compete primarily for shelters and not for females, an abundance of high-value shelters per male in both treatments may reduce the effects of sex ratios on intermale competition (Forsgren et al. 1996). Examples of shelter-related competition are found in other decapod species, such as intertidal fiddler crabs, which compete for intertidal burrows, and hermit crabs, which fight for their shells (reviewed by Hyatt 1983). Second, the frequency of encounters per individual may be a misleading measure of competition for either sex, if the costs of competitive behaviour are high and vary between the sexes (Clutton-Brock & Parker 1992). The high potential cost of contact aggression between lobsters, and a higher proportion of such encounters between males (46%) than between females (16%) may have prevented an increase in competitive aggression in male-biased conditions.

In contrast to the findings above, when data were not corrected for probabilities of encounter, they showed strong effects of sex ratio on the frequency of within- and between-sex encounters. This is not surprising. We suspect, for example, that male-male encounters were more frequent in the male-biased treatment simply because there were more males that other males could bump into than in the female-biased treatment. Our corrected data exclude any effects of density, and thus reflect the effect of sex ratio more accurately.

Sex ratio also had no effect on the duration of courtship observed (prediction 4). This may be due to the low power of the test. Conversely, the results may substantiate our previous results indicating that sex ratio has no effect on the frequency of intermale competition. Indeed, the high costs of mate defence by males may preclude lengthy pair bonds.

Mating shelters are valuable resources, both in terms of protection against predators and strong water currents in the wild, and are essential for successful mating (Atema & Cobb 1980). Variation in shelter number and quality in the wild may therefore affect the OSR. For example, if they are in shorter supply than in our experiment, this should cause greater competition among males for these resources. There should also be greater competition among females for shelter-holding males.

Our study demonstrates that adult sex ratios and time out from mate acquisition are important factors influencing the intensity of mate competition. Surprisingly, variation in sex ratio did not influence intermale competition as expected, although it did affect females. We suggest that the costs of competitive behaviour may also strongly influence the intensity of sexual selection, constraining the behavioural responses of animals to the operational sex ratio.

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