

Effects of breeding site density on competition and sexual selection in the European lobster

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The availability of breeding sites has been predicted to affect the intensity of sexual selection, including mate competition, mate choice and ultimately, variation in mating success. We tested the hypothesis that reduced density of shelters would cause an increase in the intensity of sexual selection in European lobsters, *Homarus gammarus*. However, we found little support for our predictions. For example, within-sex competition by males and by females was not more intense when shelters were scarce. Indeed, females attempted to evict one another from shelters significantly more often when shelters were common. When shelters were abundant, shelter-holding males had greater mating success than males without shelters, yet females did not show more interest towards these males during courtship encounters. Mate attraction was more strongly related to large male body size when shelters were scarce. Overall, the results suggest that reduced shelter density does not lead to more overt within-sex aggression in this species. Instead, we suggest that impacts of breeding resource availability on sexual selection may depend on the range over which resources are measured, with extreme scarcity of shelters rendering overt competition uneconomical. Furthermore, females may become more selective of male traits such as large size, which enhance male control of breeding sites and hence protection of females. *Key words*: Crustacea, mate choice, mating system, reproduction, resource defense. [*Behav Ecol* 14:396–402 (2003)]

Breeding systems are governed by the ability of one sex to gain access to members of the other sex either by direct means, such as courtship, coercion, and pre- and post-copulatory competition, or by controlling resources that are vital to reproduction (Emlen and Oring, 1977; Reynolds, 1996). The availability of individuals of each sex that are ready to mate will be determined mainly by potential rates of reproduction and biases in the adult sex ratio (Clutton-Brock and Parker, 1992; Clutton-Brock and Vincent, 1991; Okuda, 1999). Potential rates of reproduction are the maximum rates at which each sex could produce offspring if given unlimited access to members of the opposite sex, averaged over all individuals and conditions (Parker and Simmons, 1996). Classically, females of most species contribute more toward the offspring than males and therefore have a lower potential rate of reproduction. Thus, the low ratio of females to males that are ready to mate (operational sex ratio, OSR) leads to strong selection on males to compete for females (Clutton-Brock and Parker, 1992; Kvarnemo and Ahnesjö, 1996; Kvarnemo et al., 1995; Lindström and Seppa, 1996).

These connections between potential rates of reproduction, OSR, and sexual selection can be altered by the availability of breeding resources. For example, the direction and intensity of sexual selection may depend on food and nutrients (Gwynne, 1993; Reavis and Barlow, 1998; Simmons, 1992, 1994) and nest sites (Almada et al., 1995; Forsgren et al., 1996; Reavis and Barlow, 1998). When males compete to defend breeding sites from which they attract potential mates, their mating success will depend on both competition for such sites and on their ability to attract females. Given abundant breeding sites, females should have more resource-holding males to choose from and therefore be able to more fully ex-

ercise their choice of potential mates. Conversely, when breeding sites are scarce, males should compete more intensely to monopolize them (Forsgren et al., 1996; Kvarnemo and Ahnesjö, 1996).

The defense of mating sites is exhibited by several species of aquatic Crustacea (Goshima et al., 1996; Jennions and Backwell, 1996; Lawton and Lavalli, 1995). American lobsters (*Homarus americanus*) use rock crevices for breeding shelters. Shelters are used by males to attract females and for advanced stages of courtship, cohabitation, and mating. Shelters enhance the successful pre- and postcopulatory guarding of the soft-shelled female against attack after moulting (Atema, 1986; Atema and Voigt, 1995; Cowan and Atema, 1990) and help to reduce extrapair copulations by other males. Shelter-holding males attract females toward the shelter, using chemical cues in part. During courtship, the female makes repeated visits to the shelter-holding male (Atema, 1986; Atema and Voigt, 1995). This typically leads to sustained cohabitation and mating inside the shelter, lasting 4–5 days in the American lobster (Karnofsky and Price, 1989). Then there is a period of sperm retention before the fertilized eggs are extruded. Females spend a further 9–11 months in parental care, aerating the developing eggs until hatching (Atema and Voigt, 1995). Shelters are also used by both sexes for protection against strong water currents and from attacks by conspecifics.

Shelter competition in the European lobster (*H. gammarus*) is an integral part of breeding competition; males fight for and defend shelters while competing for mates (Debuse et al., unpublished data). Females may also compete aggressively with males and other females for shelters. However, they compete less strongly for mates and may be more selective in their mate choice, as expected from their greater input into offspring and corresponding lower potential rates of reproduction (Debuse et al., 1999).

Sexual selection on males may favor ornamentation or weaponry that helps them to fight for resources critical for attracting mates (Andersson, 1994). Body size has often been shown to be under sexual selection, influencing the outcome

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of contests in crustaceans (Fielder, 1965; Hyatt, 1983; Karnofsky and Price, 1989; Scrivener, 1971). Morphological characteristics that are used as weapons, such as claws, may also be correlated with dominance and are assessed by females (Andersson, 1994; Dingle, 1983; Hyatt, 1983). Another trait that may indicate male quality is fluctuating asymmetry (FA), which is measured as small random deviations from bilateral symmetry in morphological traits. Fluctuating asymmetry may indicate the genetic quality of an individual if it reflects overall developmental stability (Møller and Pomiankowski, 1993; Møller and Swaddle, 1997). In theory, high-quality males should have more symmetrical sexually selected traits, which may be correlated with their success in within-sex competition and mate acquisition.

The aim of our study was to investigate the effect of shelter density on sexual selection through male–male competition, female–female competition, and male–female interactions in the European lobster. We predicted that there should be more competition within each sex when there are fewer shelters and that this should be especially true for males because they have a higher potential rate of reproduction. In addition, shelter-holding males, especially those that attract females, should be larger, with larger claws, and perhaps less fluctuating asymmetry. We expected relationships between male morphology and mating success to be most pronounced when shelters are abundant, as females could choose among more resource-holding males.

METHODS

We conducted our experiment at the Lowestoft Laboratory, Centre for Environment, Fisheries and Aquaculture Science (CEFAS), UK, between May and August 1997. Lobsters 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 as part of a normal commercial fishing operation. They were separated by sex and held in storage tanks with continuously renewed natural sea water, either individually or in groups, due to limited storage space. Each lobster was fed with two fish (sprats, *Sprattus sprattus*) once each week for the duration of the experiment.

We used four outdoor tanks (3.8 × 1.3 × 0.9 m height), each with a 10-cm thick layer of pea-sized gravel and continuously renewed sea water. Over the study period the water temperature and salinity followed natural patterns and varied from 13.0° to 20.5°C and 29–33‰, respectively. Light was measured as photon irradiance, which is perceived by animal photoreceptors (Endler, 1990; Jones and Reynolds, 1996). Levels were manipulated by using two sets of eight 60 W and nine 15 W incandescent light bulbs. We used three light levels to represent dawn and dusk and day and night within a 24-h period, which followed the natural photoperiodicity: day lasted 13 h (3.5 μmol m⁻² s⁻¹), dawn lasted 1 h (0.3 μmol m⁻² s⁻¹), dusk lasted 3 h (0.3 μmol m⁻² s⁻¹), and night lasted 7 h (<0.1 μmol m⁻² s⁻¹). From our experience, European lobsters increase their activity sharply during the dusk period, so this period was extended for observations (see also Smith et al., 1998). We assigned each treatment to two tanks, so that two replicates could be run simultaneously. We provided clay ridge roof tiles to create shelters (30.9 × 26.5 × 12.5 cm high). High-density shelter treatments (“high shelter”) consisted of four evenly distributed shelters, providing males with an excess of shelters, and low-density shelter treatments (“low shelter”) contained one randomly placed shelter.

Six reproductively mature lobsters (three males and three females) were assigned to each treatment, with 15 replicates per treatment. The size of the lobsters represented the most

common adult sizes in the wild in the UK (85.0–104.9 mm carapace length; Bannister, 1986). For each sex, we selected one small (85.0–89.9 mm), one medium sized (90.0–94.9 mm), and one large individual (95.0–104.9 mm), and we ensured there was no difference in the mean sizes of individuals between treatments (one-way ANOVA: males: $F_{1,88} = 0.209$, $p = .649$; females: $F_{1,88} = 0.198$, $p = .658$). Males were assigned randomly to replicates with respect to their previous holding conditions. Male dominance rank is influenced by moult stage in the American lobster, and true dominance is displayed only during the intermoult (Tamm and Cobb, 1978). Only two males moulted during the experiment.

Each replicate lasted 9 days. One to two days before observations, we placed lobsters in experimental tanks to allow them to settle. After this period, we observed high and low shelter treatments in parallel on days 1, 3, 5, 7, and 9 for all but two replicates, where observations on day 9 were prevented by problems with the lights. Observation day had no effect on the frequency of encounters observed (one-way ANOVA: $F_{4,140} = 1.338$, $p = .259$). We watched each tank for 1.5 h in the dusk period, during which all individuals were observed. Individuals were identified by yellow numbered Petersen tags that were glued to the carapace and by combinations of colored elastic bands that were wrapped around the upper part of each claw without restricting claw use.

Competitive behavior

Competition was defined by eight aggressive and five avoidance behaviors (Debuse et al., 1999; Scrivener, 1971). Competitive encounters within the sexes were classified into two categories: male against another male (male–male) and female against another female (female–female). In the event of the death of an individual or a female becoming unavailable to mate (see below), the expected probabilities of encounters in a tank changed. Therefore, for each category of sexual encounters, we divided the number of aggressive encounters per individual by the proportion of all individuals of the relevant sex that could have been encountered (Debuse et al., 1999). The mean encounter rate per individual, measured as the mean number of encounters per individual over the 9-day period, was log-transformed for normality and pooled for each behavioral category and density treatment.

Ten of the 80 females extruded eggs during the experiment. For six of these, we were unable to tell when the extrusion had taken place, and because we had not seen courtship behavior we could not establish the proportion of the observation period during which they had been unreceptive to mates. These individuals were therefore excluded from the analyses. The other four females that extruded eggs had been observed courting and were therefore considered to have been receptive during that period. Females that were guarded by males were unable to compete with other individuals and so were excluded from the competition analyses for the period of the guarding. Conversely, males competed with other males throughout guarding and so were included.

Courtship and mating

We classified an individual as holding a shelter if it was observed occupying or defending a shelter. Lobsters do not remain in their shelters at all times, and they may hold more than one shelter simultaneously (see also Lawton and Lavalli, 1995). Thus, ownership could not be measured by the time an individual spent in a shelter.

We used two measures of female choice. First, we recorded male mating success (number of copulations) to compare the success of male shelter-holders with the success of other males. However, we observed only 14 incidences of mating,

Table 1
Effect of shelter density on the intensity of sexual selection on males and females due to within-sex competition and male–female interactions

Form of selection	<i>F/t/Z</i>	df	<i>p</i>	Support for hypothesis?
Male–male competition				
Encounter frequency	−0.987 ^a	28	.332	No
Encounter duration	2.281 ^a	28	.030	Opposite trend ^b
Frequency of attempted shelter evictions	−0.826 ^c	28	.409	No
Body size	0.430 ^d	1	.518	No
Claw size (absolute)	0.024 ^d	1	.879	No
Claw size (relative)	5.434 ^d	1	.028	Opposite trend ^b
Fluctuating asymmetry	2.472 ^d	1	.129	No
Female–female competition				
Encounter frequency	−0.894 ^a	28	.379	No
Encounter duration	1.673 ^a	28	.105	No
Frequency of attempted shelter evictions	−2.679 ^c	28	.007	Opposite
Male–female interactions				
Male body size	4.585 ^d	1	.044	Opposite
Male claw size (absolute)	3.626 ^d	1	.070	No
Male claw size (relative)	0.273 ^d	1	.606	No
Fluctuating asymmetry (males)	0.715 ^d	1	.408	No

Bonferroni adjustments were applied to all tests.

^a Analyzed using *t* tests.

^b Not significant after sequential Bonferroni correction.

^c Analyzed using Mann-Whitney tests.

^d Analyzed using two-way ANOVAs.

and it is likely that courting individuals also mated outside observation periods. When analyzing phenotypic traits, we therefore included advanced courtship with copulation frequency and define it throughout as “attraction.” Mate attraction was characterized as a male being involved in advanced courtship encounters, whereby the female reacted positively, regardless of which sex initiated the encounter. Courtship behavior of the European lobster was similar to that of the American lobster (Atema and Cobb, 1980), and we defined advanced stages of courtship as those that typically occur during the intermittent and permanent shelter sharing phases; these included claw pushing, tapping, or boxing between the male and female, the female placing her claw on the head of the male, the female presenting her abdomen to the male, and the male responding by jabbing or nudging the female on the side of the abdomen. We also recorded rapid pleopod fanning, but since this can occur in the early stages of courtship, we recorded it only when it was observed as part of a sequence that included the other courtship behaviors.

We measured three phenotypic characteristics that could be under sexual selection: body size (measured as carapace length), claw volume, and relative FA of rostrum teeth. An index of claw volume was calculated from length × width × depth (for exact measurement locations, see Aiken and Waddy, 1980). Claw volume was positively correlated with carapace length ($r^2 = .465$, $p < .0001$), and we accounted for this by using residuals from linear regressions between claw volume and carapace length to calculate relative claw volume. Males have larger bodies and claws than females (Debusse et al., 2001, unpublished). Relative fluctuating asymmetry of the rostrum teeth was measured as the difference in the number of teeth between the left and right sides of the

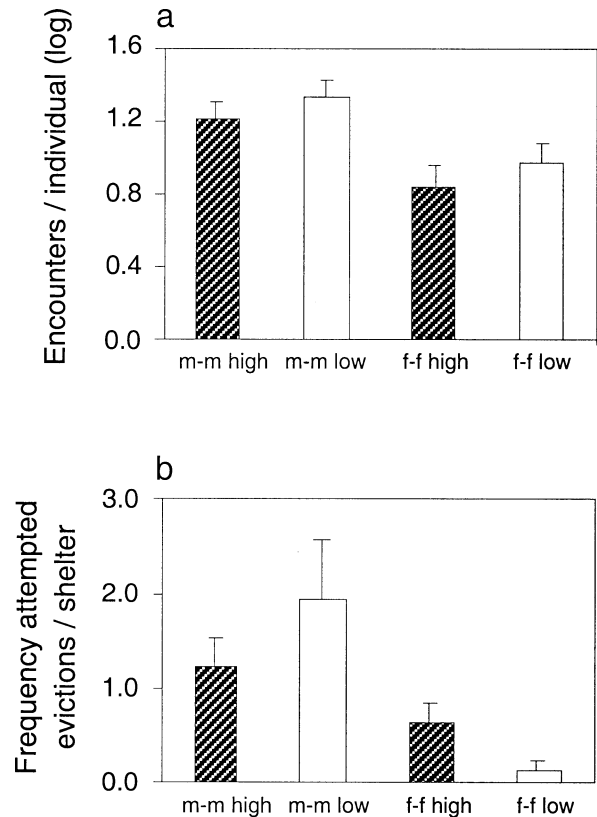


Figure 1

Intrasexual competition between males (m-m) and females (f-f) in high shelter (hatched bars) and low shelter (open bars) treatments ($n = 15$ per treatment). Values are (a) mean encounters per individual corrected for the probability of encounter + SE and (b) number of attempted evictions per shelter per observation period.

rostrum divided by the total number of rostrum teeth. The rostrum teeth asymmetry values were normally distributed with a mean value of zero, indicating an approximation to true fluctuating asymmetry.

Power of the tests was defined as $1 - \beta$, where β is the probability of accepting a false null hypothesis. All tests were two-tailed, and Bonferroni adjustments were made to all tests in Table 1.

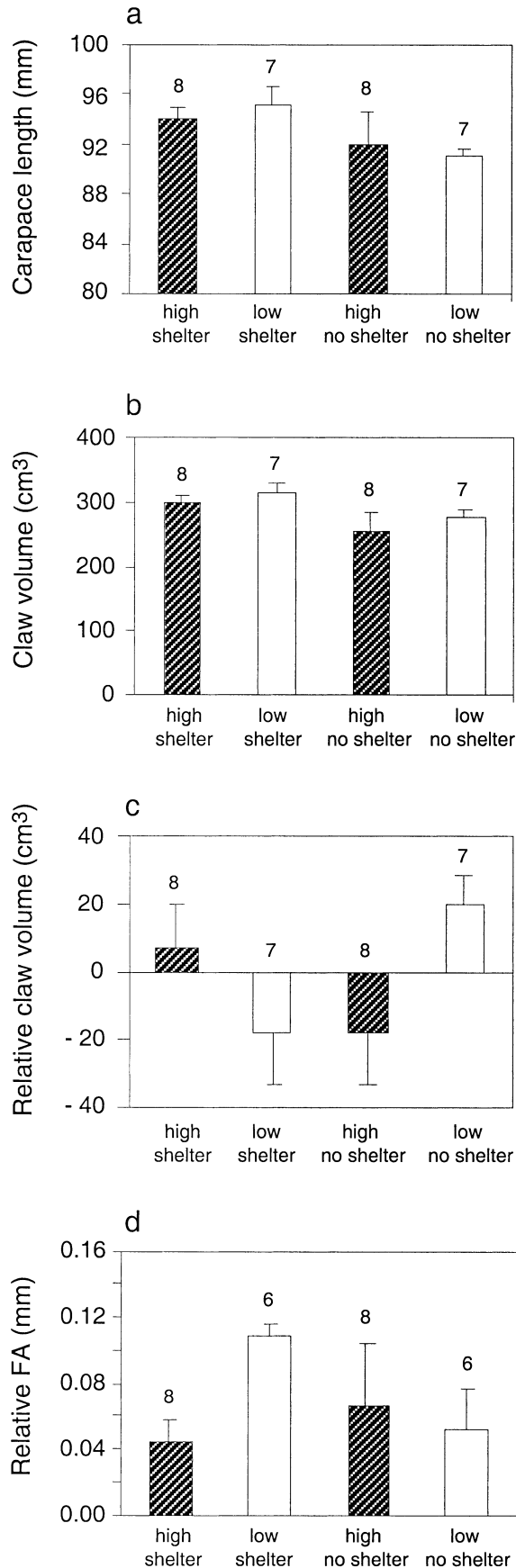
RESULTS

Differences between the sexes

Males were involved in aggressive encounters significantly more often than females (paired *t* test: $t = 3.371$, $df = 29$, $p = .002$; Figure 1a) and attempted to evict members of the same sex from shelters more frequently than did females ($t = 3.011$, $df = 29$, $p = .005$; Figure 1b).

Male–male competition

As expected, a higher proportion of males owned shelters in the high-density shelter treatment than in the treatment where shelters were scarce (high shelter: mean = 0.82 ± 0.17 , low shelter: mean = 0.31 ± 0.34 , unpaired *t* test: $t = 4.151$, $df = 28$, $p < .001$). Contrary to our prediction, male–male encounters tended to last longer when shelters were more abundant (high shelter: mean = 35.8 ± 3.5 min, low shelter: mean = 26.1 ± 2.8), although after adjusting for multiple tests with a sequential Bonferroni correction, this difference



was not significant (Table 1). Furthermore, we found no evidence for an increase in male–male competition under low shelter densities, either in terms of encounter frequency or evictions (Table 1, Figure 1, $1 - \beta = 0.8$).

The data on male morphometrics also failed to support the hypothesis that shelter abundance would affect the difference between males that did and did not defend shelters (Figure 2). This interpretation can be seen from the interaction terms presented in Table 1, which are repeated below along with full statistics from two-way ANOVAs with shelter density and shelter ownership as factors. There was no significant interaction between shelter density and shelter ownership for body size (shelter density: $F_{1,26} < 0.001$, $p = .981$, shelter ownership: $F_{1,26} = 3.454$, $p = .074$, interaction: $F_{1,26} = 0.430$, $p = .518$), for absolute claw size (shelter density: $F_{1,26} = 0.741$, $p = .397$, shelter ownership: $F_{1,26} = 5.069$, $p = .033$, interaction: $F_{1,26} = 0.024$, $p = .879$), or for FA (shelter density: $F_{1,26} = 0.980$, $p = .332$, shelter ownership: $F_{1,26} = 0.468$, $p = .501$, interaction: $F_{1,26} = 2.472$, $p = .129$). Indeed, contrary to the hypothesis, in the low shelter treatment, shelter holders tended to have proportionately smaller claws than non-shelter-holders when compared with the high shelter treatment (shelter density: $F_{1,26} = 0.225$, $p = .639$, shelter ownership: $F_{1,26} = 0.188$, $p = .669$, interaction: $F_{1,26} = 5.434$, $p = .028$; Figure 2c, Table 1), although the relationship was not significant after applying the Bonferroni adjustment.

Female–female competition

We found no evidence for a scarcity of shelters increasing sexual selection on females (Figure 1, Table 1). Indeed, attempted female–female evictions were significantly more frequent in the high shelter treatment than when shelters were more scarce (Figure 1b, Table 1).

Male–female interactions

We were surprised to find that advanced courtship interactions often took place outside of shelters, and these did not involve shelter-owning males more often than males that lacked shelters in either shelter density treatment. In the high shelter treatment, the mean proportions of shelter-holding and non-shelter-holding males that attracted interest from females were 0.13 ± 0.08 and 0.13 ± 0.13 , respectively. For the low shelter treatment, the corresponding means were 0.36 ± 0.18 and 0.21 ± 0.15 , respectively (paired t test: $t = 0.795$, $df = 6$, $p = .457$, $1 - \beta = 0.1$). Conversely, observed incidences of mating success (copulations) confirmed that shelter-holding males were more successful than non-shelter-holding males, but only when shelters were abundant (two-way ANOVA: shelter density: $F_{1,12} < 0.001$, $p > .999$, shelter ownership: $F_{1,12} = 0.801$, $p = .388$, interaction: $F_{1,12} = 12.806$, $p = .004$; post-hoc: $p = .056$). Shelter holders that mated were, however, no larger than those shelter holders that did not mate in the high shelter treatment (mated shelter holders: 93.8 ± 1.7 , unmated shelter holders: 94.5 ± 1.3 ; paired t test: $t = -0.265$, $df = 4$, $p = .808$, $1 - \beta = 0.1$).

Males that concurrently held more than one shelter tended to attract more females than males holding single shelters

Figure 2

Relationship between shelter ownership and male phenotypic traits in high shelter (hatched bars) and low shelter (open bars) density treatments. Traits represented are (a) carapace length, (b) absolute claw size, (c) claw size relative to carapace length, and (d) relative fluctuating asymmetry of rostrum teeth. Values are mean trait size ± SE.

(logistic regression: $r^2 = 3.257$, $p = .071$). However, males holding multiple shelters did not mate with more females than other males (logistic regression: $r^2 = 1.569$, $p = .210$).

Contrary to our initial expectation, a scarcity of shelters led to more pronounced female choice, with females attracted to significantly larger males, with a tendency toward larger claws, than when shelters were abundant (Figure 3, Table 1). The statistics from two-way ANOVAs are as follows: body size: shelter density: $F_{1,22} = 0.114$, $p = .739$, shelter ownership: $F_{1,22} = 2.257$, $p = .147$, interaction: $F_{1,22} = 4.585$, $p = .044$; absolute claw size: shelter density: $F_{1,22} = 0.764$, $p = .391$, shelter ownership: $F_{1,22} = 1.755$, $p = .199$, interaction: $F_{1,22} = 3.626$, $p = .070$. The claw size trend disappeared when body size was controlled (two-way ANOVA: shelter density: $F_{1,22} = 0.643$, $p = .431$, shelter ownership: $F_{1,22} = 0.019$, $p = .892$, interaction: $F_{1,22} = 0.273$, $p = .606$; Table 1). We found no relationship between shelter abundance and selection for males with low FA (two-way ANOVA: shelter density: $F_{1,20} = 0.097$, $p = .759$, shelter ownership: $F_{1,20} = 1.309$, $p = .266$, interaction: $F_{1,20} = 0.715$, $p = .408$; Figure 3d, Table 1).

DISCUSSION

The pattern of male–male competition and morphometric variation did not support the hypothesis that sexual selection should be more intense when shelters are limited (Table 1). Similarly, female–female competition and interactions between the sexes either contradicted or did not support our expectations.

Male–male competition

The lack of increase in male competition under low shelter conditions could be due to challenges between males becoming uneconomical at low resource abundance (e.g., Grant et al. 2000). Indeed, one might expect a dome-shaped relationship between abundance of breeding resources and male–male competition, with the highest competition at intermediate levels of shelters, with competition decreasing again when resources are abundant. Thus, at the low density of shelters used here, dominance of shelter holders may suppress challenges from subordinates (Huntingford and Turner, 1987), particularly if the value of the shelters was higher for owners (Leimar and Enquist, 1984). Furthermore, when more shelters were available, some male lobsters defended more than one at a time (see also O'Neill and Cobb, 1979) and attracted more females than did males that held single shelters.

There was no effect of shelter abundance on the strength of selection for body size or FA of shelter owners. Overall, male shelter holders tended to be larger than those males that did not hold a shelter, a finding that matches other studies showing that differences in body size are important in predicting contest outcomes (Archer, 1988; Lindström, 1992; Huntingford et al., 1995). Lee and Seed (1992) suggested that claw size, rather than body size, may be a better predictor of competitive ability. Claws are important as weapons in intermale conflicts (Rosenberg, 1997; Sneddon

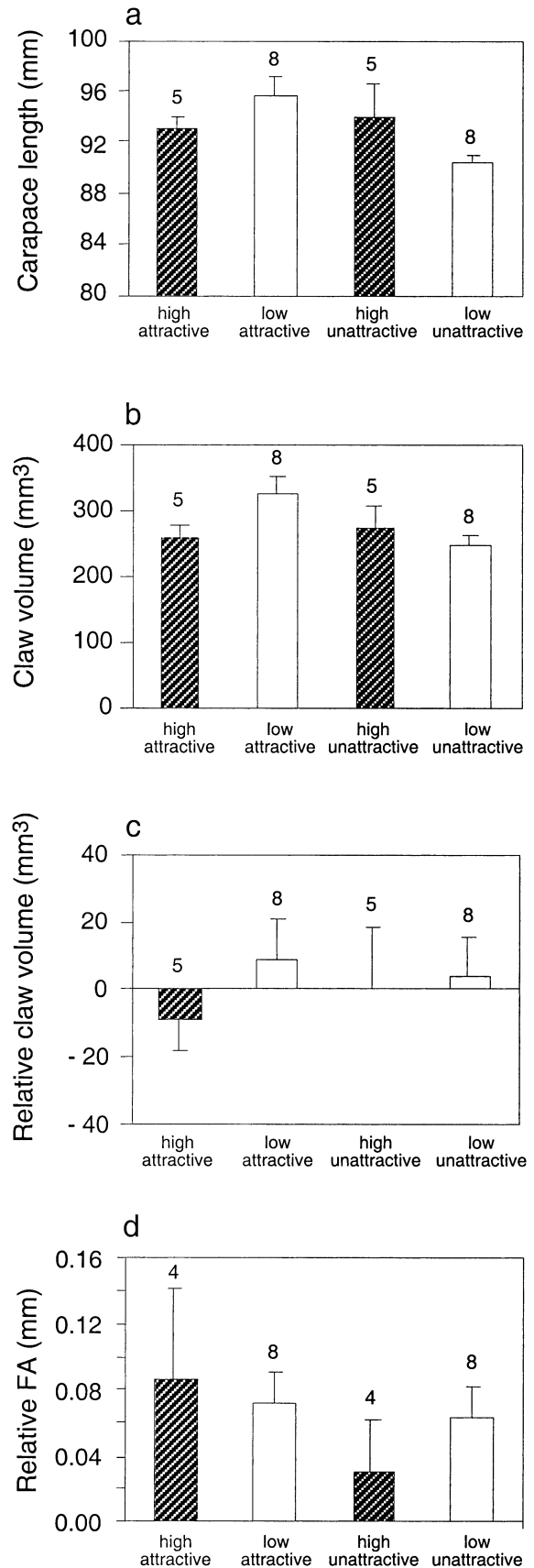


Figure 3

Relationship between male attractiveness to females and male phenotypic traits in high shelter (hatched bars) and low shelter (open bars) density treatments. Traits represented are (a) carapace length, (b) absolute claw size, (c) relative claw size, and (d) relative fluctuating asymmetry of rostrum teeth. Values are mean trait size + SE.

et al., 1997) and may also signal fighting ability (Andersson, 1994). However, we found that although shelter holders had larger claws, these were not larger relative to body size.

In some species, FA of morphometric traits may signal the overall quality of an individual (Kodric-Brown, 1997; Møller, 1992; Møller and Swaddle, 1997), though this is a controversial topic. A lesser degree of FA may indicate higher quality both in terms of fighting ability (Sneddon and Swaddle, 1999; Thornhill, 1992) and mating success (Hunt et al., 1998; Kodric-Brown, 1997; Tsubaki and Matsumoto, 1998). Our results suggest that the relative FA of the rostrum teeth is not an accurate indicator of competitive ability and that other morphological traits such as body size are more important.

Female–female competition

As with male–male competition, competition between females did not support the hypothesis that competition would be more intense when shelters were scarce. Indeed, we found the opposite result for attempts by females to evict other females from shelters. The same arguments may apply to females as for males concerning the ability of a single individual to maintain control over shelters when these are scarce. Overall, the frequency of competition was lower between females than between males, as expected from the large difference between potential reproductive rates of the sexes (Debuse et al., 1999).

Male–female interactions

The discrepancy between mating success of shelter-holding males and their initial attractiveness to females in the high shelter treatment indicates that although shelters are important for breeding, they may not be vital for attracting mates where shelters are common, unless a male holds more than one shelter concurrently. Females may choose males based on dominance status using visual or chemical cues, which reflects the male's likelihood of obtaining a shelter for reproduction. Furthermore, it is possible that some females were using the shelters for protection rather than for reproduction.

Larger males were more attractive to females at low shelter densities than when shelters were abundant. Although there was a tendency for shelter holders to be larger than males without shelters in both treatments, females showed no attraction for male shelter holders over other males at low shelter densities, suggesting that females were attracted to larger males, regardless of shelter ownership status. We would expect females to be less selective when choosing mates at low shelter densities, unless females choose males on criteria other than current shelter ownership, such as their ability to defend outside a shelter or their future likelihood of acquiring a shelter.

Conversely, shelter-holding males experienced higher mating success at high shelter densities than when shelters were scarce. Mated shelter-holding males were not significantly larger than shelter holders that did not mate, suggesting that shelter ownership, rather than body size, was more important for mating success when shelters are abundant. Our results show that morphometric measures may not be reliable predictors of male mating success in all cases (Topping and Millar, 1999). Chemical cues may also be important, as females may use them to distinguish mate quality and competitive ability (Atema, 1986; Bushmann and Atema, 1997).

In conclusion, we found little support for predictions about relationships between resource abundance and sexual selection. Indeed, overt competition within each sex was less intense when shelters were scarce, and females were more attracted to large-bodied males. We suggest that dominance interactions may have suppressed overt aggression at the low

densities of breeding resources tested here and that females may have become more selective of males that were able to achieve such dominance.

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