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Male parasitism and intrasexual competition in a burrowing barnacle

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Summary. In sexually dimorphic animals, large male body size is often associated with direct interference competition among males for access to females or resources used in reproduction. In contrast, small male body size may be associated with indirect scramble competition among males for temporal or spatial access to females. Minute, "parasitic" males of the acrothoracican barnacle *Trypetesa lampas* (Hancock) appear to compete with one another for permanent attachment sites on the external body of the female. Several spatial patterns suggest indirect male-male competition: 1) males were consistently aggregated on the anterior surface of the female ovarian disc; 2) the average distance from attached males to the site of insemination correlated positively with local male density; 3) average male body size on a female decreased as a function of male density; 4) the distribution of males on the left and right hand sides of the female ovarian disc was more even than expected, suggesting that males avoided crowded settlement sites. The number of males attached to a female increased with female body size and matched a null model in which males colonized female "targets" of differing areas. These results suggest that competition between males primarily affected settlement sites and male body sizes within, rather than among, females. Male parasitism may have evolved through both sexual selection for efficient access to females (Ghiselin 1974) and natural selection for reduced burrow density in a space-limited habitat (Turner and Yakovlev 1983).

Key words: Acrothoracica – Male parasitism – Sexual selection – Male-male competition

Body size differences between females and males are often associated with sexual selection and the evolution of reproductive behavior (Darwin 1874). Among primates, for example, the intensity of male-male competition increases with the degree to which males exceed females in adult body size (Alexander et al. 1978). Large body size in other animals may confer many competitive advantages: large males may hold larger, more productive territories (Howard 1978; Alcock 1979), secure more copulations (Howard 1980; LeBoeuf and Reiter 1988), successfully guard females from other males (Borgia 1981; Fincke 1984), and be more successful in individual male-male combat (Johnson 1982; Clutton-Brock et al. 1988).

For invertebrates, the typical pattern is for females to exceed males in body size. In these cases, small male body size does not imply a lack of male-male competition. Instead, male-male competition for females may not be expressed as direct interference among small males. Small males may secure matings by stealth (Gross and Charnov 1980), female mimicry (Shuster 1989), or by more efficient access to females (Berry and Shine 1980). These tactics are most obvious in species with discrete male morphs, but may be present as well in species with monomorphic males or with males showing continuous variation in body size.

In this study we present indirect evidence for male-male competition in one of the most extreme examples of sexual size dimorphism in nature: dwarf, "parasitic" males of the acrothoracican barnacle *Trypetesa lampas* (Hancock). In the Acrothoracica, the male is a tiny dwarf that attaches permanently to the exterior mantle surface of the female, then fertilizes her through the mantle cavity opening. In *T. lampas* as many as fifteen males have been found attached to a single female (Kühnert 1934).

Male parasitism has evolved independently in several taxa. For the purposes of this study, we defined a parasitic male as an extremely small dwarf living within or attached to the body of the female as an obligate associate. It usually lacks appendages and mouthparts, as well as a digestive, circulatory, and excretory system. The body often consists only of gonadal tissue and an intromittent organ, and it is the primary male form in a dioecious species. "Complemental males" (Darwin 1854)

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in some hermaphroditic species have a similar morphology, but we are restricting our discussion to gonochoristic forms.

In this type of mating system, direct interference competition between males is unlikely, because males do not have the ability to sequester or guard females (Ghiselin 1974). Instead, male-male competition is likely to be pre-emptive: males may compete indirectly for a limited number of settlement sites from which insemination is more likely to be successful.

We show that the spatial distribution of attached males of *T. lampas* within females is highly non-random, both with respect to other males and to the site of insemination. These spatial patterns are consistent with the hypothesis that males are competing for preferred attachment sites on females. We also consider the selective forces that may be responsible for the evolution of this extreme sexual size dimorphism.

Materials and methods

Life history of Trypetesa lampas

Immature females excavate permanent burrows in gastropod shells held by hermit crabs (Hancock 1849). They feed with a much reduced cirral net, reach sexual maturity within 6 to 9 months, and live for 2 to 3 years (Turquier 1972). A single female may carry several broods of eggs in her lifetime (Kühnert 1934). Embryos pass through the typical barnacle stages of egg, nauplius, metanauplius and cypris. Like other barnacles, but unlike many other acrothoracicans, embryos of *T. lampas* are released as free-swimming nauplius larvae (Kühnert 1934; Tomlinson 1969). Most other acrothoracicans brood their larvae up to the final cyprid stage (Tomlinson 1969).

Male cyprids enter the female burrow aperture and pass in a posterior direction along left or right hand sides of the attachment process. The attachment process is a knob of cement and shed exoskeleton on the mid-anterior margin of the ovarian disc that projects to the ceiling of the female burrow. Males then select a settlement site on the surface of the female ovarian disc, usually posterior to the attachment process (Fig. 1). Most of the exterior surface of the ovarian disc, if not all, appears suitable for larval settlement.

Males molt to the adult stage and reach sexual maturity within a few days of settlement (Turquier 1972); the lifespan of the male is probably less than 3 or 4 months (Kühnert 1934). In *T. lampas*, the weight of a single male is about one five-hundredth that of the female (Spivey 1979). The male body consists of only a single testis, vas deferens, and extensible penis. The female is inseminated through the mantle cavity opening (Darwin 1854), and individual males may fertilize several successive broods of a single female (Turquier 1972). Sperm storage by females has not been studied in the Acrothoracica, but probably does not occur.

Collection and measurement techniques

We collected specimens of *T. lampas* from shells of the Florida conch *Strombus alatus* Gmelin occupied by the hermit crab *Pagurus impressus* (Benedict). During February 1983, we gathered 80 shells from benthic trawl samples in Apalachee Bay, Florida, northeastern Gulf of Mexico. Two hundred seven females were randomly sampled from these shells and removed from their burrows by treatment with 5% HCl (Tomlinson 1969).

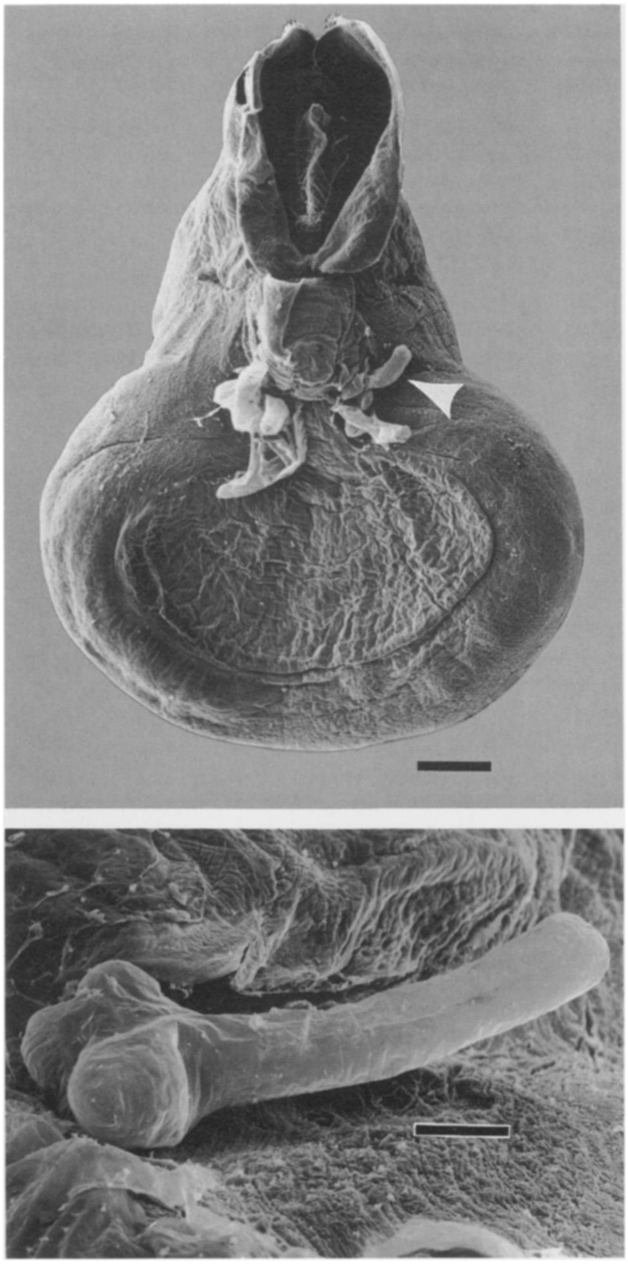

Fig. 1. Mature female and male of *Trypetesa lampas*. *(Top)* A female, removed from burrow, showing mantle cavity opening and large, circular ovarian disc. Arrow shows one of four dwarf males located on the disc region posterior to the attachment process. Scale bar = 0.5 mm. *(Bottom)* Mature dwarf male attached to above female, position marked by arrow. Scale bar = 0.1 mm

Outline drawings of female ovarian discs were made with camera lucida and measured with a HIPAD digitizer. For each female, we measured the total ovarian disc area, number and position of attached cyprids and metamorphosed males, and the distance from the attachment base of each male to the female mantle cavity opening, the site of insemination (Fig. 2). We defined the "median male" for each female by ranking the attached males according to their distance from the mantle cavity opening. We measured the area forward of the median male by drawing an imaginary line perpendicular to the long axis of the female. This area was converted to a percentage of the total female ovarian disc area. We also measured the (contracted) penis length of each male.

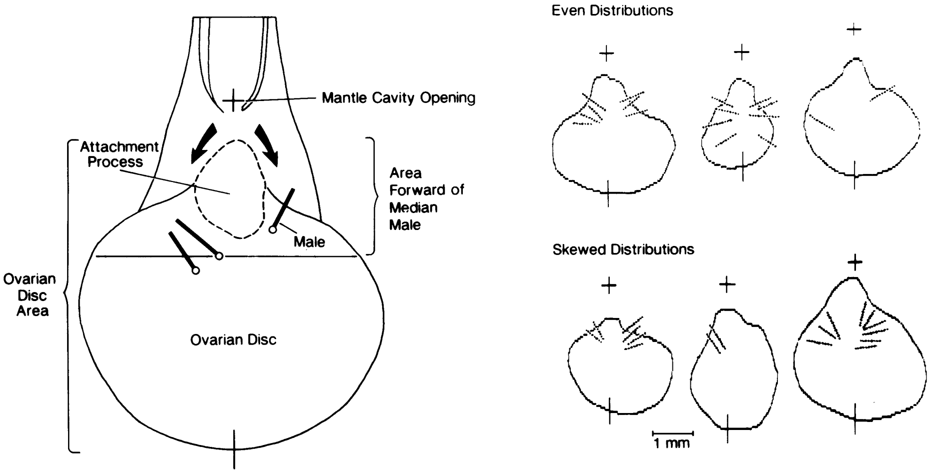

Fig. 2. Diagram of ovarian regions of female *Trypetesa lampas* showing positions of dwarf males and measurements taken. *(Left)* Female is suspended from roof of burrow interior by column of cement and shed exoskeleton (the attachment process), which divides the ovarian disc into left and right hand sides along the longitudinal axis of body. Male cyprids enter burrow aperture, move across exterior surface of female, and reach the settlement surface of the ovarian disc, where they attach and metamorphose into dwarfs. Arrows indicate probable pathways taken. The attachment point of the male is usually found at its inward-most end *(open circles)*. *(Right)* Digitized drawings of ovarian discs, showing even and skewed distributions of attached males. Attachment distance is the straight-line distance from the attachment base of the male to the mantle cavity opening (+)

Statistical analyses

We used these data to test for non-random distributions of males, both between and within individual females. Between females, we tested two null hypotheses to account for the observed numbers of attached males. The first null hypothesis is that male density is fit by a Poisson distribution (Pielou, 1974). This hypothesis assumes that males settled independently of one another, and that all females represented equiprobable settlement sites.

The second null hypothesis is that males settled independently of one another, but the probability of settlement was proportional to female surface area (Coleman et al. 1982). To generate the predictions from this model, we used a Monte Carlo simulation. Each male was randomly placed on a female, with the probability of placement being proportional to female ovarian disc area. No female was allowed to accumulate more than 11 males, the maximum number observed on any single female. Next, we tabulated the number of females with 0, 1, 2, 3, 4, or ≥ 5 attached males. We repeated this simulation 200 times to generate the expected number of females in each male abundance class. For both the equiprobable and proportional model, we compared the observed and expected numbers of females with a Chi-square test. If males avoided crowded competition sites, there should be significantly fewer females with 0 males than expected under one or both of the models.

To analyze the settlement distance of males, we used a stepwise multiple regression approach. For each female, we used the average distance of attached males as the response variable, and male density, average male size, and female area as the predictor variables. If competition between males influenced settlement distance, the coefficient for male density should be significant and positive, even after accounting for the effects of female area and male size.

We used a similar analysis to evaluate the effects of area, distance and density on average male body size. Male body size was defined as contracted penis length. To examine the relationship between *individual* male body size and settlement distance, we correlated these two variables on females with 7 or more attached males.

We also analyzed settlement distances across females by plotting a histogram of the percentage are forward of the median male. If male settlement were random with respect to the insemination site, the distribution of median distances among females should be symmetric, with a mode at 50%.

These tests assume that, other things being equal, males that settle closer to the mantle cavity opening have a higher fertilization success than males that settle more distantly. The penis of the dwarf male is highly extensible, so the assumption may not be true at all spatial scales. Nevertheless, attachment distance is known to be important to fertilization success in barnacles (Barnes 1953; Hurley 1973).

Although anterior settlement may be optimal for access to the female, crowding from neighboring males could reduce successful fertilization. We tested for a pattern of crowding by analyzing the distribution of males on the left and right hand sides of the female ovarian disc. We designated females with more than one male as "even" or "skewed", based on a count comparison of males on the two sides of the attachment process.

Even distributions are those with an equal number (to the nearest integer) of males on the two sides. Skewed distributions are those with an unequal split of males on the two sides. As an example, if a female has seven attached males, a 4–3 split would represent an even distribution, whereas a 5–2, 6–1, or 7–0 split would represent a skewed distribution. If males settled independently of one another, with equal probability of choosing the left or right hand side, the expected frequency of skewed and even distributions can be calculated as a binomial distribution.

Let n equal the number of attached males. If n is an even integer, let $x = (n/2)$. The probability of an even split is

$$P_e = \binom{n}{x} (0.5)^n$$

and the probability of a skewed split is

$$P_s = 1.0 - \binom{n}{x} (0.5)^n .$$

If n is an odd integer, let $x = n/2 + 0.5$. The probability of an even split is

$$P_e = 2\binom{n}{x} (0.5)^n$$

and the probability of a skewed split is

$$P_s = 1.0 - 2\binom{n}{x} (0.5)^n$$

We multiplied these probabilities by the number of females in each n-male class to give the expected number of females with even and skewed distributions of males. We pooled adjacent cells to maintain cell expectations above 5.0 (Sokal and Rohlf 1981). Observed and expected numbers were compared using the Chi-square test. The test for the interaction between male abundance class and skewness is the difference between the total Chi-square and the additive Chi-square. This interaction Chi-square has three, not two, degrees of freedom because the cell expectations are derived from the binomial equation and not from the marginal totals (D. Meeter, pers. comm.). If males settled on the two sides of the ovarian disc randomly and independently of one another, the observed number of females with even and skewed counts should follow the binomial distribution. However, if males were unable or unwilling to settle on the most crowded side of the disc, even distributions should predominate.

Results

Twenty-four percent of the gastropod shells collected were occupied by *T. lampas* females. The average burrow density was 30.75 burrows/shell (114 maximum), although not all burrows were occupied. Most burrows were concentrated at high density in the columella of the shell. Fifty-five percent of the females sampled had males attached. Of these, 63% contained two or more males. These patterns differ significantly from those predicted by a Poisson distribution ($x_5^2 = 186.3$; $p < 0.001$). Specifically, there were too many females with no males and too few females with 5 or more males to match the predictions of the random, equiprobable placement model (Fig. 3). Although the Chi-square test is marginally significant ($x_5^2 = 13.1$; $p < 0.05$), the data are much better fit by the predictions of the proportional area model. The statistical significance is caused entirely by an excess of females with four attached males (observed = 16, expected = 7.2). For both models, there were more females with no males than predicted (Fig. 3).

The distribution of attached males was highly skewed towards the anterior of the female ovarian disc (Fig. 4). For the majority of females, the median male was cemented to the anterior-most one third of the disc. If settlement were random and proportional to area, the distribution should be symmetrical with a peak at 50%.

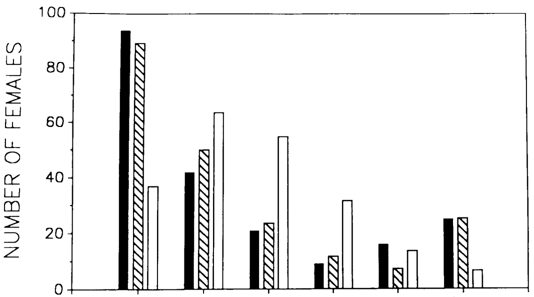

Fig. 3. *Filled bar* = observed number of females with different numbers of attached males. *Open bar* = expected number of females, assuming male settlement is independent and equiprobable (Poisson distribution). *Shaded bar* = expected number of females, assuming male settlement is independent and that the probability of settlement is proportional to female area

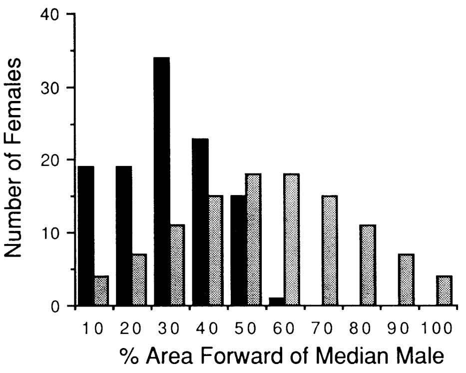

Fig. 4. The percentage area of the female ovarian disc forward of the median male. Black histogram bars give the number of females in each 10-percentile class ($n = 113$). The percentage area is the fraction of the total female ovarian disc area that is anterior to the attachment point of the median male. Shaded histogram bars give the expected number of females in each 10-percentile class if male settlement were random across the entire surface of the ovarian disc (Kolmogorov-Smirnov $D = 0.53$, $p < 0.01$)

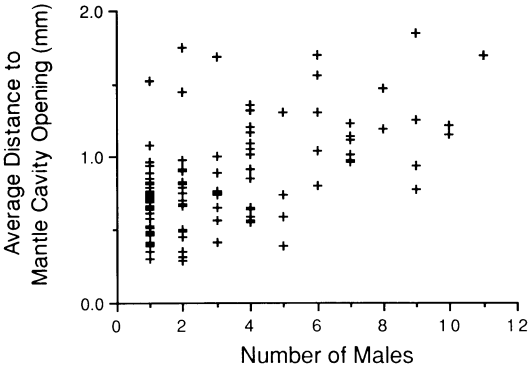

Fig. 5. Local male density and the average distance from each male to the site of insemination. Each point represents the number of males on a single female and the average distance from those males to the female mantle cavity opening ($r = 0.56$, $p < 0.001$; $n = 113$)

Although most males settled on the anterior of the female ovarian disc, the distance from each male to the site of insemination depended on male density. The average attachment distance of males increased as a function of local male density (Fig. 5). Thus, uncrowded males tended to be attached closer to the site of insemination than did crowded males.

Average attachment distance was also positively correlated with average male size, and with female area. In contrast, only male density and attachment distance were significant predictors of average male size (Table 1). After accounting for variation due to attachment distance, male density correlated negatively with male body size. Although average male body size and attachment distance were correlated *between* females, the pattern did not hold *within* females. For females with 7 or more attached males, there was no significant relationship between individual male size and attachment distance (Table 2).

Table 1. Multiple regression of average settlement distance, average male body size, male density and female ovarian disc area. Coefficients ($p < 0.05$) are given for the best-fitting models based on a step-wise multiple regression (backward elimination). $n = 113$ females. R^2 is given for the total model

Dependent variable	Attachment distance	Male body size
Independent variables		
Attachment distance	–	0.1600
Male body size	0.6852	–
Male density	0.0214	−0.0125
Female area	0.0610	N.S.
Intercept	0.2161	0.4511
R^2	0.6678	0.1595

Table 2. Correlation (r) between male body size and distance to site of insemination for female with 7 or more males

Shell #	Specimen #	# of males	r	p
16	1	10	0.051	0.888
54	15	10	0.256	0.474
5	3	9[a]	−0.077	0.844
5	1	9	0.598	0.089
5	11	9	−0.116	0.766
16	2	9	0.256	0.505
5	4	8	−0.269	0.519
64	2	8	0.132	0.755
5	2	7	0.249	0.590
16	6	7	−0.286	0.533
51	8	7	−0.689	0.087
54	10	7[a]	0.119	0.799
64	1	7	−0.350	0.441

[a] Specimen also contained 2 attached cyprids

Table 3. The number of females with even and skewed distributions of parasitic males attached to the left and right hand sides of the ovarian disc. Even distributions are those in which the number of males was split evenly between the two sides (1–1, 1–2, 2–2, etc.). Skewed distributions are those in which the number was unequal on the two sides (2–0, 3–0, 3–1 or 4–0, etc.). Values in parentheses are the numbers expected if the settlement of males were random on the two sides. Data for females with 5 or more males were combined to raise the expected values above 5.0. Data are given for the total number of metamorphosed males and newly-settled male cyprids on each female, but the results are similar if cyprids are excluded from the calculations

Numbers of males	Even	Skewed
2	14	7
	(10.50)	(10.50)
3	8	1
	(6.75)	(2.25)
4	11	5
	(5.99)	(10.01)
≥5	15	10
	(11.07)	(13.93)
total	48	23
	(34.31)	(36.69)

The distribution of males on the two sides of the attachment process was highly non-random. Across all abundance classes of males, there were significantly more even distributions than expected by chance ($x_1^2 = 10.57$, $p < 0.01$; Table 3). This pattern would arise if males consistently chose the least crowded side of the disc for settlement. There was no interaction between evenness and abundance class ($x_3^2 = 1.88, p > 0.05$), suggesting that males avoided crowding to the same degree in low and high density conditions.

Discussion

Four spatial patterns are consistent with the notion that males compete with one another for attachment sites on a female: 1) males were strongly aggregated towards the anterior of the female ovarian disc (Fig. 4); 2) attachment distance correlated positively with local male density (Fig. 5); 3) males were distributed on the two sides of the female ovarian disc more evenly than expected by chance (Table 3) average male body size decreased as a function of male density (Table 1).

Alternative mechanisms other than male-male competition are less satisfying explanations for these patterns. For example, on a single female, gregarious larval settlement (Crisp 1979) might cause males to be aggregated close to the anterior of the ovarian disc. But gregarious settlement cannot explain the consistent anterior placement of the median male across many different females (Fig. 4). Anterior distributions might also arise if the posterior area of the ovarian disc were simply unusable as a settlement surface. This hypothesis seems unlikely because the anterior and posterior regions of the disc surface appear similar (Fig. 1), and because we have found individual males attached 75% of the distance back from the mantle cavity opening.

An alternative explanation for the correlation between attachment distance and density (Fig. 5) is that the pattern is due to allometric constraints imposed by female or male body size. Although both of these factors are also correlated with attachment distance, the multiple regression analysis indicates that density explains a significant component of variation in settlement distance, even after size effects are accounted for (Table 1). Allometric constraints also cannot account for the negative relationship between male density and male body size.

Alternative explanations for the distribution of males on the two sides of the female are that males choose a settlement site on the basis of available area, accessibility, or suitability, rather than on the basis of local male density. But if males were responding to these factors alone, the results would be biased towards skewed distributions. Predominance of even distributions (Table 3) implies that cyprids assess male density before choosing a settlement site. Barnacle cyprids often probe and explore potential settlement surfaces before permanent attachment (Crisp 1961; Turquier 1970; Lewis 1978), so it is not unrealistic to believe they have the potential to assess local male density, particularly when considering the elaborate sensory structures they possess (Nott and Foster 1969; Walley 1969).

Not all distribution patterns are consistent with the simple hypothesis of male-male competition. Male density can be explained parsimoniously by a random settlement model based on differences in female area. Such a model might imply an ultimate space limitation for males, or simply a passive settlement system in which females function as "targets" of different areas. In either case, the colonization process allows males to make several hierarchical choices: among patches (gastropod shells), among females within a patch, and among settlement sites within a patch. The results presented here suggest that interactions among males primarily affect the choice of settlement sites on a single female.

The significant positive correlation between average male body size and average settlement distance (Table 1) suggests that small males tend to settle closer to the insemination site than large males. However, this interpretation is not supported by correlations of individual male size and settlement distance within individual females (Table 2). On the other hand, the multiple regression analysis does indicate that average male body size decreases as a function of male density, which again suggests a competitive interaction. These correlations are somewhat surprising because males do not feed after settlement and are not thought to grow. A complete interpretation of these results would require information on the relationships among male density, male body size, settlement distance, and fertilization success.

Trypetesa lampas exploits a specialized, patchy habitat, where the dynamics of local hermit crab populations affect the availability of gastropod shells for colonization (White 1969). Under these circumstances, the male dispersal model (Ghiselin 1974) predicts the evolution of dwarfing because there is no longer a premium on large male body size as an object of female choice or as an advantage in direct male-male interactions. Instead, males indirectly compete for spatial and temporal access to females. Small male body size and precocious sexual maturity are advantageous under these circumstances. In support of this hypothesis, Høeg (1991) also found evidence for pre-emptive male-male competition in certain Rhizocephala with parasitic males: the male trichogon sheds a cuticle armed with spines that permanently blocks the female receptacle and prevents additional males from entering and fertilizing the female.

An alternative hypothesis for understanding small male body size is to consider the ecological implications of dwarfing (Shine 1989). Sexual size dimorphism may evolve if resources are limiting, so that intraspecific competition leads to niche specialization by each sex (Slatkin 1984). Burrowing space is likely to be in short supply because female density within shells can be high, and burrows continue to occupy space even after the death of the female. Under these high-density conditions, selection may favor dwarf males that attach directly to the female. The cost to the male may be the lost opportunity for mating with more than one neighboring female. However, this cost may be balanced by the energetic gains from foregoing burrow construction and investing in somatic tissue. Tomlinson (1969) stressed the limited settlement area available to acrothoracicans, and Turner and Yakovlev (1983) invoked a similar mechanism to explain the evolution of dwarf males in a teredinid bivalve that burrows into seagrass rhizomes.

Thus, both sexual selection for efficient access to females ("male dispersal" in the terminology of Ghiselin 1974) and natural selection for coexistence in a space-limited habitat (Turner and Yakovlev 1983) may have contributed to the evolution of parasitic males.

Finally, a definitive understanding of the evolution of parasitic males in the Acrothoracica requires knowledge of the phylogeny of the group. Although acrothoracicans are clearly among the most primitive barnacle taxa, their evolutionary origins are obscure (Newman 1987). The sexuality of primitive cirripeds is diverse (Charnov 1987), and the ancestors of the Acrothoracica may have been dioecious, hermaphroditic, or hermaphroditic with small, complemental males.

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