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**Sex Size Ratios and Their Influence
On the Mating Success of Two
Calanoid Copepod Species**

Gabriella Grad

**A Thesis
in
The Department
of
Biology**

**Presented in Partial Fulfillment of the Requirements
for the Degree of Master of Science at
Concordia University
Montréal, Québec, Canada**

April 1989

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ISBN 0-315-49098-5

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ABSTRACT

Sex Size Ratios and Their Influence on the Mating Success of Two Calanoid Copepod Species

Gabriella Grad

Mating experiments using 182 individual pairs of Diaptomus birgei Marsh and 153 pairs of D. leptopus Forbes were video-taped in the laboratory. The following were measured and scored: attempted capture of the female by the male, time to successful capture and mounting, duration of copulation, spermatophore placement, time to clutch extrusion, metasomal lengths of all individuals and sex size ratios (female:male lengths) of all pairs. It was found that mating success was a function of sex size ratios for both D. birgei and D. leptopus. Photographic analysis of both species showed that males always held onto female genital segments in the vicinity of the spines with their right fifth legs. Pearson correlations were calculated comparing metasomal lengths to a variety of genital parts. The strongest relationships were found with female genital segment width, at the level of the spines for both species, and right fifth leg claw length for D. birgei. These data help support the hypothesis that sex size ratios and mating success may be related in one species though not in the other. Ecological differences between D. birgei and D. leptopus which could promote differences in reproductive strategies are discussed.

ACKNOWLEDGEMENTS

I would like to thank 'Sir' Ed Maly for supporting and believing in me and giving me a chance to work in his lab. Sincere thanks to Henry van Leeuwen for giving me a working hypothesis I could expand on and thoroughly enjoy. Thanks to Dr.'s Daphne Fairbairn (for remaining on my committee) and Mary Maly, as well as Richard Preziosi for their statistical insight, to Dr. J.D. McLaughlin for being a 'real' scientist, to Bob Kirner for his support and inspirational assistance, Dany Lacroix and Al Elliott for their chauffeuring, as well as Suzanne Plante, Chris Doucet and Shelley Watson for their camaraderie. Thanks also to Scott France, Todd Minchinton, Simon Pedder and Hank (again) for making Maly's Mob such a special group to be a part of. Special thanks to R.J.A. for being there to listen when I needed him.

Many thanks also go to Dr. Craig Williamson for agreeing to be my external supervisor.

DEDICATION

This thesis is dedicated to my ever supportive
mother, Aline Grad.

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INTRODUCTION

Sexual size dimorphism is a phenomenon commonly found in a large variety of animals, from primates to protozoans. Many hypotheses have been proposed to explain size differences among the sexes for many organisms. The two most commonly used hypotheses are discussed in a paper by Clutton-Brock and Harvey (1977): that sexual size dimorphism allows the sexes to exploit different niches (Selander 1966) and that dimorphism has arisen as a result of differential competition for mates (Darwin 1871; Trivers 1972; in Clutton-Brock and Harvey 1977).

SELECTION FAVORING LARGE MALES

It would seem that the second hypothesis mentioned above is most widely accepted in these cases. For example, Clutton-Brock and Harvey (1977) suggested that there was reasonable evidence that sexual dimorphism in body size was related to differences in breeding competition between the sexes in primates. They found some indication that dimorphism in body size was greatest in species where inter-male competition was most intense; monogamous species showed the smallest degree of dimorphism and strongly polygynous species, the greatest. Some authors (Cheverud et al 1985) have argued that the majority of the variation

among primate species is due to phylogeny and scaling. Others (Gaulin and Sailer 1984) state that there has not yet been a convincing description of the mechanism by which allometric considerations alone, in the absence of sexual selection, could produce the patterns of dimorphism observed.

Packer and Pusey (1982) found that the largest and more vigorous male lions consorted most often with oestrous females and that these differences in competitive ability did result in differential male reproductive success.

Anderson and Fedak (1985) found that the largest male grey seals may on average sire 10 times as many offspring as the smallest breeding males. In the case of elephant seals, the largest and strongest males win the biggest harems and in any one year, all the matings are performed by just a few males (LeBoeuf 1972).

Clutton-Brock et al (1979) found that fighting success and reproductive success in red deer populations were closely related. They also found that weight and fighting ability were closely related. Wilkinson and Shank (1976) reported that 5 to 10 per cent of musk ox bulls were killed during the 1973 rut, and that the dead bulls were mostly young or elderly adults. The data in the former two articles suggest again that the strongest and most vigorous males would have the highest mating success.

Jarman (1974) studied sexual size dimorphism in over 20 species of African antelope ranging from males weighing

109% of female weight in oribi to over 150% in impala, greater kudu, Uganda kob, buffalo and eland. Jarman suggested that the degree of sexual dimorphism increased with the individual's maturation, both physically and within the hierarchy of mating rights.

There can also be selection on male size in the absence of male-male competition. An example of this can be found in two studies of different cricket species (Sakaluk 1985, Simmons 1988). Both authors found that female crickets show a strong preference for mating with large males. This preference occurs because females remove the sperm ampulla soon after consuming the spermatophylax, the size of which is correlated to male size, and thus penalize males that provide smaller nuptial meals. Thus mate choice (it is the female cricket which mounts the male) can be a powerful selective force on male size. Yet, since selection can also favor large, more fecund females (Dodson 1987), sexual size dimorphism in crickets does not occur under normal conditions (Simmons 1987). However dimorphism was reported by Simmons (1987) as a result of intense competition. In this case, females were found to be larger than males.

SELECTION FAVORING LARGER FEMALES

If males have nothing to defend, such as groups of females, territories, or resources, then male-male

competition would be low. In these cases it is thought that selection is strongest on and favors large females because eggs are expensive, and the bigger the female, the more eggs she can lay (Dodson 1987). A good example of this is found in the anemone fish, a protandrous hermaphrodite, which starts out as a male, and as it grows may undergo a sex change to the now more profitable sex - a female (Frickle and Frickle 1977).

Sexual size dimorphism favoring females can also be found in woodpeckers (Selander 1966) and falcons (Storer 1966). Selander demonstrated a relationship between degrees of sexual dimorphism and sexual divergence in foraging behaviour of the strongly dimorphic Hispaniolan Woodpecker and the moderately dimorphic Golden-fronted Woodpecker. Storer similarly found that dimorphism was greatest in the smallest species, Sharp-skinned Hawk, intermediate in Cooper's Hawk, and least in the Goshawk, the largest species. Since the size of a predator is clearly related to the size of its prey, and since the number of species and individuals of available small prey is greater, Storer hypothesized that sexual size dimorphism was due to competition for food and differential niche utilization, both inter- and intraspecific. He also hypothesized that the increased dimorphism in smaller species could be due to the greater number of potential predators which might subdue a smaller female at the nest.

Wheeler and Greenwood (1983) suggest that since

females of many bird species, including raptors, are known to increase in weight prior to egg laying, female size should be a compromise between selective forces acting to optimise their hunting performance and those acting to maximize their reproductive output. A larger and more powerful female will experience less alteration and more gradual change in her wing loading and therefore less impairment of flight performance in carrying a given breeding increment. Wheeler and Greenwood therefore interpret sex differences in diet primarily as a consequence of the initial evolution of reversed sexual dimorphism through the mechanisms outlined above.

ASSORTATIVE MATING

Selection can strongly favor sexual size dimorphism with cases where males are either substantially larger or smaller than females. Why then, has it been so uncommon while searching through the literature, to find extreme cases of sex size ratios (size of larger sex : size of smaller sex)? A possible explanation for this, apart from the obvious physical constraints on body size, is the lock and key theory of copulation. In reviewing works by authors studying invertebrate homogamy (such as assortative conjugation in Paramecia (Jennings 1911)), Willoughby and Pomerat (1932) stated that those investigators are of the practically unanimous opinion that in the forms

investigated by them, homogamy is closely conditioned by the physical impossibility of copulation between animals widely divergent in size.

There are a great many examples of assortative mating, or homogamy, in the literature. Frogs and toads (Howard 1980, and Willoughby and Pomerat 1932, Davies and Halliday 1977, respectively) have shown that assortative mating occurs: large males mating with large females. The authors attributed this homogamy to high male-male competition (in the woodfrog study (Howard 1980), males outnumbered females 5.6 to one) and to the ability of large males being able to dislodge smaller males already in amplexus.

Scheiring (1977) found that intermediate sized cerambycid beetles were physiologically better suited for mating, and that therefore size was an important component of mating success in both males and females. McCauley and Wade (1978) showed that though adult soldier beetles interact at random, size was an important factor in predicting both mating success and mate choice. Pinto and Mayor (1986) also found mating to be size assortative in several species of blister beetles, and promote possible explanations for their findings. In two of the species, the male's abdomen and genitalia at the posterior end of the body, and the antennae and palpi at the anterior end are involved in courtship concurrently. Observations of these species, as well as numerous others with similar

displays, indicate clearly that when the male is substantially larger than the female the lack of coincidence of anatomical parts prevents normal courtship delivery. These findings clearly provide evidence for the lock and key theory of copulation.

Much work has also been done on the mating systems of crustacea. Hughes and Matthiesson (1962) reported some observations of American lobster mating behaviour. They noted that a large male was invariably unsuccessful in attempting to mate with a female considerably smaller than he, whereas a small male could mate successfully with a much larger female. Also, when two males were placed in the same tank with a female in receptive condition, they would compete for the right to mate, with the larger and more aggressive male eventually driving the other one off.

Swartz (1976) showed that mating in the xanthid crab was homogamous. The average sex size ratio of mated pairs (in terms of carapace width) was 1.5. Males were always found to mate with females smaller than themselves. This size discrimination in copulation was attributable to the agonistic character of pre-Grab behaviour (initial approach and pairing at the end of which the male always grabs the female with his chelae). Swartz also stated that the size discrimination reflected the influence of relative size on dominant-subordinate relationships during normal agonistic interactions.

Data on fiddler crabs is contradictory. Greenspan

(1980) found that females of one species were highly selective in mating, while males were not. She also found that females would select a male whose size was correlated with hers. On the other hand, Christy (1987) found that females of a second species consistently chose males whose burrows were larger and deeper than those they rejected, but that they did not select males on the basis of size.

Stein (1976), studying sexual dimorphism in crayfish chelae, found that the proportions of successful copulations were greatest when the differences between the carapace lengths of males and females was between 0 and +4 mm. The chelae appeared most important for reproductive activities and secondary for prey manipulation and defense, since size of chelae is reduced in non-mating males during the summer. In sexual encounters, males used their chelae to grasp and hold females during copulation. Since males with large chelae could interact more successfully with larger, more fecund females, they would have an increased fitness and be selected for.

In an early study of selective coupling in gammarids, Crozier and Snyder (1923) stated that the assortative mating they found was due to the fact that the mutual fitting of two individuals, requisite for conjugation, was mechanically possible only when those individuals were of similar size. A later study by Adams and Greenwood (1987) suggested that assortative mating was an artifact of loading constraints. They showed that relatively large

males had an advantage because they could swim against stronger currents when carrying a mate. At high current speeds, the male/female size ratio which forms is significantly greater than at low current speeds. In field collections, size ratios of pairs were higher in streams than in lakes for a number of species. They also suggested that in sites where the male/female ratios were not high, assortative coupling was probably due to male preference for larger, more fecund females. A more recent study by Ward (1988) showed that males adjusted precopula duration with females of different sizes to equalize their reproductive returns (number of eggs fertilized per day of precopula). Ward also found that there was a significant selection intensity for a smaller male/female size ratio.

PURPOSE AND BACKGROUND

The purpose of this thesis was to investigate sexual size dimorphism of two species of calanoid copepods, Diaptomus birgei Marsh, 1894 and D. leptopus Forbes, 1882. Some work has already been done on the topic using different species (Bayly 1978, Maly 1978, Geddes and Cole 1981, Gilbert and Williamson 1983, Maly 1983, 1984a, b, DeFrenza et al 1986, Chow-Fraser and Maly 1988). There have been three hypotheses proposed to explain the observation that sex size ratios in species of calanoid copepods are relatively constant and female biased (females

are generally larger than males).

Bayly (1978), studying Australian copepods, found that sex size ratios in temporary ponds were much greater than those in permanent bodies of water. He postulated that the high degrees of sexual size dimorphism found in species only inhabiting temporary ponds could be attributed to lack of predation. Selection would then favor the largest, most fecund females. If the risk of predation by either planktonic or nectonic predators is high, there would be selection for low sexual dimorphism. In this way, predation would not threaten reproductive success through differential loss of either sex.

Bayly (1978) also used the general hypothesis put forward by Selander (1966) that selection for increased female size would presumably decrease competition with males for similar sized food particles. He similarly suggested that competition for limited food resources could be a selective force against size overlap in co-occurring species.

It was this second hypothesis, along with the many examples of such non-overlapping species size assemblages (Cole 1961, Sandercock 1967, Geddes and Cole 1981, Maly 1978, Jacoby and Youngbluth 1983, Maly 1984a, b) which led to the suggestion of the third selective force - mating ability. Studies have shown that copepods make interspecific mating errors in laboratory conditions (Katona 1973, Jacoby and Youngbluth 1983, Maly 1984b). A

hypothesis was put forth by Maly (1984b) arguing that if male calanoid copepods chose mates on the basis of size, two similar-sized species would be unable to co-occur due to the waste of time and energy used in interspecific copulation unless intraspecific mating was restricted temporally or spatially. Such a hypothesis could be used to further explain the extent of both size dimorphism and the size assemblages of co-occurring species found in nature. Mating ability as a function of size could also explain such findings as those of Carillo and Miller (1974). They found that Atlantic and Pacific populations of a marine copepod could not interbreed. The major difference between the two populations was size, yet they did not consider it as a possible factor in their results.

As was mentioned previously, sex size ratios (mean female : male metasomal lengths) are found to be species specific and stable, given constant conditions, even though absolute sizes vary seasonally (Bayly 1978). Maly (1978) showed that the sex size ratio of D. shoshone remained remarkably constant in time and space, though the actual sizes of the animals varied. A study by Hart and McLaren (1978) found that copepods mated in a size assortative fashion. Using field data, DeFrenza et al (1986) showed that for each of three species, D. minutus, D. oregonensis, and D. birgei, there appears to be an optimal sex size ratio. In natural populations, as the ratio approached the optimum, the amount of sexual activity was found to

increase. Activity in this case referred to the number of females with attached spermatophores or clutches, as compared to the total number of females in the sample. These observations suggest that selection plays an active role in maintaining species sex size ratios. The fourth species studied by DeFrenza et al (1986), D. leptopus, showed no such trend. Since sexual activity did not have a single peak, the authors suggested that size was less of a factor in mate selection for D. leptopus than it was for the other three species.

OBJECTIVES

Using two of the species from sites included in the analysis of DeFrenza et al (1986), a laboratory study was performed to test the hypothesis that copepods mate more successfully at their commonly observed optimal sex size ratios. In order to support any arguments which could be made relating metasomal lengths to mating ability, it was decided to collect evidence to determine if measurements of male and female copepod genitalia are correlated to overall body size.

The main objective of this study was to attempt to answer the following questions:

- 1) Does D. birgei mating success peak at a sex size ratio close to 1.199?
- 2) Is D. leptopus mating success equal at all sex size

ratios?

3) Is mating success a function of individual size for either sex or species?

4) What is the relative importance of male and female genitalia in both species in terms of mating?

and

5) Are male and female genitalia which are important in mating highly correlated to metasomal lengths for both sexes and species?

Data in concurrence with the above questions would also be in concurrence with the findings of DeFrenza et al (1986), would add to evidence that these ratios are controlled by natural selection and would strengthen the hypothesis of Maly (1984b) that mating may play a role in co-occurrence patterns.

MATERIALS AND METHODS

COLLECTION

Diaptomus birgei were collected from a small pond in St. Joachim, Quebec ($45^{\circ} 27' 15''\text{N}$, $72^{\circ} 31' 20''\text{W}$) and from a larger pond (B4) on Nun's Island ($45^{\circ} 27' 15''\text{N}$, $73^{\circ} 33' 30''\text{W}$). Neither of the D. birgei ponds freeze to the bottom in the winter. Diaptomus leptopus were collected from two ponds in Morgan's Aboretum, St. Anne's, Quebec. The first is a temporary pond, Quarry pond ($45^{\circ} 25' 45''\text{N}$, $73^{\circ} 52' 30''\text{W}$), which dries by the end of June. The second, Hill pond ($45^{\circ} 25' 50''\text{N}$, $73^{\circ} 56' 45''\text{W}$), is permanent and sometimes freezes solid in the winter. D. leptopus do not survive at Hill pond in the winter months. All ponds were sampled using a Wisconsin plankton tow net (80 μm mesh size). In the summer, tows were taken diagonally while winter tows were vertical. Summer samples of D. birgei were taken on four occasions from late July to mid August, 1986, eight other samples were taken from mid September, 1986 to late April, 1988. D. leptopus were sampled in the summers of 1987 for morphometric work and 1988 (ten times) for mating experiments.

MATING EXPERIMENTS

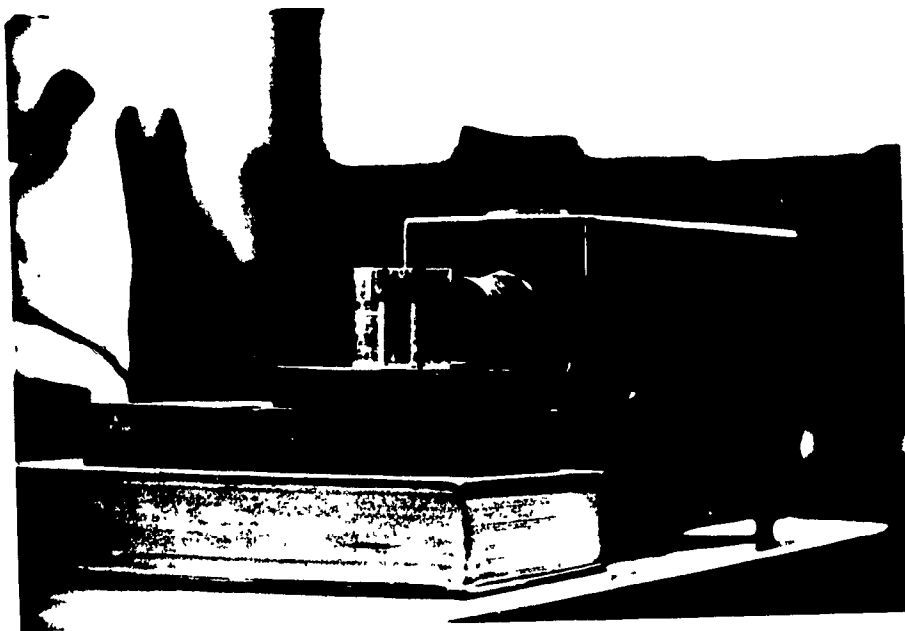
Live animals were brought back to the laboratory in 20L plastic carboys. Mature males and gravid females (carrying mature oocytes) were separated and isolated in 1L beakers containing filtered pond water. This was done to prevent the animals from mating within at least 12 h before their use in an experiment. Only gravid females were used in experiments.

Individuals were paired either randomly or according to their sizes to ensure sufficient matings were tried to cover as wide a range of sex size ratios as possible. In the experiments where pairs were not chosen at random, live measurements were taken. Each individual was placed in a Pyrex 9-spot plate in one drop of water. As much water as possible was then removed. The size of the copepod - now rendered almost immobile - was estimated using a micrometer mounted on a Jena dissecting microscope at 50X magnification. The individual was then placed into a plastic vial containing 30 ml of filtered pond water.

In the mating experiments, a male was placed into a standard polystyrene cuvet containing approximately 1.5 ml filtered pond water and allowed to acclimate for 5 min. Only males which would swim more than 1 cm above the bottom of the cuvetts were used. Males which remained on the bottom of the cuvetts were discarded. A gravid female was then added. Females were used whether or not they were very active. The pair would then be video-taped using a Hitachi closed-circuit television camera, a Hitachi 5 head

VHS video tape recorder, and viewed on a 53 cm Hitachi monitor (Fig. 1) until mating was completed or for a maximum of 80 min. The viewing period was determined through preliminary experiments. Up to three pairs were run at one time. A stopwatch was placed next to the monitor and was only started after all the females were placed in the cuvetts and the volume in each cuvet was equilibrated. If mating occurred, time elapsed before commencement of mating and copulation duration were noted. The pair was then removed from the cuvet. The male was placed into a small plastic vial containing 30 ml filtered pond water and the female was placed in a Pyrex 9-spot plate and observed using the Jena microscope. The female was scored for placement of a spermatophore immediately after removal from the cuvet. It was also noted whether or not the spermatophore was full of spermatozoa. The female was then checked every few minutes so that approximate time for the spermatophore to empty and subsequent clutch to be produced (if any) could also be determined. Diaptomus birgei females were given at least 3h to produce a clutch, while D. leptopus females were given at least 4h. Differentiation was made between fertilized and unfertilized clutches; unfertilized eggs would disintegrate and appear as a grey mass in the clutch, whereas fertilized ones would remain distinct and dark. The female was then placed into a vial containing 30 ml of filtered pond water. Individual copepods were killed at a

Figure 1. Photograph (A) shows the maximum of three cuvetts being video-taped by the closed-circuit camera. Photograph (B) shows the black and white image that would appear on the monitor and the position of the stopwatch used to time all experiments. Copepods can be seen on the monitor - gravid females can most easily be seen due to the eggs they carry.



A



B

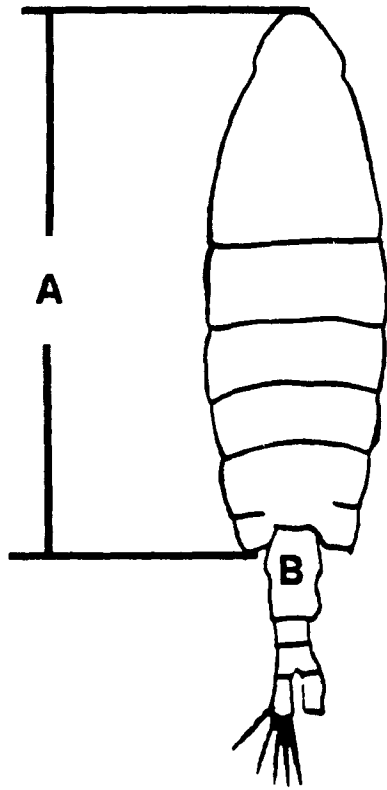
later time using a 30% formaldehyde solution and their metasomal lengths were measured (Fig. 2). Diaptomus birgei were measured using a micrometer mounted on a Bausch and Lomb dissecting microscope at 30X to the nearest 0.033 mm, while D. leptopus were measured using a micrometer mounted on the Jena microscope at 50X to the nearest 0.0185 mm.

The pairs which were used in the analysis consisted of any that had either mated, or wherein the male had made at least one attempt at copulation with the female during the allotted period. Attempts were identified through characteristic approach behaviour - the male's swimming pattern would change from a smooth motion to short bursts of activity towards the female (Jacobs 1961). A male exhibiting approach behaviour would always approach the female from below and would swim towards her in a spiralling path to properly align his antennules for use in copulation. Only pairs where the male clearly attempted to catch the female at least twice were considered. Mating experiments were performed from 9 am to 1 am. Since Williamson and Butler (1987) observed no patterns of diel periodicity in egg laying, hence in mating, for D. pallidus, I did not expect mating to be affected by time of day in the two species studied here.

STATISTICAL ANALYSIS

Once the individuals were measured, sex size ratios

Figure 2. The general drawing of a calanoid copepod was taken from Ward and Whipple (1959). Distance (A) is the metasomal length, from head to tip of metasomal wings, which was measured for both species and sexes. Structure (B) is the genital segment.



were calculated and logarithmically transformed for use in statistical analysis. The four summer samples and eight fall and winter samples of D. birgei were each pooled for lengths of males and females, as were the ten summer D. leptopus samples. To establish that though average size of sample D. birgei may change seasonally, sex size ratios remain constant, t-tests for independent samples were performed to determine whether metasomal lengths differed between seasons, and a Mann-Whitney test was performed to determine whether sex size ratios vary significantly between seasons. Data for the t-test consisted of all individuals from the 182 pairings while the data for the Mann-Whitney test consisted only of the random mating pairings, since all other pairs were manipulated in order to yield extreme ratios. Site differences between St. Joachim and Nun's Island were also tested even though the sample size of Nun's Island pairs ($n = 8$ in the summer and $n = 4$ in all other samples) was very small.

Student t-tests were also performed to determine whether male and female lengths of D. leptopus differed between the two sites. A Mann-Whitney test was used to determine if D. leptopus sex size ratios differed at Hill and Quarry ponds. Since all sampled D. leptopus pairs were chosen at random, individuals from all 153 pairings were used in the analysis. Seasonal changes in male and female lengths as well as sex size ratios over the summer period were also tested using single factor ANOVAs and Student-

Neuman-Keuls tests. The Quarry samples were compared to Hill samples taken before and after July 14, by which date Quarry had dried.

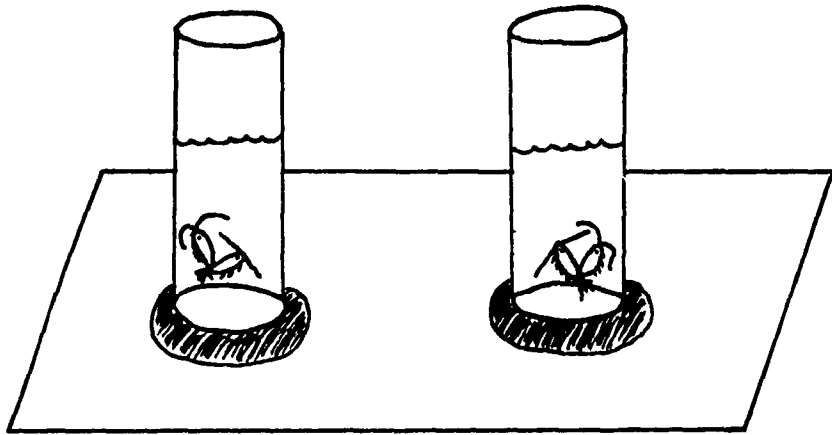
Frequencies of matings that produced a fertile clutch (successful matings) were plotted against sex size ratio classes. Log likelihood ratio (G) tests, Fisher's Exact tests (when sample sizes were too small for G), and Spearman Rank correlations were performed to compare mating success at different sex size ratio classes, as well as at different length classes of males and females for both species. Log likelihood ratio and Fisher's Exact tests were also used to compare D. leptopus spermatophore placement (or lack thereof) with male and female length classes. G-tests of independence, using Williams' correction for 2 x 2 tables (Sokal and Rohlf 1981), were performed if significant differences were found between mating success and sex size ratio with the log likelihood ratio test to determine which classes differed significantly from each other.

Pearson correlations were calculated, comparing time to mating in minutes, to logarithmically transformed sex size ratios, as well as male and female lengths for both species. Stepwise regression and Pearson correlations using SPSSX statistical package were used to analyze relationships between duration of mating and sex size ratios, as well as male and female lengths for both species.

PHOTOGRAPHIC ANALYSIS

At the end of August and during September, 1987, photographs of copulating D. leptopus and D. birgei were taken using a Wild inverted microscope at 100X. First, the wide end of a Pasteur pipette was cut using a piece of quartz to a length of approximately 1.3 cm. The glass cylinder was then mounted on a depression slide using silicone (Fig. 3), to create a holding chamber of very small volume (0.3 ml). Copulating pairs were obtained by placing a large number of live copepods into a plastic pan measuring 30 cm in length by 20 cm in width by 4 cm in height. As soon as a copulating pair was observed, they would be sucked up into the wide end of a Pasteur pipette. The pair were then put into a holding chamber for observation using the Wild microscope with camera attachment. The pair was observed until they stopped moving and could be focused on, at which point they would then be photographed. Any photographed pair was kept until copulation ended. The male and female were then killed using a 30% formaldehyde solution and their metasomal lengths were measured using the Jena microscope. Measurements were accurate to within 0.0185 mm. Sex size ratios of each pair were calculated. Enough pairs were photographed so that the copulatory position of each species could be determined. All pairs in which the male

Figure 3. The drawing shows two holding chambers on a depression slide, each containing a drop of water and a copulating pair of copepods.



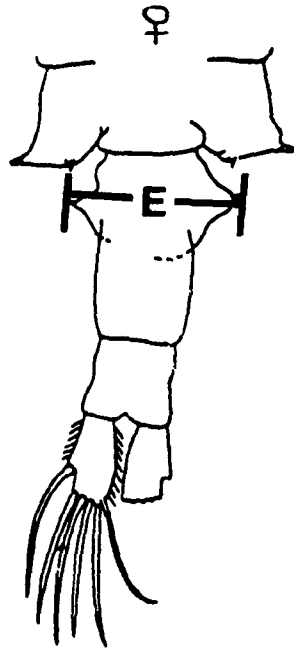
let go of the female before they could be photographed were discarded.

Photographs were examined to determine which aspects of the genital morphology were most important in mating.

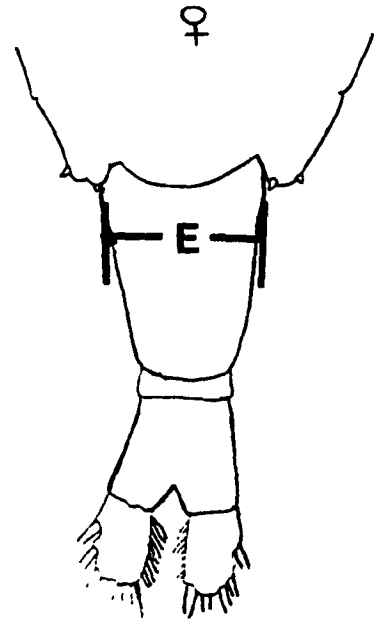
CORRELATION ANALYSIS

On May 14 (Hill and Quarry), August 18 (Nun's Island), and September 19 (St. Joachim), 1987, 100 males and 100 females were randomly sorted from live samples. These animals were then preserved using a 30% formaldehyde solution. At a later date, measurements of male and female genital morphology deemed most important in mating were taken using the Wild microscope. A sample size of 50 individuals was used for each correlation because the r values tended to remain constant after about 30 measurements. Pearson correlations were used to compare genital morphology to metasomal lengths. The widths of female genital segments at the level of the spines (Fig. 4A, B) were measured at 100X, accurate to 0.00651 mm. The lengths of male left fifth legs as well as the claws and segments of the right fifth legs (Fig. 4C, D) were measured at 200X, accurate to 0.003255 mm. Male and female metasomal lengths were measured at 30X, and those measurements are accurate to within 0.0217 mm. This analysis was done for both species at each of the four locations used in the mating experiments.

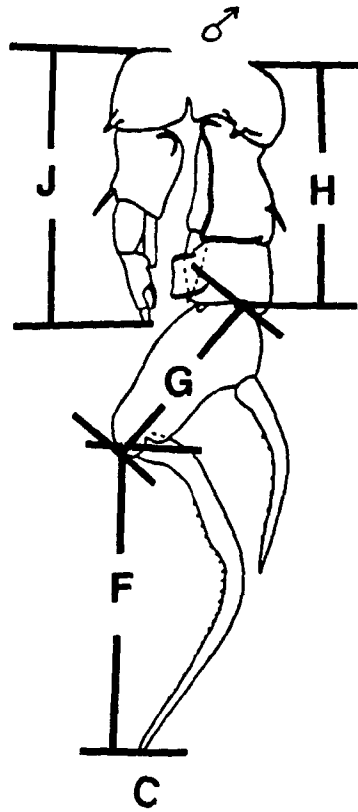
Figure 4. The morphological drawings are taken from Ward and Whipple (1959). Drawings (A) and (C) are D. birgei female segments from the metasomal wings downward, and male fifth leg pair, respectively. Drawings (B) and (D) show the same morphological aspects of D. leptopus. Distances (E) are measures of female genital segment spine widths. Distances (F) are male right fifth leg claw lengths, (G) are large segment lengths and (H) are the remainders of the right fifth leg lengths. Distances (J) are left fifth leg lengths.



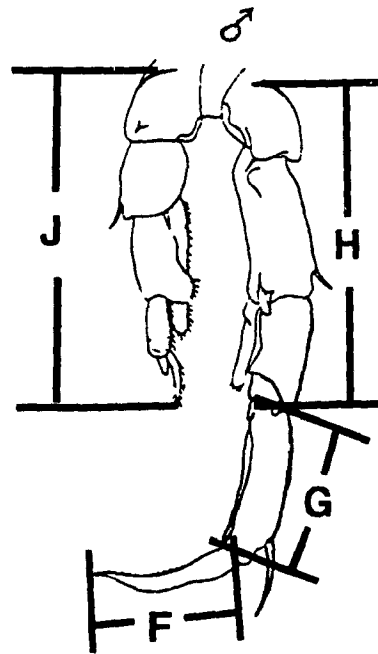
A



B



C



D

RESULTS

SEASONAL AND SITE DIFFERENCES OF *Diaptomus birgei*

The metasomal lengths of summer individuals were significantly smaller than those measured during other seasons of the year (Table 1). Student's t-test for independent samples yielded values of -15.174 ($P < 0.001$) for females and -11.582 ($P < 0.001$) for males. Accordingly, the two sets of data were kept separate in subsequent analyses. Though length changed with season, the average sex size ratio calculated for animals measured in the summer was the same as that calculated from all other samples (1.22, SD = 0.07, $n = 62$ and 1.22, SD = 0.05, $n = 47$ respectively). A normal approximation for the Mann-Whitney test statistic showed no significant differences between seasons in the sex size ratio ($Z = 0.434$, $P > 0.05$).

Site differences also occurred. Female lengths at Nun's Island were greater than those at St. Joachim ($t = 3.965$, $P < 0.005$) though male lengths were not ($t = 0.065$, $P > 0.5$). Nun's Island pairs were nevertheless used since they could generate large sex size ratios needed to test a wide range, and since samples from that pond were so small.

Table 1. Sample sizes, means, standard deviations and ranges are given for a number of variables.

	n	X	SD	Range
Metasomal lengths (mm)				
<u>D. birgei</u>				
Summer				
Males	62	0.92	0.04	0.84 - 0.99
Females	62	1.12	0.06	0.99 - 1.25
Winter				
Males	120	1.00	0.05	0.80 - 1.11
Females	120	1.26	0.06	1.09 - 1.39
<u>D. leptotus</u>				
Quarry				
Males	42	1.06	0.04	0.96 - 1.15
Females	42	1.25	0.05	1.11 - 1.35
Early Hill				
Males	25	1.09	0.07	0.85 - 1.15
Females	25	1.26	0.05	1.11 - 1.35
Late Hill				
Males	86	0.98	0.03	0.93 - 1.07
Females	86	1.14	0.04	1.06 - 1.30
Time to Mating (min.)				
<u>D. birgei</u>				
Summer	51	21.76	20.24	0.47 - 78.67
Winter	108	12.17	14.60	0.35 - 72.60
<u>D. leptopus</u>				
Before July	58	15.17	18.40	0.28 - 68.72
After July	82	22.32	20.36	0.95 - 77.75
Duration of Copulation (min.)				
<u>D. birgei</u>				
Summer	51	6.65	2.48	3.05 - 12.93
Winter	108	8.32	4.47	0.17 - 18.22
<u>D. leptopus</u>				
Before July	58	2.73	1.52	0.83 - 10.08
After July	82	1.96	0.60	0.63 - 3.80

SEASONAL AND SITE DIFFERENCES OF Diaptomus leptopus

When Student's t-tests for independent samples were calculated comparing parameters at Hill and Quarry over the whole sampling period, significant differences were found. Female lengths were significantly larger ($t = 7.682$, $P < 0.001$) at Quarry than they were at Hill (Table 1). Males were also significantly larger ($t = 5.146$, $P < 0.001$) at Quarry than at Hill (Table 1). Sex size ratios were slightly different at both sites ($\bar{X} = 1.18$, $SD = 0.07$, $n = 42$ at Quarry, $\bar{X} = 1.16$, $SD = 0.06$, $n = 111$ at Hill). A normal approximation for the Mann-Whitney test statistic showed significant differences ($Z = 1.975$, $P < 0.05$).

When summer samples were divided into three groups—Quarry, and Hill before and after July 14, I found that the Hill and Quarry samples taken before July did not differ. Single factor ANOVAs showed that the three groups differed in both male and female lengths ($F = 73$, $F = 129.5$, $P < 0.001$, respectively). Student-Neuman-Keuls tests showed that samples from Hill and Quarry taken before July did not differ in either male or female lengths (Table 2). Yet, both these samples differed from the Hill samples taken later in the summer (Table 2). Due to the seasonal size differences, data from early and late summer were not grouped for any further analysis. When the sex size ratios were separated into groups, no differences could be found using single factor ANOVA ($F = 2.05$, $P > 0.5$).

Table 2. Student-Neuman-Keuls test results.

The categories are Quarry (2), early Hill (3) and late Hill (1). Levels of significance are q (0.05,150,P) for females and q (0.01,150,P) for males. dX is the difference between the means of both groups tested.

	dX	SE	q	P	q_{crit}
Males					
3 X 1	0.104	0.007	14.86	3	4.2
3 X 2	0.029	0.008	3.63	2	3.7
2 X 1	0.075	0.006	12.50	2	3.7
Females					
3 X 1	0.123	0.007	17.57	3	3.4
3 X 2	0.009	0.008	1.13	2	2.8
2 X 1	0.114	0.006	19.00	2	2.8

MATING SUCCESS

Pairs ($n = 40$ for D. birgei, $n = 25$ for D. leptopus) where the male exhibited no evidence of approach behaviour were excluded from the analysis. Although the exact placement of the spermatophore on the female's genital pore was not determined, in only 6 cases was a spermatophore not placed after copulation in D. birgei matings. On the other hand, D. leptopus males failed to place spermatophores on females a total of 15 times. Of the spermatophores placed, all D. leptopus spermatophores and all but 2 D. birgei spermatophores were found to contain spermatozoa once the pair separated and the female had been isolated.

Each of the three possible mating outcomes (with fertile clutch, with infertile or no clutch, and attempt) was scored in 9 sex size ratio classes for D. birgei (Table 3) and 10 classes for D. leptopus (Table 4). The log likelihood ratio test comparing number of successful to unsuccessful matings in each class yielded a value of 18.462 ($P < 0.025$) for D. birgei, indicating that there were significant differences among the classes (Table 5). When mating attempts were excluded from the analysis, significant differences among the classes were still found ($G = 16.408$, $P < 0.05$). G-tests of independence yielded differences between the classes (Table 3). Classes labeled 'c' are significantly different from classes labeled 'a'.

Table 3. Diaptomus birgei sex size ratio class data including sample sizes of successful matings (yielding fertile clutches) and unsuccessful matings (yielding infertile or no clutches, as well as attempts). Explanation for the class is in the text.

Sex size ratio classes	Successful matings	Unsuccessful matings		Class
		Infertile clutches	Attempts	
(n)	n	n	n	
1.0670 - 1.1220 (12)	3	7	2	a
1.1220 - 1.1482 (10)	6	2	2	b
1.1482 - 1.1749 (13)	9	4	0	c
1.1749 - 1.2023 (20)	12	7	1	c*
1.2023 - 1.2303 (27)	17	8	2	c
1.2303 - 1.2589 (21)	12	6	3	c*
1.2589 - 1.2882 (26)	8	15	3	a
1.2882 - 1.3183 (26)	8	15	3	a
1.3183 - 1.5814 (27)	9	11	7	a
Total (182)	84	75	23	

Table 4. Diaptomus leptopus sex size ratio class data including sample sizes of successful matings (yielding fertile clutches) and unsuccessful matings (yielding infertile or no clutches, as well as attempts). Sp is indicative of spermatophore placement.

Sex size ratio classes	Successful matings	Unsuccessful matings		Attempt n
		Infertile clutches	Attempt n	
(n)	n	sp n	no sp n	n
1.0470 - 1.0715 (5)	1	2	2	0
1.0715 - 1.0965 (14)	6	8	0	0
1.0965 - 1.1220 (23)	5	13	4	1
1.1220 - 1.1482 (22)	2	17	0	3
1.1482 - 1.1749 (34)	7	21	1	5
1.1749 - 1.2023 (22)	2	18	2	0
1.2023 - 1.2303 (15)	2	12	1	0
1.2303 - 1.2589 (5)	0	2	1	2
1.2589 - 1.2882 (4)	0	1	2	1
1.2882 - 1.4780 (9)	1	5	2	1
Totals (153)	26	99	15	13

The 'b' class is not significantly different from any other. An asterix represents significance at the 0.01 level, all other differences are significant at the 0.05 level. No significant differences were found among the classes for D. leptopus when data from Hill and Quarry were clumped, nor were differences found when Hill was tested alone (Table 5). Though when Spearman Rank correlations were calculated, a significant negative relationship was found between sex size ratio class and percent mating success for D. leptopus (Table 6). This was the only significant correlation. Percentages of successful matings plotted against sex size ratio classes illustrate the range over which D. birgei and D. leptopus can most successfully mate (Figs. 5 and 6 respectively).

The log likelihood ratio and Fisher Exact tests comparing number of successful to unsuccessful matings at different male and female length classes for both species yielded significant differences only for summer male and winter female D. birgei (Table 5). The tests were also used to compare proper spermatophore placement in D. leptopus at different male and female length classes. No significant differences were found (Table 5) indicating that ability to place a spermatophore did not differ according to length. It should be noted that only pairs which mated for at least 0:30 min. were used in this analysis, mating attempts were not included.

The stepwise regression analysis comparing duration of

Table 5. Log likelihood ratio and Fisher's Exact test results comparing mating success and spermatophore placement to the variables listed below. The level of significance used is = 0.05.

	G	crit. val.	P
<u>D. birgei</u>			
Mating Success vs.			
Sex size ratio	18.462	15.507	0.025
Male length			
Summer	6.746	5.991	0.05
Winter	0.774	7.815	NS
Female length			
Summer	5.941	7.815	NS
Winter	10.117	5.991	0.01
<u>D. leptopus</u>			
Mating Success vs.			
Sex size ratio			
Grouped	8.902	9.488	NS
Hill	6.627	9.488	NS
Male length			
Before July	P> 0.055*	0.05	NS
After July	0.732	5.991	NS
Female length			
Before July	P> 0.076*	0.05	NS
After July	2.284	5.991	NS
Spermatophore Placement vs.			
Male length			
Before July	1.612	3.841	NS
After July	P> 0.332*	0.05	NS
Female length			
Before July	0.111	3.841	NS
After July	P> 0.319*	0.05	NS

* Calculated P for Fisher's Exact test.

Table 6. Spearman Rank correlation results comparing % mating success to the variables listed below. The level of significance is =0.05

	rs	r crit.	P
<u>D. birgei</u>			
% Mating Success vs.			
Sex size ratio	-0.244	0.700	NS
Male length			
Summer	0.410	1.000	NS
Winter	0.319	0.886	NS
Female length			
Summer	0.714	0.886	NS
Winter	-0.232	0.886	NS
<u>D. leptopus</u>			
% Mating Success vs.			
Sex size ratio	-0.683	0.648	0.05
Male length			
Before July	0.885	0.886	NS
After July	-0.036	0.786	NS
Female length			
Before July	-0.146	0.738	NS
After July	0.056	0.648	NS

Figure 5. Mating success as a function of sex size ratio classes for D. birgei. The numbers above the bars represent the total sample size of successful and unsuccessful matings in each class.

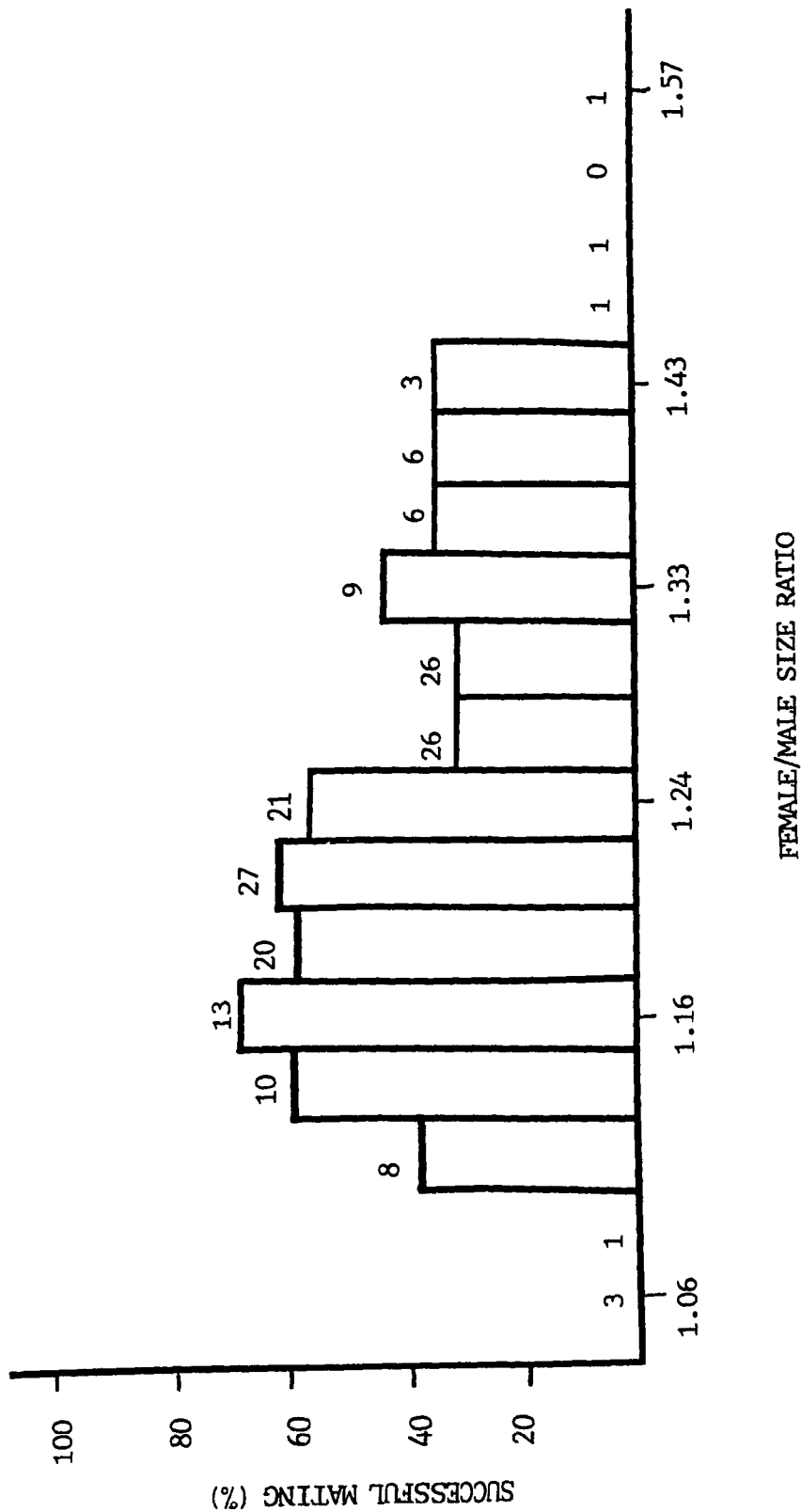
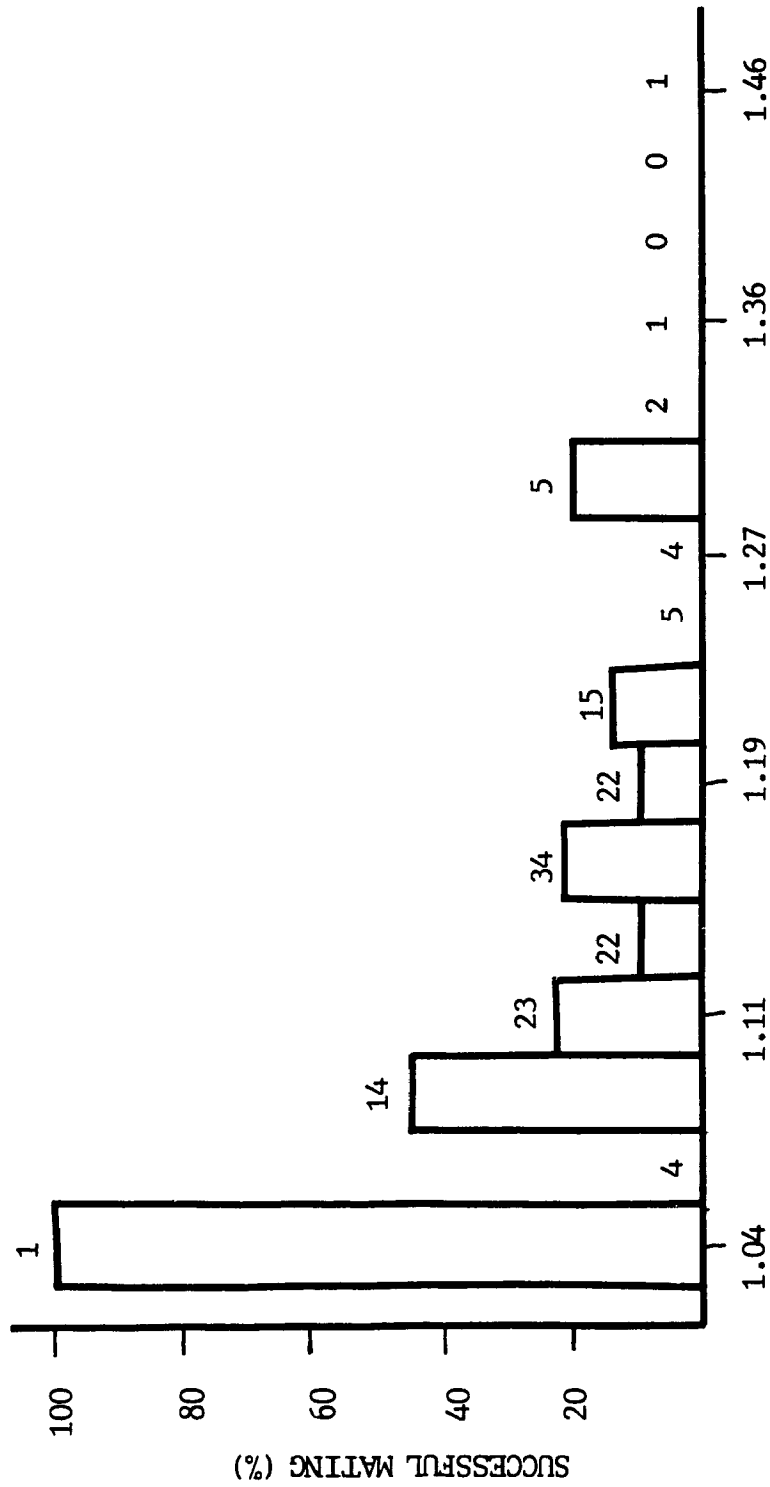


Figure 6. Mating success as a function of sex size ratio classes for D. leptopus. The numbers above the bars represent the total sample size of successful and unsuccessful matings in each class.



FEMALE/MALE SIZE RATIO

copulation to logarithmically transformed sex size ratios yielded no relationship between these two variables for either species. Correlation coefficients comparing time to mating and duration of copulation to logarithmically transformed sex size ratios, as well as male and female lengths were calculated for both species (Table 7). Only correlations where the coefficient of determination (r^2) was greater than 0.10, were considered to be of biological significance. None of the values in Table 7 are biologically significant. It should be noted that one pair of D. leptopus copepods, which were left in the cuvet after their 80 min. period had elapsed, mated 10 min. later and were used in the analysis.

MATING PHOTOGRAPHY

Of the 14 D. birgei and 13 D. leptopus pairs photographed, 12 and 10 pairs, respectively, were found to have the same mating positions. The other photographs were of insufficient quality to determine positions accurately. A representative picture of each species along with a drawing (taken mostly from Ward and Whipple 1959) can be found in Figs. 7 and 8. The sex size ratio ranges over which the photographs were taken were 1.151 to 1.288 for D. birgei and 1.015 to 1.232 for D. leptopus. From these photographs and my knowledge of the mating sequence, I determined that the male's fifth pair of legs and the

Table 7. Pearson correlations comparing time to mating, and duration of copulation in minutes to the variables shown below.

	r	n	rcrit*	P
Time to vs.				
<u>D. birgei</u>				
Sex size ratio	0.006	158	0.159	NS
Male length				
Summer	0.034	51	0.273	NS
Winter	-0.159	107	0.190	NS
Female length				
Summer	0.052	51	0.273	NS
Winter	-0.104	107	0.190	NS
<u>D. leptopus</u>				
Sex size ratio	0.196	140	0.168	0.05
Male length				
Before July	-0.251	58	0.259	NS
After July	-0.181	82	0.217	NS
Female length				
Before July	0.263	58	0.259	0.05
After July	-0.033	82	0.217	NS
Duration vs.				
<u>D. birgei</u>				
Sex size ratio	0.163	158	0.159	0.05
Male length				
Summer	0.234	51	0.273	NS
Winter	-0.051	107	0.190	NS
Female length				
Summer	0.326	51	0.273	0.02
Winter	0.142	107	0.190	NS
<u>D. leptopus</u>				
Sex size ratio	0.064	140	0.168	NS
Male length				
Before July	-0.089	58	0.259	NS
After July	0.093	82	0.217	NS
Female length				
Before July	0.027	58	0.259	NS
After July	-0.049	82	0.217	NS

* Level of significance is 0.05

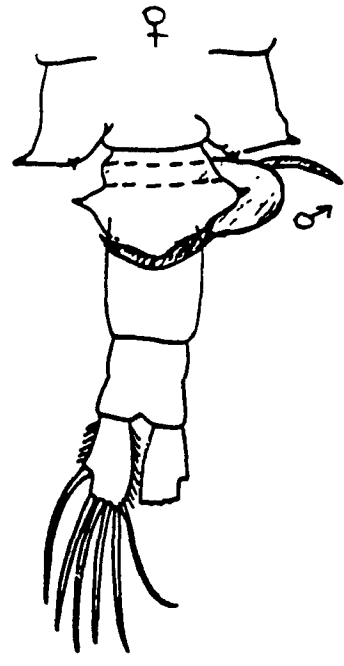
Figure 7. Photograph (A) shows a mating pair of D. birgei. Drawing (B) shows female morphology from the metasomal wings downward (Ward and Whipple 1959). A representation of the male's holding position on the female's genital segment is indicated by the shaded in right fifth leg of the male.



♂

♀

A

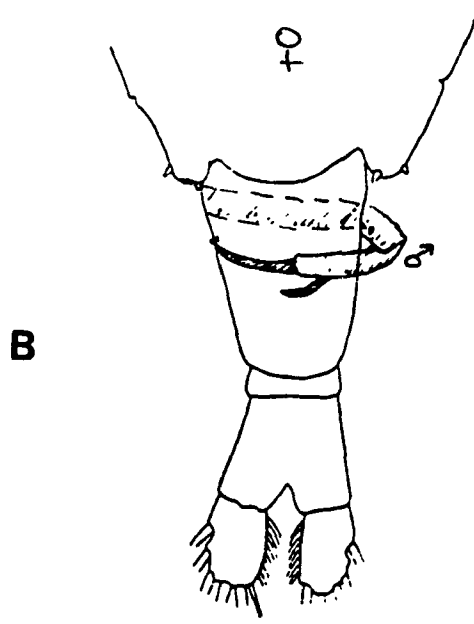
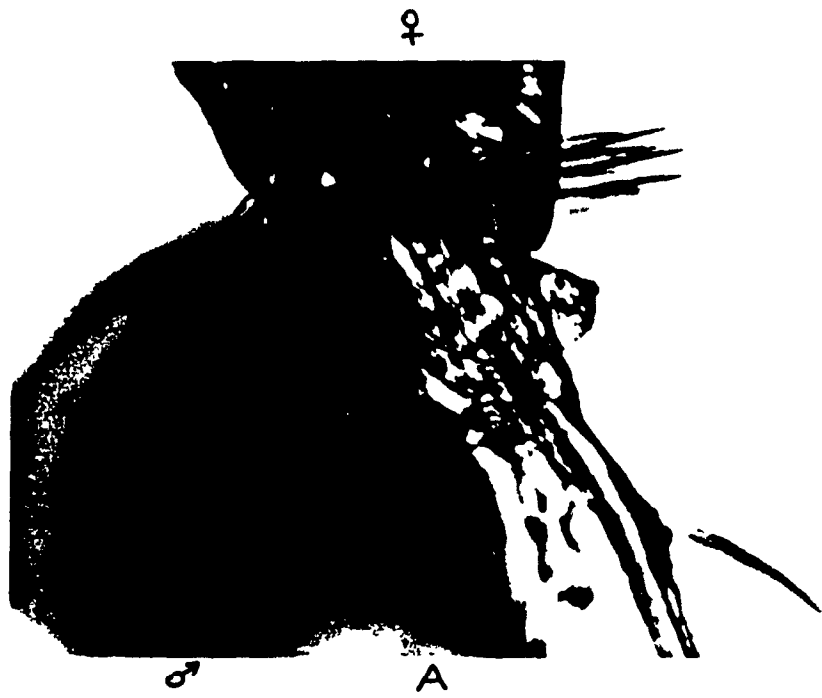


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♂

B

Figure 8. Photograph (A) shows a mating pair of D. leptopus. Drawing (B) shows female morphology from the metasomal wings downward (Ward and Whipple 1959). A representation of the male's holding position, on the female's genital segment is indicated by the shaded in right fifth leg of the male.



female's genital segment at the level of the spines were the aspects of morphology which were most important in mating.

MATING AND MORPHOLOGY

Pearson's correlation coefficients were calculated, comparing genital spine width in females (E), as well as right fifth leg claw (F), large segment (G), and rest of leg length (H), and left fifth leg length in males (J), to metasomal length (Tables 8 and 9), (Fig. 4). Female genital segment width was highly correlated to metasomal length for both species. Male claw and large segment lengths were correlated to metasomal lengths for D. birgei but not D. leptopus.

Table 8. Pearson correlations comparing metasomal length to different genital parts of D. birgei.
Sample size is 50 for all comparisons.

Metasomal length vs.	r	² r	p*
Females			
Spine width			
St. Joachim	0.596	0.356	0.001
Nun's Island	0.498	0.248	0.001
Males			
Claw length			
St. Joachim	0.475	0.225	0.001
Nun's Island	0.669	0.448	0.001
Large segment length			
St. Joachim	0.300	0.090	0.05
Nun's Island	0.517	0.267	0.001
Rest of right leg			
St. Joachim	0.221	0.049	NS
Nun's Island	0.269	0.072	NS
Left leg length			
St. Joachim	0.293	0.086	0.05
Nun's Island	0.245	0.060	NS

* rcrit (0.05) = 0.276, rcrit (0.001) = 0.447

Table 9. Pearson correlations comparing metasomal lengths to different genital parts of D. leptopus. Sample size is 50 for all comparisons.

Metasomal length vs.	r	² r	P*
Females			
Spine width			
Hill	0.925	0.855	0.001
Quarry	0.759	0.576	0.001
Males			
Claw length			
Hill	0.170	0.029	NS
Quarry	0.313	0.098	0.05
Large segment length			
Hill	0.058	0.003	NS
Quarry	0.173	0.030	NS
Rest of right leg			
Hill	0.094	0.009	NS
Quarry	0.078	0.006	NS
Left leg length			
Hill	0.200	0.040	NS
Quarry	0.146	0.021	NS

* rcrit (0.05) = 0.276, rcrit (0.001) = 0.447

DISCUSSION

SEASONAL AND SITE DIFFERENCES

The increase in size of D. birgei over the winter months (Table 1) was expected. Hart and McLaren (1978) found an increase in body length and egg size of copepods during the cold season as well as a decrease in development rate. Though length of both sexes significantly changed with season, the average sex size ratio did not change significantly over the sampling period. Enough data was not obtained to determine whether sex size ratios differed between St. Joachim and Nun's Island ponds. It should be noted that DeFrenza et al (1986) report the ratios to be the same at both sites.

Seasonal changes in length also occurred in D. leptopus. Male and female lengths as well as sex size ratios were not significantly different at Hill and Quarry at the beginning of the summer, but as the summer wore on and Quarry dried up, the copepods at Hill became significantly smaller (Tables 1 and 2). This decrease in size might have been due to a crowding effect in Hill pond or to the increase in temperature from 22° in June to 29° in early July. Density and temperature have both been found to be negatively correlated to body length in calanoids (O'Brien et al 1973, Klein Breteler and Gonzalez

1988). DeFrenza et al (1986) found that the sex size ratio at Quarry (sampled only once and being equal to 1.136) fell within the sex size ratio range found at Hill (sampled 12 times and being 1.115 - 1.179). In this study, the sex size ratios at the two sites differed by only 0.02 units and when the samples were separated by season, no differences in sex size ratios between the two sites were found.

MATING SUCCESS

Mating behaviour of copepods has been studied by many authors (Gauld 1957, Jacobs 1961, Sawchyn and Hammer 1968, Roff 1972, Katona 1975, Blades 1977, Corkett and McLaren 1978, Hart and McLaren 1978, Blades and Youngbluth in Kerfoot 1980, Watras and Haney 1980, Jacoby and Youngbluth 1983, Watras 1983a, Williamson and Butler 1987, Uchima and Murrano 1988, and Lonsdale et al 1988). The mating behaviour observed in this experiment was the same as described by those investigators. Mating would start with the male approaching the female caudally, in short quick swimming bursts while spiralling in order to properly align his antennules. When the male was close enough to the female, he would grasp her caudal ramii with his right geniculate antennule. This position was termed Precopula 1 by Watras (1983a), and was maintained for as long as 2:21 min. in D. birgei and 0:21 min. in D. leptopus. Normally,

Precopula 1 would only last for an instant. The male would then swivel around and grasp the female's genital segment with his long right fifth leg. At this point the animals are back to back in a position termed Precopula 2 by Watras (1983a) (Figs. 7 and 8). The male would then place an extruded spermatophore on the genital pore of the female using his shorter left fifth leg. Once he had done this, he would release his grasp and swim away. Fertilization is internal and, since all the females used in the experiments were gravid, the female then released her eggs into a clutch sac. Diaptomid copepods can only produce one fertile clutch per mating (Watras and Haney 1980, Watras 1983a, Williamson and Butler 1987). This and the fact that all individuals were isolated before their use in mating experiments, ensured that the clutches produced in the experiments were due to the matings observed.

The data for mating success of D. birgei indicate that there is a range of sex size ratios over which mating in that species is most successful (Fig. 5). The G-tests showed that mating success is a function of sex size ratios. The range encompasses the predicted 'optima' of 1.216 for St. Joachim and 1.223 for Nun's Island as well as the average observed ratio of 1.199 found in both ponds (DeFrenza et al 1986). All of these ratios are within the range of average sex size ratios (1.157 to 1.238) reported by DeFrenza et al (1986) (Fig. 5). This suggests that mating success may be a selective force responsible for the

sexual size dimorphism observed in nature.

The data for D. leptopus mating success indicate that length is a less important factor (Fig. 6). Unlike D. birgei, D. leptopus showed no significant differences in mating success among sex size ratio classes. However, a significant negative correlation was found between percent mating success and sex size ratio class indicating that as the ratio decreases, mating success increases. Yet the data show no significant peak. The range of average sex size ratios reported by DeFrenza et al (1986) for D. leptopus was 1.115 to 1.179. It should be noted that this range does not include the sex size ratios at which mating is highest (Fig. 6). This suggests that mating is not an important selective force affecting size dimorphism in this species in the two ponds tested. Therefore, over the range of sex size ratios tested, the data for D. birgei and D. leptopus support the results of DeFrenza et al (1986) who demonstrated that size was an important determinant of mating success in D. birgei but not as important in D. leptopus.

Significant differences in mating success among summer male and winter female D. birgei lengths were also found (Table 5). These differences may be due to different reproductive strategies among the sexes during alternate seasons, which can not be readily accounted for at this time. Since no significant correlations were found for these data (Table 6), the possibility of alternate

reproductive strategies seems unlikely. The data in Tables 5 and 6 show that actual length does not influence relative reproductive success of individuals in D. leptopus.

Though a strong selective force acting on D. birgei sex size ratios seems to be mating ability, other selective forces may also affect the sex size ratio. Intraspecific competition for limiting food resources may be one of the selective forces acting on male and female size distributions to yield a large sexual dimorphism (Bayly 1978). In this case, however, we would expect to find a sex size ratio larger than that observed since D. birgei can mate nearly as successfully at a ratio of 1.244 as at the ratio found in nature (1.22).

D. birgei is most often found in relatively large lakes and ponds containing fish (Carter et al 1980, Smith and Fernando 1978, this study). There may be predation in the St. Joachim pond due to the large population of creek chubs inhabiting it. In their early stages of life, these fish are known to be visual predators and to prey on plankton (Scott and Crossman 1973). The only other possible planktonic food source are small species of cyclopoid copepods which are never found in abundance, making it logical to assume that D. birgei is preyed upon. It is also expected that there is predation at Nun's Island due to the large number of fish species inhabiting the pond. According to theory, the sex size ratio would then be expected to be close to unity, or in this case, closer

to the lower end of the mating success range, such as 1.13. Since I did not find this, I do not believe that predation has been affecting the sex size ratio appreciably.

A factor which may be causing the size dimorphism is selection for the largest possible females relative to the males. Maly (1983) found a significant positive correlation between clutch size and female cephalothorax lengths for Diaptomus birgei, indicating that the larger females would have the higher reproductive potential; many others report a similar relationship between length and clutch in other species (Smyly 1968, Maly 1973, Corkett and McLaren 1978, Hofmann 1979). I can again argue, that if female reproductive success was a strong selective force, we would expect to see greater size dimorphism than is observed. Since the observed dimorphism is at the upper end of the mating success range, this type of sexual selection can not be dismissed.

In order to hypothesize as to why D. leptopus mating success is not an important function of sex size ratio, we must first know more about the ecology of this species. D. leptopus is mostly found in shallow, possibly temporary ponds which usually contain no planktivorous fish (Cole 1961, Hazelwood and Parker 1961, Sawchyn and Hammer 1968, O'Brien et al 1973, Carter et al 1980, Watras and Haney 1980, Watras 1983b). The same is true of 11 D. leptopus ponds sampled in our region. Sawchyn and Hammer (1968) found that there were overlapping generations of D.

leptopus in a pond that they studied. In examining plankton samples from a few D. leptopus ponds in our area, it was often observed that adult sizes could vary greatly within a sex as opposed to between the sexes. This led us to believe that copepods of very different sizes came from two distinct generations which were overlapping. Since D. leptopus from the two ponds sampled in this study must mate quickly before their habitat expires, it would be advantageous for small males to be able to mate with females twice their size from another generation as opposed to females only 1.14 times their size from their own generation. The need to copulate quickly may have been enough of a driving force to ensure that size was not very important in mating.

The selective force which may act on the sex size ratio, keeping it rather close to unity, is predation. Chaoborus americanus is a predator found in both Hill and Quarry ponds, the fourth instar of which preys on D. leptopus adults (Melville and Maly 1981). Predation pressure exerted by these instars may be strong enough to keep sexual size dimorphism lower than that found in D. birgei. Selection for the largest possible females relative to the males, as well as intraspecific competition for limiting food resources would both yield high degrees of sexual dimorphism. Since the dimorphism observed in D. leptopus is higher than would be expected if mating success was the only selective force acting upon it, the two latter

forces may be affecting size in this species.

From Tables 3 and 4, one can determine the average mating success of both species. Out of 159 matings viewed for D. birgei, 84 were successful, yielding a success rate of 52.83%. On the other hand, out of 140 matings viewed for D. leptopus, only 26 fertile clutches were produced. This yields a success rate of 18.57%. Attempted matings were not included in these calculations. Watras (in Watras and Haney 1980) found the success rate of copulation for D. leptopus to be 20%. The question of why D. birgei might have a mating success rate more than twice that of D. leptopus will be addressed below.

Time to mating was not highly correlated to either sex size ratios or male and female sizes for either species (Table 7). Though significant correlations were found between D. leptopus sex size ratio and female size at Hill, the coefficients of determination were less than 0.10 in both cases ($r^2 = 0.0384$ and 0.0713 , respectively). It was therefore decided that these correlations did not have any biological significance. Due to the small volume of the container, I believe that the male was aware of the female before copulation was attempted since the pair would occasionally bump into each other. After watching these copepods for many hours, it would seem that a factor which influenced time to mating was both male and female readiness to mate. It should be noted that the copepod density in the mating chambers (cuvets) is equivalent to

1.3×10^6 individuals m^{-3} . Though this density is unnaturally high, I do not believe that any behavioural artefacts concerning actual copulatory behaviour would result. Blades (1977) stated that the basic copulation movements of Centropages typicus appeared to be identical in both a large holding container and a deep-well depression slide.

It was thought that time to mating may have been an important variable for several reasons. Firstly, if females produce pheromones (Katona 1973), then large females may produce more pheromones than smaller ones. It would then be expected that a male would sense the presence of a large female more rapidly than he would a small female and that mating would occur more rapidly. Secondly, since copepods are most sensitive to water disturbances ahead of them (Gill and Crisp 1985) and if larger males produce greater disturbances as they swim than smaller males, a female may be able to detect them approaching her and escape their grasp. Mating experience might play a role in how quickly and from what direction a male approaches and is able to grasp a female. Thirdly, if copepod mating is size assortative, as stated by Hart and McLaren (1978), then males might be able to judge the presence of a 'right-sized' mate by the disturbances she produces while swimming and copulate quicker than they would if they judged the female to be 'wrong-sized'.

It is important to note that significant correlations

might have been found if time to first attempt had been recorded instead of time to mating. Many males had to approach females more than once before being able to attain the Precopula 1 position. Unfortunately, time to first attempt was never noted.

The stepwise regression analysis was done comparing duration of copulation to logarithmically transformed sex size ratios because I was not sure what type of relationship these two variables would have. In actuality, due to the great amount of variance in duration times (Table 1), no relationships existed between the variables for either species. When Pearson correlations were calculated comparing duration of copulation with sex size ratios as well as male and female lengths, two significant positive correlations were found (Table 7). The first correlation with D. birgei sex size ratio is not biologically significant. The second correlation with D. birgei summer female length has an r^2 of 0.106. Since no correlation was found for female length in the winter samples, the summer correlation may be due to the small sample size.

It was thought that duration of copulation might be related to sex size ratios, especially in D. birgei where size was important in mating. This relationship was not found. Photographs of mating D. birgei and D. leptopus pairs show that over a large sex size ratio range, all males hold onto the spines of the female's genital segment

with their right fifth legs. The smaller left fifth leg is used to place the spermatophore onto the female's genital pore. Therefore, it was thought that at a large sex size ratio, a small male may require more time to place the spermatophore properly - his success would depend on his reach. On the other hand, at a small sex size ratio, a large male should be able to place the spermatophore in the correct area rather quickly because the left fifth leg can articulate, giving him maneuverability.

PHOTOGRAPHY AND MORPHOLOGY

It was interesting to discover that both D. birgei and D. leptopus males always held onto the female genital segments at the level of the spines. This suggests that the spines on females are important aspects of their morphology. The fact that the males' fifth pair of legs were important in mating was already well established by the many researchers mentioned previously (page 54). The importance of the males' right geniculate antennule was ruled out, not in terms of mating but just in terms of size because males were almost always able to attain Precopula 1 and 2, no matter what the sex size ratio was.

The correlations between morphology and metasomal lengths (Tables 8 and 9) showed that female genital spine widths for both species and male right fifth leg claw lengths for D. birgei had the strongest relationships with

body length. It was expected that spine width would be highly correlated in both species from observations of photographs taken. If males always hold onto female spines during copulation, then selection would be expected to play a role in maintaining that morphology. Male right fifth leg claws are important characteristics in identification of different species and the ability of a male to hold onto a female is directly related to the length of his right fifth leg, including the claw. It was therefore also expected that claw length and body length be strongly correlated for D. birgei since mating success was a function of sex size ratios in that species. The fact that claw lengths were not correlated to body size in D. leptopus may be due to the fact that sex size ratios played little part in mating success.

A possible explanation of why D. birgei's rate of mating success is more than twice that of D. leptopus can now be given. We must first consider the average copulation duration times of these two species: 7.78 and 2.28 min, respectively (Table 1). It is possible that the difference in duration times is related to morphological differences between the species. Perhaps D. birgei males can hold onto females for longer periods of time because those females have very large spines (Fig. 4) and the males can get a good grip. D. leptopus males may not be able to hold onto females for as long because those females have tiny spines and the males' hold is not strong enough for

him to resist slipping. It should be noted that due to the shape of D. birgei males' claws, their right fifth legs can wrap around almost 100% of the females' genital segments and closely follow their contours. This is not true of D. leptopus males (refer to photographs in Figs. 7 and 8). It is therefore proposed that the better grip D. birgei males can get on females may enable them to attain higher reproductive success.

It should be noted that duration of copulation may be related to mating success. Jacoby and Youngbluth (1983) found that in three species of Pseudodiaptomids, the species with the longest copulation duration time (76.8 min.) also had the highest mating success rate (88%). On the other hand, the species with the lowest duration (32.9 min.) had the lowest success rate (18%) and the intermediate species (duration 44.7 min.) had an intermediate success rate (54%).

It is also possible that morphology plays a part in mate recognition. In preliminary mating experiments done in 1984 by members of our lab, D. birgei was found to make the fewest mating mistakes. Four species (D. minutus, D. oregonensis, D. birgei, and D. leptopus) were used. All the possible pairwise comparisons of males and females were made and the number of spermatophores placed per pair per day were calculated. D. birgei males were found to place the smallest number of spermatophores on females of the other three species. A possible reason for this could be

that D. birgei males did not recognize females of the other species as being mature, once in the Pécopula 2 position since none of them have large spines on their genital segments.

Why do D. birgei and D. leptopus have species specific morphology and mating success rates? Many factors other than those discussed above may have affected copulation success and may have shaped the reproductive strategies of the two species. One of these factors is predation. It is possible that if predation pressure on a species is strong, mating duration, and consequently mating success, would decrease since a mating pair is a more obvious target than a single copepod. As mentioned before, both D. birgei and D. leptopus are preyed upon, both in the habitats sampled in this study as well as others. It is possible that predation pressure on D. leptopus by the invertebrate Chaoborus is greater than the pressure exerted on D. birgei by planktivorous fish. It is not known if D. leptopus is selectively preyed upon in its habitat. If predation on D. leptopus is greater than on D. birgei, then the lower mating success of D. leptopus may be attributable to predation pressure. It is also possible that predation on D. leptopus was greater in the past (evolutionarily speaking) due to its large size and that its reproductive strategies were shaped long ago.

Other factors such as copepod longevity, in terms of number of clutches produced in a lifetime, the amount of

time a female remains in the gravid condition, and density (individuals per liter) may also play a part in the reproductive strategies of a species. For instance the longer a female lives, the more clutches she can produce. The size of the clutches depends on such variables as female length, food availability, and temperature (Hazelwood and Parker 1961, Roff 1972, Armitage et al 1973, Maly 1973, O'Brien et al 1973, Corkett and McLaren 1978, Hart and McLaren 1978, Maly 1983, Williamson and Butler 1987). In samples collected over the past summer, the average clutch size of D. leptopus at Hill and Quarry was 30 eggs, while that of D. birgei at Nun's Island was 18 eggs. A D. leptopus male would only have to inseminate half as many females as a D. birgei male for equal fitness, all other things being equal. The longevity, in terms of time, is stated as 11 weeks for D. leptopus (O'Brien et al 1973) and 15 weeks for D. birgei (Walton 1985). Therefore, a D. leptopus male with half the mating success of a D. birgei male, in terms of fertile clutches sired, should be able to produce roughly as many offspring. Unfortunately, it is very difficult to verify the importance of longevity since it can vary greatly in different habitats and seasonal conditions.

What may be a more important factor is the frequency at which a female can be found in the gravid condition. Watras (1983b) found that D. leptopus females were gravid 75% of the time. By grouping data collected over the

summer for both D. birgei and D. leptopus, I found that 20.5%, and 37.6% of all females sampled were gravid, respectively. It was also much more common to find clutched and gravid females in the D. leptopus samples. That condition was all but non-existent in the D. birgei samples. Since D. leptopus females would more readily be in the condition to mate than D. birgei females, males of D. leptopus would not suffer in their reproductive potential as much as D. birgei males if they mated unsuccessfully with any given female. A D. leptopus male who can more easily find a gravid female to mate with, may not need to have a high mating success rate. On the other hand, D. birgei males would lose greater reproductive potential if their mating success was as low as that of D. leptopus because gravid females are not as common. It could be argued that D. leptopus females are found gravid more often because D. leptopus males have a low mating success. When comparing summer samples, 9.8% of all D. leptopus females were clutched, as compared to 20.5% of all D. birgei females. A possible explanation for the difference in numbers may be that D. leptopus females drop their clutches more often and sooner than D. birgei females, again suggesting that predation pressure may have molded reproductive strategy since a clutched female is very conspicuous. Of the 26% D. birgei females which dropped their clutches, 18.5% dropped them when handled with a pipette. Of the 39.6% D. leptopus females which

dropped clutches, 28.3% dropped them when handled (unpublished summer data). So the relative scarcity of clutched D. leptopus females in preserved samples may be due to their dropping the eggs in a frenzy to avoid the formaldehyde used to kill them.

The same arguments as those used for amount of time spent gravid, can be used in reference to copepod density in a given body of water. If the density of individuals in a lake is low, then so are the chances of a male finding a reproductively available female. The density of D. leptopus in the shallow temporary ponds in which it is found could be much higher than that of D. birgei in deeper ponds and lakes. Actual densities were never taken over the sampling period. Low mating success of D. leptopus males would not hinder them in terms of reproductive potential since they would be able to easily find another mate. This may not always be the case for D. birgei in larger bodies of water.

A factor not yet addressed is competition for food. In theory, such competition would select for greater dimorphism between the sexes. It is possible that sexual size dimorphism in both D. birgei and D. leptopus has been shaped by such competition, yet no data are available on the food sources and their quantities in the ponds sampled. It should be noted that food has to be a limiting resource for competition to take place. There is little data in support of competition for food in copepods. Chow-Fraser

(pers. comm.) studied the gut contents of two species, D. minutus and D. oregonensis, which are two of the species most often found to co-occur (Rigler and Langford 1967). Size displacement was found to occur in these species in a few ponds in our region. There was a greater difference in size between them in sympatry than there was between them in allopatry: D. minutus was smaller and D. oregonensis was larger in sympatry. Though when the gut contents of sympatric and allopatric individuals were examined, no differences in diet could be found (Chow-Fraser unpublished data). Thus the difference in size of the sympatric populations was evidently not due to resource partitioning.

It is important to realize that, ecologically speaking, all the above factors probably played a role in the formation of the mating success and reproductive strategies of D. birgei and D. leptopus. All factors should be considered before trying to isolate any one as a major driving force for the behaviours and observations which we make.

CONCLUSIONS

D. birgei and D. leptopus were found to have quite different reproductive strategies, to which their morphologies were related. The possible selective forces which may have led to the formation of these strategies were discussed. Mating success and duration of copulation, two important aspects of reproduction, were found to be related - as duration increased, so did the success rate of the species. All the factors discussed which may have selected for the species specific strategies were hypothesized to be inversely related to mating success and duration (Table 10). As the data in Table 10 show, the only variable which does not seem to fit the data given for D. birgei and D. leptopus is longevity. As was discussed earlier, since longevity varies greatly with habitat, it was not thought to play a large role in selection. Also, the data stated here came only from one source for each of the species.

In order to discover whether or not the relationships between the variables given in Table 10 are true, similar data would have to be gathered on many more species. If those species also show the same direct relationship between mating success and duration of copulation, and similar inverse relationships between mating success and such things as habitat, predation, and amount of time females are gravid, then we could predict the reproductive strategies of a species if enough is known about it.

Table 10. Summary of life history tactics and their relationships with mating success for both species.

Variable	Mating Success*	<u>D. b.</u>	<u>D. l.</u>
Sex size ratio		1.22	1.15
Mating success		52.83%	18.57%
Importance of length in mating		No	No
Importance of sex size ratio in mating		Yes	No
Female spines		Large	Small
Duration of copul.	↑ ↑	7.78 min	2.28 min
% time gravid	↑ ↓	~20.5%	~37.6%
Clutch size	↑ ↓	~18 eggs	~30 eggs
Habitat size	↑ ↓	Large	Small
Predation	↑ ↓	Fish	<u>Chaoborus</u>
Longevity	↑ ↓	~15 weeks	~11 weeks

*Arrows show relationship between variable and mating success.

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