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Pre-copulatory guarding and the evolution of sexual size dimorphism in asellus aquaticus L

Pollitt, R.A.P

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PRE-COPULATORY GUARDING AND THE EVOLUTION OF

SEXUAL SIZE DIMORPHISM IN ASELLUS AQUATICUS L.

R.A.P. POLLITT

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ABSTRACT

Sexual selection and assortative mating are examined in two field populations of the fresh-water isopod Asellus aquaticus. The ability of males to carry the female in the pre-copula pair under adverse conditions was investigated experimentally, this ability was related to the weight of the female in the pair. The implications of female size as a loading constraint on males, the evolution of sexual size dimorphism and the significance of assortative mating are discussed.

ACKNOWLEDGMENTS

CHAPTER 1: INTRODUCTION

1.1   Sexual Size Dimorphism

Sexual dimorphism is a common phenomenon in the natural world; in anisogamous species the definition of sex is based upon which of two types of gamete is produced (Parker, Baker and Smith, 1972). Accompanying the production of these different but complementary gametes will be the physiology and anatomy of gamete formation, structures essential to their successful propagation and the development of the subsequent zygotes. The principle effect that this dimorphism should have on the size of the sexes was noted by Darwin in his theory of sexual selection (Darwin, 1871), and later by others e.g. Ghiselin 1974. Since females usually invest more in reproductive output they should evolve to be larger than males. This being the case then additional hypotheses are required to account for the evolution of increased male size. Traditionally the selective pressure presented to account for the dimorphism is male-male competition for females. Little attention is given to the influence that the size of females may have on the size of males.

Amongst the mammals and birds the male is usually the larger sex, and studies generally relate this to the degree of male-male competition or polygyny (Clutton-Brock, Harvey and Rudder, 1977). Outside these groups male-male competition exists but the most frequent form of sexual size dimorphism has females as the larger sex.

When the investment in reproduction, following fertilization, is greater for one sex than the other there exists a bias in the operational sex ratio such that the sex investing less is available for pairing at a

greater frequency than the sex with the higher investment. Females usually invest more in reproduction than do males (parental care by males can raise the male investment e.g. Fish, some Anurans). Pre- or post copulatory guarding of females by males might arise as a result of the male competition amongst males (Parker 1970(b)).

Sexual size dimorphism is present in many guarding species but the pattern is not consistent with increased male size due to male-male competition. So in some species there is high male-male competition precopulatory guarding but the female, which carries the male in the guarding phase, is the larger sex, i.e. Bufo bufo (Davies and Halliday 1977), Locusta migratoria (Parker, Hayhurst and Bradley 1974, Uvarov 1966) and Sepsis cynipsea (Parker 1972). In other species the male supports the female during guarding and is the larger sex i.e. Gammarus pulex (Birkhead and Clarkson, 1981 , Adams and Greenwood, 1983) Asellus aquaticus (Ridley and Thompson 1979 and Manning 1975), and Thermosphaeroma thermophilum (Schuster 1979). The dungfly, Scatophaga stercoraria, performs post copulatory guarding, the male, which may carry the female in flight, is the larger sex (Parker, 1970(a), Borgia, 1981).

Adams and Greenwood (1983) investigated pairing in Gammarus pulex, and they proposed a hypothesis with general implications for other species where the male and female are attached before, during or after copulation. They argued that female size will influence the size of males not through sexual selection but through natural selection operating on ecological factors associated with survival of the pair. Solely in terms of size related fecundity males should choose the largest female but if a male increases the probability of survival and fertilization by selecting a female smaller than itself, then males

following that pattern will be selected for. Female size will be selected for gamete production whilst male size will be selected for carrying, or being carried by, females.

Yonow (1983) worked on the potential loading constraint that male Asellus aquaticus bear when guarding females, she found that the weight ratio influenced the mobility of males in pairs.

This study aimed to develop the ideas of the earlier work and to examine the effect of different female sizes on the mobility of paired males.

1.2.1   A brief life history of Asellus aquaticus (Crustacea:Isopoda)

Asellus aquaticus is a freshwater isopod widely distributed through northern temperate Europe (Williams 1962). It inhabits ponds and slow moving streams living on the substrate amongst the detritus which harbour the bacteria upon which they feed.

Viviparous young are produced in broods following two peaks of breeding around April and September; Asellus aquaticus unlike the closely related A. Meridianus does not have a complete cessation of breeding during July and August (Steel 1961).

Offspring from the first broods of the year form the larger cohort of a bimodal population. They develop and reproduce in September, then they overwinter and breed again in the spring (Steel 1961). The smaller cohort develop more slowly over winter and reproduce later in the spring breeding phase. The size of breeding pairs drops as the season progresses (Ridley and Thompson, 1979).

Females rear a brood in the marsupium following fertilization.

After the release of the brood the females die (Steel,1961). Males

appear to be sexually active for longer than females though no

evidence was found in the literature for multiple mating by males.

Males die off sooner than females (Ridley and Thompson. 1979). The

latter remaining as brooding individuals for up to forty days.

1.2.2   Reproductive biology of Asellus aquaticus

Asellus undertake extensive precopulatory guarding (up to 11

days, Manning 1975). The male holds the female to its ventral surface

with the modified fourth pair of paraeopods (see Figure 1). During

this period both animals continue to feed and move (Unwin,1919). At

rest or in slow movement the female will have contact with the substrate

but when the pair move more quickly the female is held clear of the

substrate and the male is responsible for movement. After the

abdominal moult of the female, but before she completes the whole

moult the male inseminates her (Unwin,1919). Within 24 hrs of the

onset of the moulting phase the oostegites will enlarge and harden so

precluding fertilization. Female Asellus are unable to modify the

onset of the moult according to the presence or absence of a male

(Thompson and Manning, 1981). Fecundity, as assessed by egg number in the

brood, is proportional to female size (Steel, 1961).

1.3.1   Sex determination in Asellus broods

Steel (1961) quotes Seitz (1953) as recording that Asellus

aquaticus will sometimes produce monogenic broods. However, Steel

(1961) found that at the end of the first peak of breeding when young

are released the sex ratio when determinable is 1:1. A set of

experiments was established to determine whether females produced

monogenic broods (half the females producing males and the other half

producing females would give a 1:1 ratio), and to investigate whether
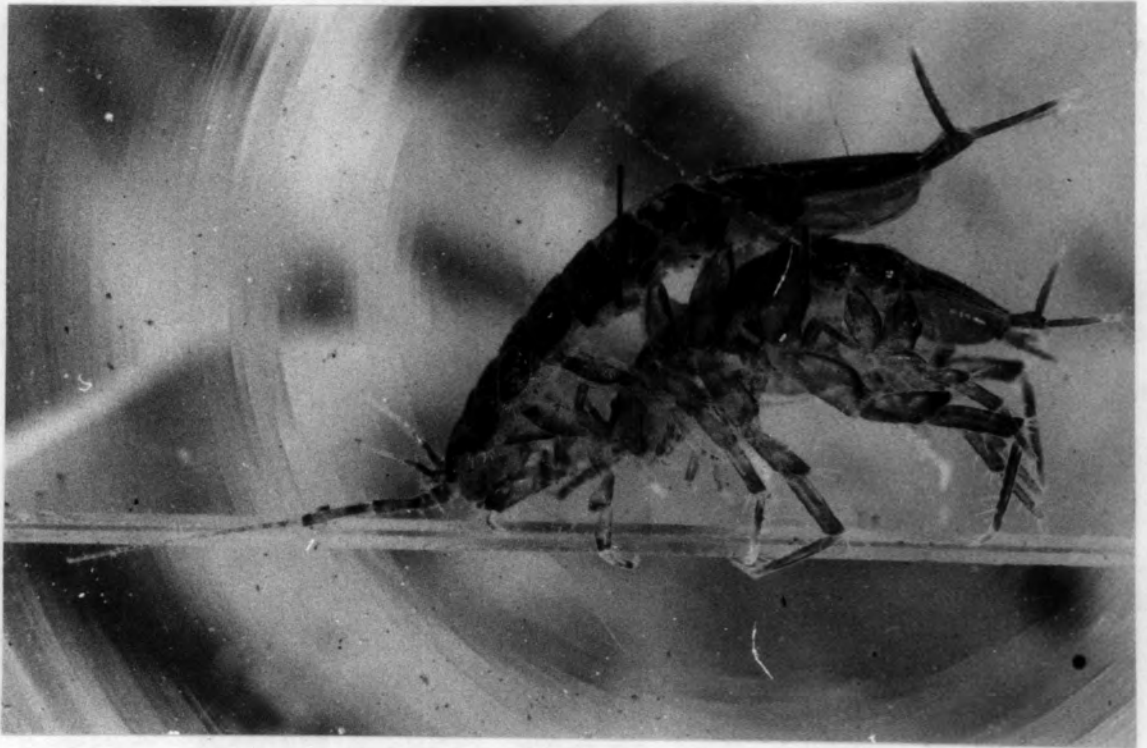
Figure 1: Pre-copula pairing in Asellus aquaticus.
The male, above the female, is resting on five pairs
of walking legs; nos. 1, 2, 5, 6& 7. The 4th pair
(marked with the arrow) holds the female, which but
for her 7th pair of legs is clear of the substrate.
The male in this picture weighs 16.1 mg (mean weight
of males in expts. 1&2 = 27.5 $\pm$ 11.7), the female
weighs 8.2 mg (mean weight of females in expts. 1&
2 = 11.8 $\pm$ 5.7), both live weights.

variables such as female weight or temperature affected the composition of the brood.

1.3.2 Mating frequency and male longevity

In terms of male mate choice on the basis of female size (fecundity) and proximity to oviposition, Manning (1980) and Thompson and Manning (1981) consider the time budget and the fertilizations per unit time to be important; not only should males maximise the reproductive output, they should maximise the rate. Knowledge of the mating frequency, do males mate more than once? and the effect if any upon longevity would be of importance in analysing mate choice decisions* by male Asellus.

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* Use of the word 'decision' is shorthand to denote a genetically determined propensity to respond in a predictable manner to a given situation - it does not assume any level of cognitive reasoning, just as 'choice' is a label for the selection of mates not a subjective consideration of qualities.

CHAPTER 2: METHODS

2.1 Sampling of Asellus

Asellus was collected from two locations, Brasside ponds in County Durham and Jesmond Dene, Newcastle-upon-Tyne.

Brasside ponds (grid ref.: NZ 2845) are a series of small elongate subsidence pools in meadow land over the site of a former brickworks; a fuller description of the site is given in Fitzpatrick (1968). A stream runs through the meadow but the ponds are isolated during the summer months. The ponds are approximately 0.5m in depth with a bed of leaf litter and rooted macrophytes. Asellus was collected from the pond edges amongst the emergent macrophytes (chiefly Typha latifolia and horsetails).

Jesmond Dene (grid ref.: NZ 2566) contains a small tributary of the River Tyne at Newcastle. Asellus was sampled from a stretch which lay between two waterfalls where the river was approximately 5m wide and 0.6m in depth. The bed of the river was unsuitable for net sampling and so Asellus was taken from the submerged vegetation (primarily the exposed roots of grasses and herbs) along the bank.

Samples were taken by working a hand net through the vegetation. At Brasside a standard two sweeps with a 1mm mesh pond net was used. At Jesmond Dene the procedure was slightly different, a standard action was employed but sampling continued until 25 pairs had been collected (all pairs were removed from each sweep). This procedure was used because 25 was, approximately, the greatest number of pairs which could be handled in the laboratory before the females began moulting. After the moult the female mates and the pairing phase ends.

Samples were hand sorted in the field and each pair was placed in a separate tube. Brasside samples were returned to the laboratory for further sorting to remove single animals. Individuals were kept together in tanks containing aerated pond water with leaf litter provided as food. Pairs were kept isolated from other pairs in small beakers with pond water and leaf litter.

.Early samples (Brasside 3/5, 16/5) were measured, to the nearest 0.5mm, from rostrum to telson. This technique was found to be unwieldy, requiring the animal to be sandwiched between two microscope slides. In addition, the range of lengths and accuracy of measurement restricted the degree to which the variation within the population could be described. Subsequent samples were weighed to the nearest 0.1mg using a microbalance. Live weight was recorded, animals being dried with tissue before weighing.

Individual animals from the Brasside samples were sexed using the description given in the F.B.A. key (Gledhill, Sutcliffe and Williams, 1976). For the sizes involved in the sample distinguishing the sexes on the basis of the pleopods was relatively easy. Brooding females could be identified as such by the presence of the yellow marsupium visible from below. Brasside samples were sorted for size, sex and reproductive status; paired, brooding or other. Jesmond Dene samples, all of which were paired, were sorted for size and sex.

Individuals from both sampling stations were chosen at random (1 per sample) to check that the species used throughout was <u>Asellus aquaticus</u> (Gledhill et. al. 1976). No other species of <u>Asellus</u> was found during the study.

2.2   Brood size and sex ratio of offspring

Brooding females from samples, dated 3/5 and 16/5, were measured and placed in separate, covered, beakers with pond water and leaf litter. Brooding females collected on 3/5 were kept at a constant 8°c (the water temperature in the field when they were collected was 9°c), those collected on the 16/5 were kept at 15°c (water temperature when collected was 12°c). Both sets of females were kept in 18 hrs light: 6 hrs dark.

2.3   Mating Frequency and male longevity in the laboratory

Single animals collected on 16/5 were held in an aerated tank, with food provided. After 7 days the pairs which had formed were removed then weighed and measured; these animals were assumed to be in breeding condition (or approaching it in the case of females).

To test the effect on male longevity of mating frequency males and females from the pairs were separated and placed into pots in the following combinations (male : female); 1:, 1:5, 5:1. Replicates were used. The pot size was varied to hold the basal area per Asellus constant ($40cm^{2}$ per animal). Leaf litter was added and the water depth in all the pots was kept at 1.5cm. Conditions were kept constant at 15°c, and 18 hrs light : 6 hrs dark. Progress was monitored 2-3 times a week.

In addition to the preliminary run described above a further experiment was carried out with a sample taken from Brasside ponds on the 20/5. The Asellus from pairs formed in the field were separated and rapidly measured. Those in the size ranges 9-11cm (male) and 5.5-7.5cm (female) were used in the second experiment; size is related to age in crustaceans and the aim was to limit the experiment to one age class. The ratios used were; single males, then (male; female) 1:1, 1:5 and 1:3. In the last set (1:3) brooding females were replaced by receptive females

(i.e. those in a pair with another male) from the laboratory stock. The experimental conditions were as described above. The pots were monitored regularly and deaths, pairings and brooding were recorded.

2.4 Male Mobility

For an experimental analysis of the loading factor which females represent to males field caught pairs were used. Pairs collected on the 30/5 were taken from Brasside ponds, all subsequent pairs were taken from Jesmond Dene.

The apparatus used for the two experiments described in 2.5 and 2.6 is illustrated in Figure 2. The channel was made of perspex and is identical to the one used by Yonow (1983), Adams and Greenwood (1983). The water in the channel was impelled by a paddle-wheel powered by a Gryphon type E electric motor set at its lowest gear. This generated a current speed of 5.4 ± 0.6 cms^{-1}, the current was monitored using a Kent mini-flow speed probe.

Along length 1 of the channel (see Figure 2) a centimetre scale 45cm in length was placed beneath the perspex stream bed so that run distances could be measured to the nearest 0.5cm. Above the scale, in the stream, was placed a strip of roughened perspex which formed the substrate, this allowed more purchase for males than did smooth perspex (Yonow 1983). Enclosing this run were two perspex walls (approximately 12cm high), these walls directed movement against the current and, in most cases, prevented males reversing their direction or making any lateral movement (lateral movement was undesirable because, a) it was not directed against the current, and b) it was not possible to measure but might interfere with the accurate timing). The channel formed was 1.5cm wide and 40cm long. The stream was filled with tap water to a depth of 10cm, aerated and allowed to dechlorinate for 3 hrs before the first run.

Figure 2: (i)
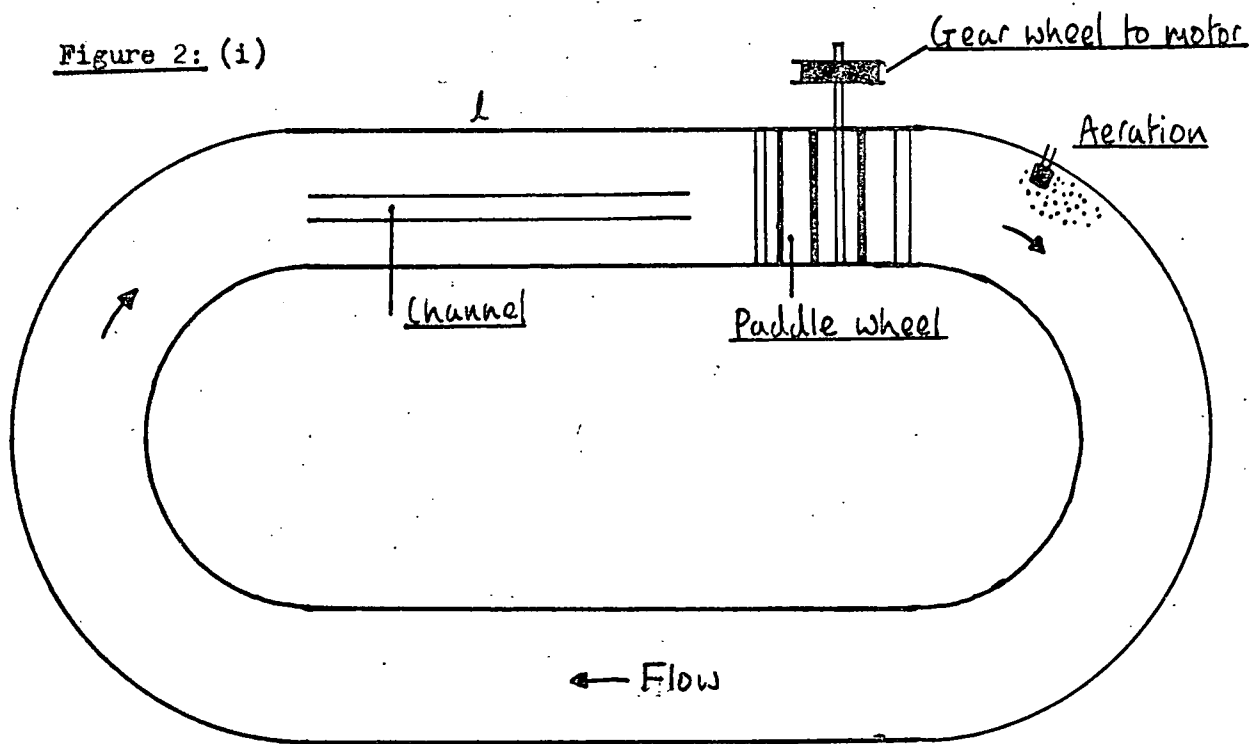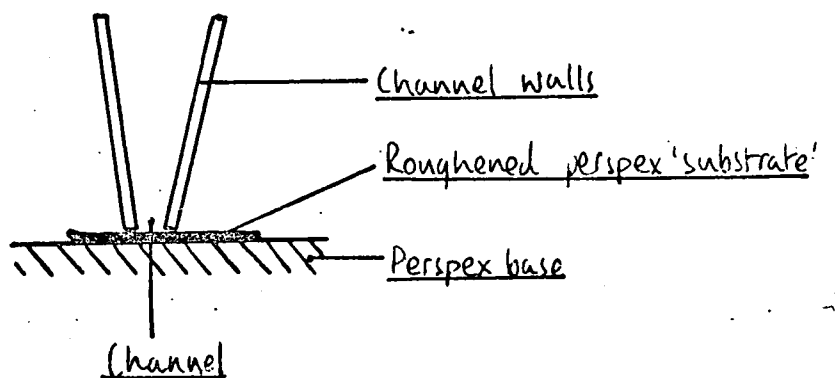

Figure 2: Diagramatic representation of the apparatus
used to test male mobility;

      (i) layout of the artificial stream with
         channel along length 1 (no scale),

      (ii) cross-section of the channel in
         which animals were placed.

Figure 2: (ii)

2.5   Experiment 1 (May 30 - June 13)

Field caught pairs were allowed to acclimate for 2 hours to laboratory conditions in labelled pots of dechlorinated water, laboratory temperature was 17°c.

The runs were conducted one pair at a time. Typically the pair would be introduced to the start of the run channel on a wet paint brush and , orientated so that the pair faced the direction of the current (rostrum first). When the pair appeared stable the motor which generated the water current was switched on, at the same time a clock was started which timed the duration of the whole procedure. The duration of runs was restricted to 5 minutes to reduce the potential effect of fatigue; the male was used for a further run (when separate) in the second part of Experiment 1.

To calculate the speed of a pair or that of a single male two records of movement were required; the total distance moved against the current, and the time spent moving against the current. The former was calculated from observation of the point of start and finish of the run, the latter was recorded by use of a hand held stop watch (timing to 0.1s) which timed the bouts of movement to give a cumulative total. No attempt was made to analyse discrete movements comprising a run, or the variety of sequences of movements between runs of different pairs. At the completion of a run, or when 5 minutes had elapsed, the motor was switched off and the pair were removed and returned to their labelled pot. When the first runs for a whole batch i.e. those pairs collected on one sampling trip, were completed the pairs were separated and both animals were weighed (live weight).

Using the technique described for pairs, males alone were put into the artificial stream and their performance was assessed under the same conditions of current and duration used for pairs.

2.6 Experiment 2 (June 22 - July 19)

In Experiment 2 field caught pairs were treated as in Experiment 1 to establish conditions of temperature and oxygen content in the water. The first run was performed with field formed pairs as described in 2.5. When the first runs were completed pairs were separated and weighed. After weighing, new pairs were formed for Part II of Experiment 2. Males were kept in their original labelled pots, females (from the pairs of Part I) were selected and placed with males according to the weight of the female the male was previously paired with. A random procedure for the selection of the female in Part II was not adopted because the numbers used in each batch were small (n = 8-20). Although repetitions of previous pairings might have given some insight into the repeatability it would have diminished the scope of the investigation. Instead an effort was made to provide a variety of size differences between the female in Part I and the female in Part II.

Most new pairs coupled readily, about 20% (14 out of 71) did not. New pairs were kept in dechlorinated tap water with leaf litter and left overnight. A second run was performed on the day following pairing, using all new pairs, in the manner used for field caught pairs (see 2.5).

CHAPTER 3: RESULTS

3.1   Sexual size dimorphism

Biometric data from the sampling period 3/5 - 19/7 are given in Tables 1-3, and Figures 3-6. Most of those data refer to a subgroup within the population which is males and females in breeding condition. This subgroup was considered the most relevant because the work in Experiments 1 and 2 was concerned with paired animals.

The first sample was taken from a population of <u>Asellus</u> at Brasside ponds. The results, which are presented in Figure 3, show that males are significantly larger (longer) than females (N=25, t = 6.822; p <0.001).

The distribution of sizes through the range (5mm - 11mm) appears normal for both sexes, though it is likely, on evidence from other surveys (Steel 1961, Fitzpatrick 1968), that between 5.0 and 5.5mm lies the minimum size retainable by the 1mm mesh of the net. These surveys report that the post-winter population is described by two size frequency curves which represent offspring from two breeding peaks; the early peak (late spring) forms the larger size curve recorded in this survey. The late peak (September) forms the smaller size curve and is not recorded in this survey. This bias toward one group is unlikely to affect the study because, as Figure 3 illustrates, breeding was restricted to the larger individuals of each sexual group. Non-breeding females showed a peak at around 6.0-6.5mm, breeding females (paired and brooding) peaked at 7.0-7.5mm. Breeding males were concentrated in the upper size range 8.0mm.

Weight was considered to be unsuitable for describing the size range of the first sample (see above) because brooding females would be likely to be slightly heavier than similarly proportioned non-brooding females which were not carrying developing offspring. Nevertheless weights were recorded

Table 1 : The mean weight (mg) of (i) males and (ii) females in samples; 3/5 and 26/5 - 19/7.

(i) MALES

CASE	DATE	N	MIN.	MAX.	MEAN	S.E.
Brasside	3/5	18	14.3	35.0	22.0	5.5
Expt. 1	26/5-13/6	73	13.0	77.7	30.3	13.5
Expt. 2	22/6-19/7	52	11.5	48.9	24.1	7.8

(ii) FEMALES

CASE	DATE	N	MIN.	MAX.	MEAN	S.E.
Brasside	3/5	18	7.6	28.2	13.1	5.6
Expt. 1	26/5-13/6	73	7.2	31.4	13.7	5.4
Expt. 2	22/5-19/7	52	4.4	32.5	9.3	5.4

Table 2 : The mean weight ratio of pairs from samples described in table 1.

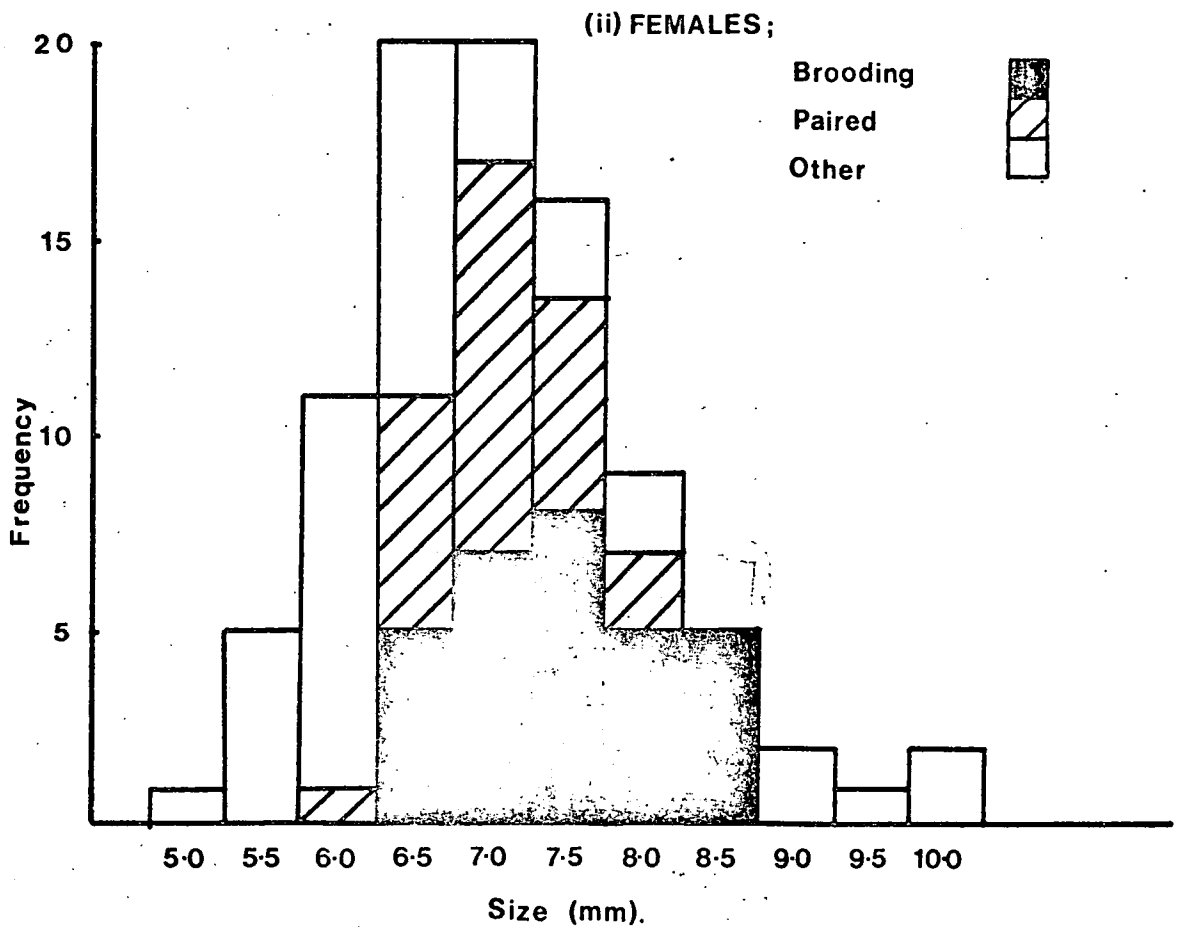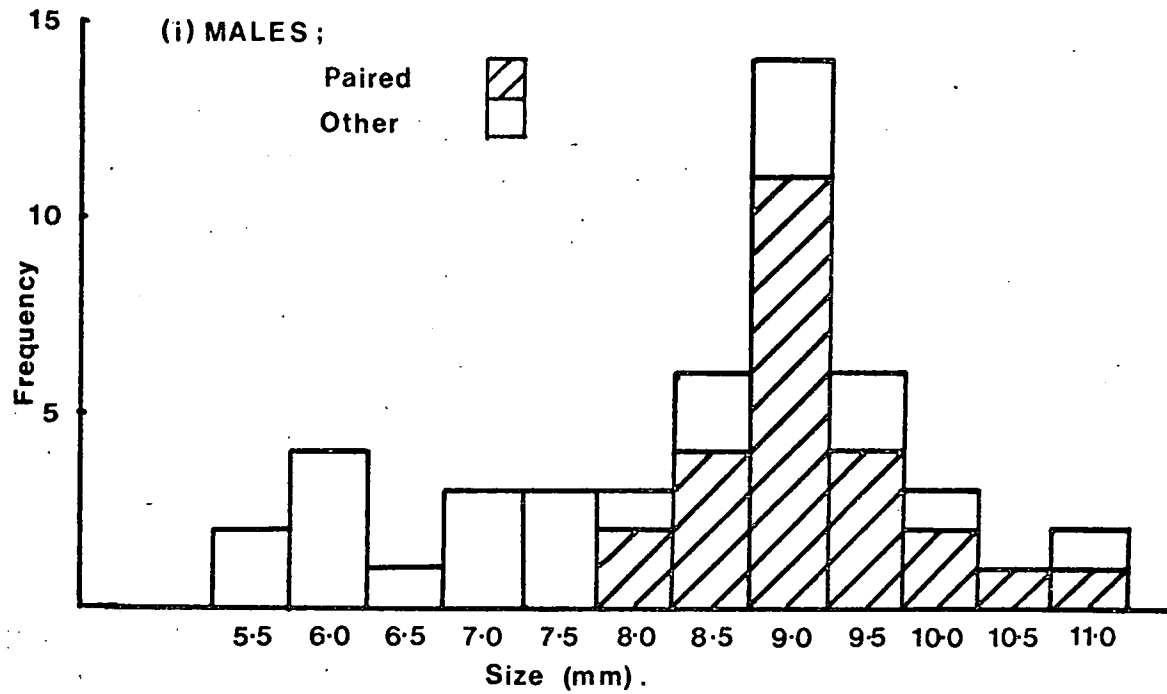| CASE	DATE	N	MIN.	MAX.	MEAN	S.E.
Brasside	3/5	18	1.03	2.98	1.80	0.44
Expt. 1	26/5-13/6	73	1.24	3.95	2.27	0.66
Expt. 2	22/6-19/7	52	1.01	7.19	2.95	2.60

Figure 3: Size (length) frequency distribution of Asellus,
from Brasside ponds , collected 3/5 ;

        (i) Males , paired and unpaired .

        (ii) Females , brooding ,paired and unpaired .

and, excluding brooding females, the weights correlated significantly with the corresponding length measurements (N = 57, r = 0.9682; p <0.001, Figure 4). Both males and females fell on the same curve but at different positions. Steel (1961) reports that below the weights found in this study the relationship between weight and length is non-linear.

Samples from the 16/5 onwards were weighed. These samples are summarised in Figure 5, where the degree of sexual size dimorphism in pairs is clearly shown (see Figure 6(i)). A pairwise t-test between male and female weight for each sample gave significant differences between the two sexes. Figure 6(ii) shows the average weights of the sexes for each sample in Experiments 1 and 2.

3.2   Assortative mating

With or without sexual size dimorphism assortative mating for size could occur wherever there was size variation in sexually mature animals of both sexes. Possible patterns of assortative mating are described in the introduction (Chapter 1). Statistically the degree of assortative mating (if a linear relationship operates) can be detected by a correlation coefficient between the weights of males and females in pairs.

An absolute difference between male and female weights would not be sufficient to indicate assortative mating. The previous section (3.1) made it clear that males are bigger than females so in random mating a size difference between the sexes with the male the larger partner would be the commonest type of pairing. Assortative mating could be exaggerated by the presence of sexual size dimorphism; in Asellus the size ranges of the sexes overlap but positive assortative mating for size will tend to preclude the generally smaller sex (females) being the larger member in a partnership.
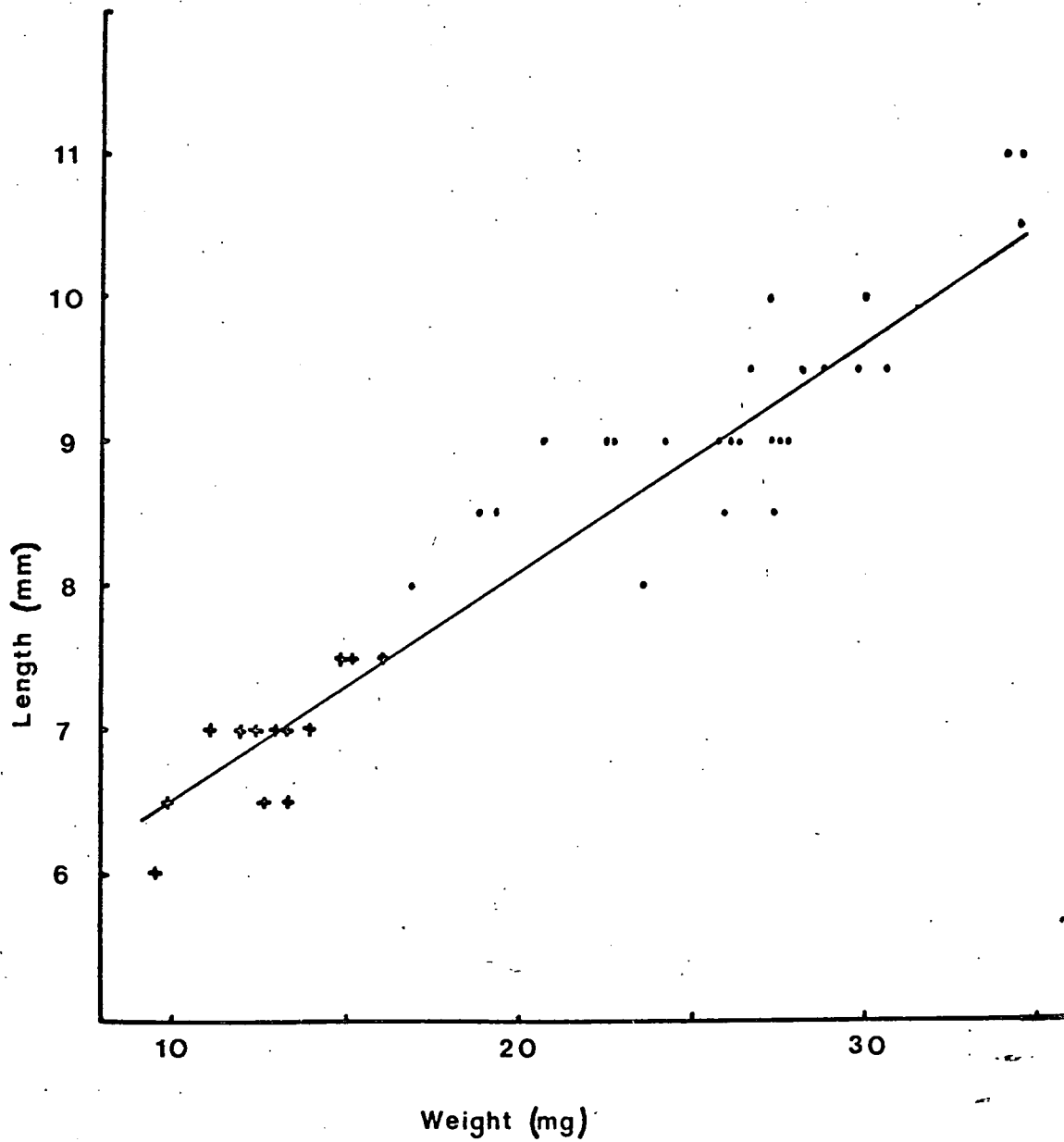
Figure 4: The relationship between length (mm)
and weight (mg) in _Asellus aquaticus_ collected
3/5; males (•) and females (+).
N = 39, r = 0.9682, P <0.001.
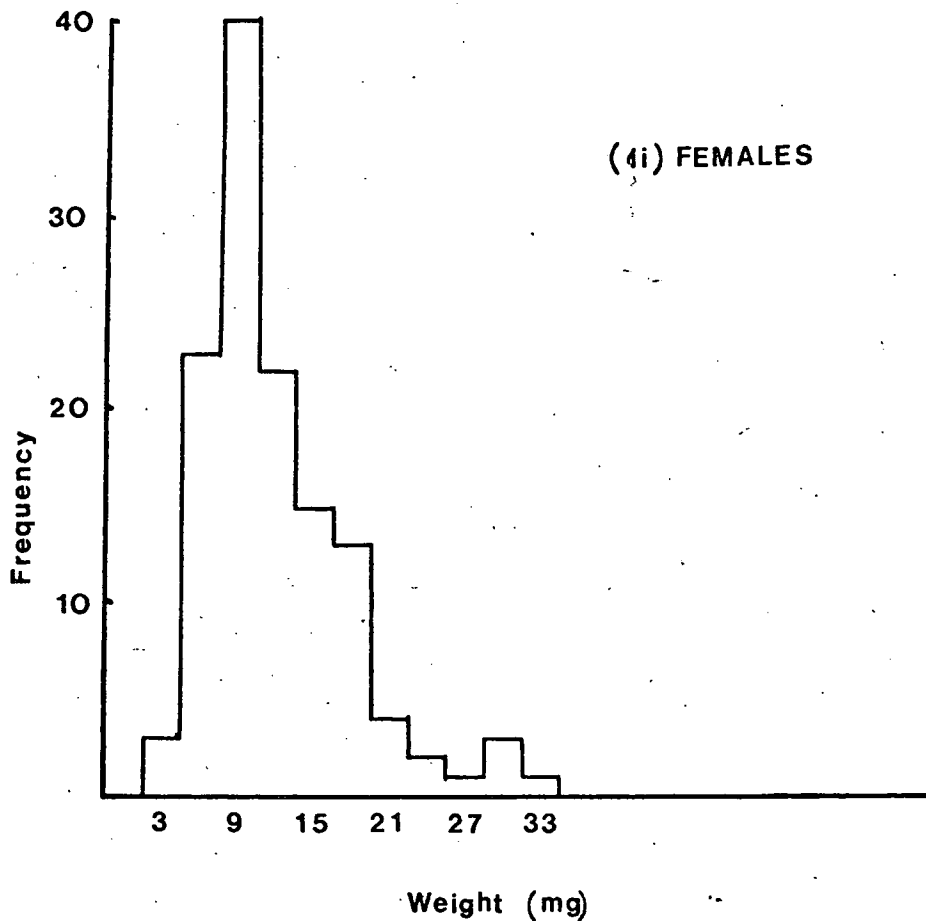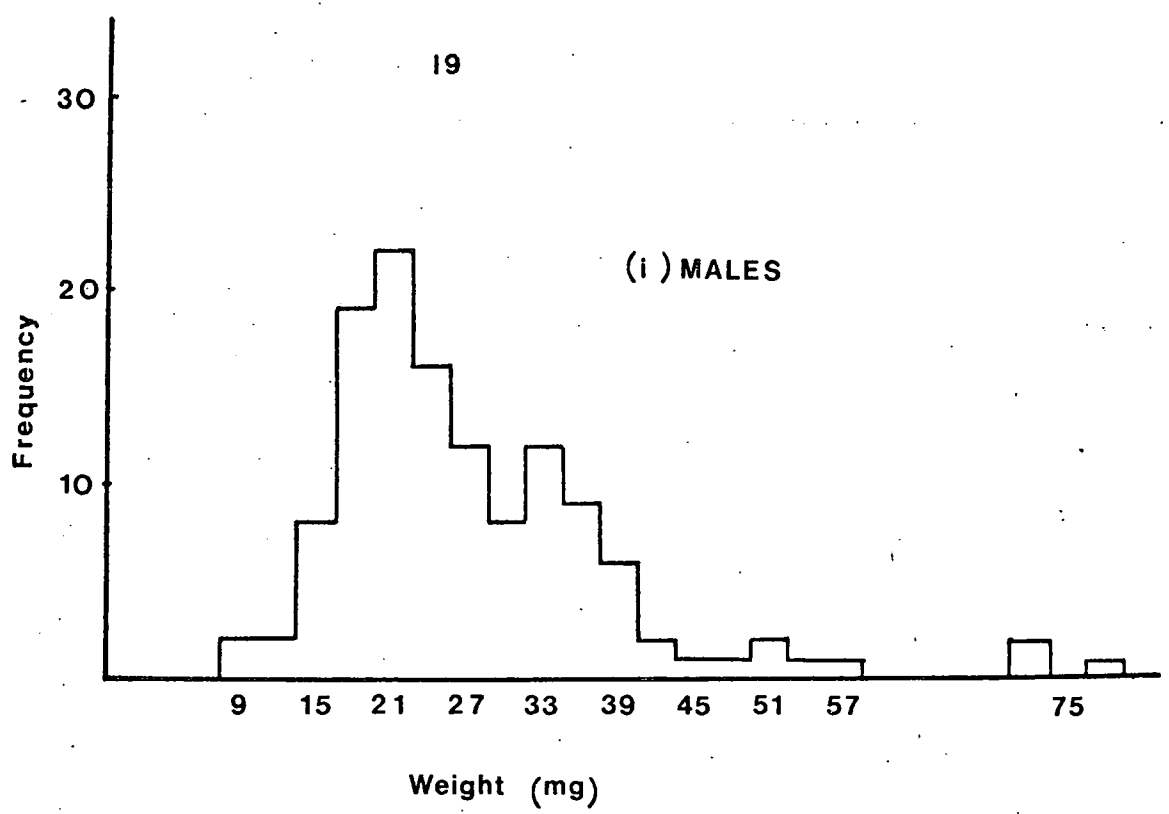
Figure 5: Size frequency distribution of Asellus
from Brasside ponds and Jesmond Dene collected
30/5 - 19/7; (i) males and (ii) females; all paired.
Analysis of sample means by paired 't' test;
N = 127, 't' = 19.135, P < 0.001.
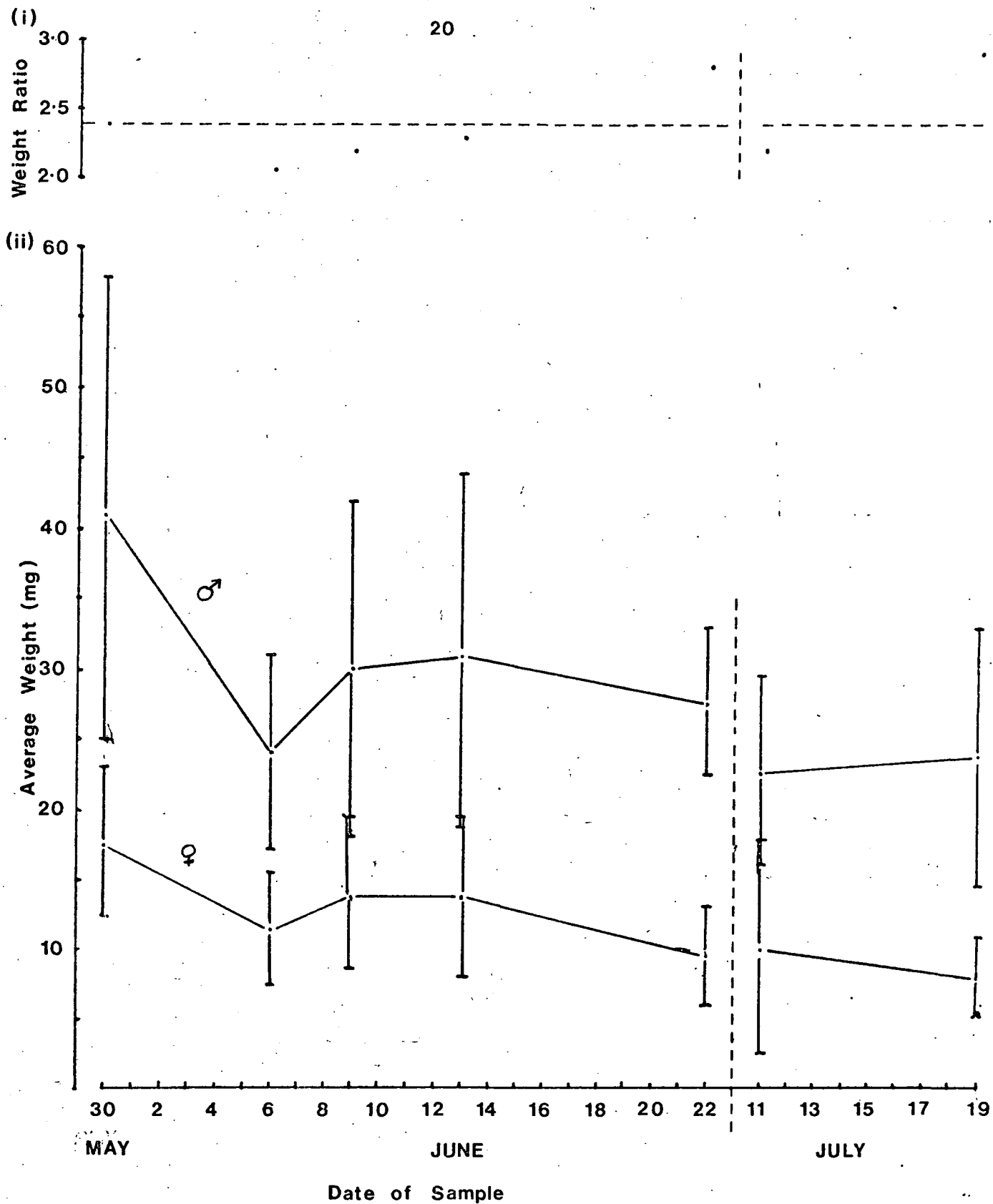
Figure 6: The sizes of male and female _Asellus_ in samples
collected for experiments I & II .

        (i) The mean weight ratios ,male : female , for each sample .

        (ii) The mean ($\pm$ 1 S.E.) weights of males (upper curve) and
            females (lower curve) for each sample .

In the first sample investigated (3/5) there was no significant correlation between male and female lengths. In this case the use of length classes rather than weight may have reduced the level of resolution i.e. seven classes of male size and five female size classes. The general trend of most subsequent samples was for positive assortative mating with respect to size. This relationship between the size of males and females in pairs has been observed by others (Ridley and Thompson 1979, Yonow 1983). Table 3 lists the correlation between sizes in pairs. Three out of ten of the samples mentioned in Table 3 do not show assortative mating, but they were all small samples ($11 < n < 24$). Grouping these small samples together as they were used in Experiments 1 and 2 shows that Asellus were mating assortatively; small males tended to be paired with small females, see Figure 7. Further inspection of Figure 7 suggests that the degree of assortative mating which, if calculated by the proximity to a perfect correlation of the male-female weight relationship, was not the same across the male weight range. Toward the lower range of male weights the cluster of points is close to the regression line (b in Figure 7), as male weight increases the variance in female weights with which they are paired increases. Large males mate less assortatively than do smaller males. In random mating the small males would be expected to pair, on occasion with females in the upper size range - this did not happen.

The weight ratio values are summarized in Table 2, the mean values show that in pairs males were 2 to 3 times heavier than the female (see also Figure 5(i)).

3.3   Male performance in relation to female weight

Observations prior to the experiments described in methods, 2.5 and 2.6, support the assertion made by Yonow (1983) that males contribute most

Table 3: Correlation between male weight and female weight
for each sample used in experiments 1 & 2, and one sample
of laboratory paired animals (not included in totals).

Correlated variables;male and female weights.

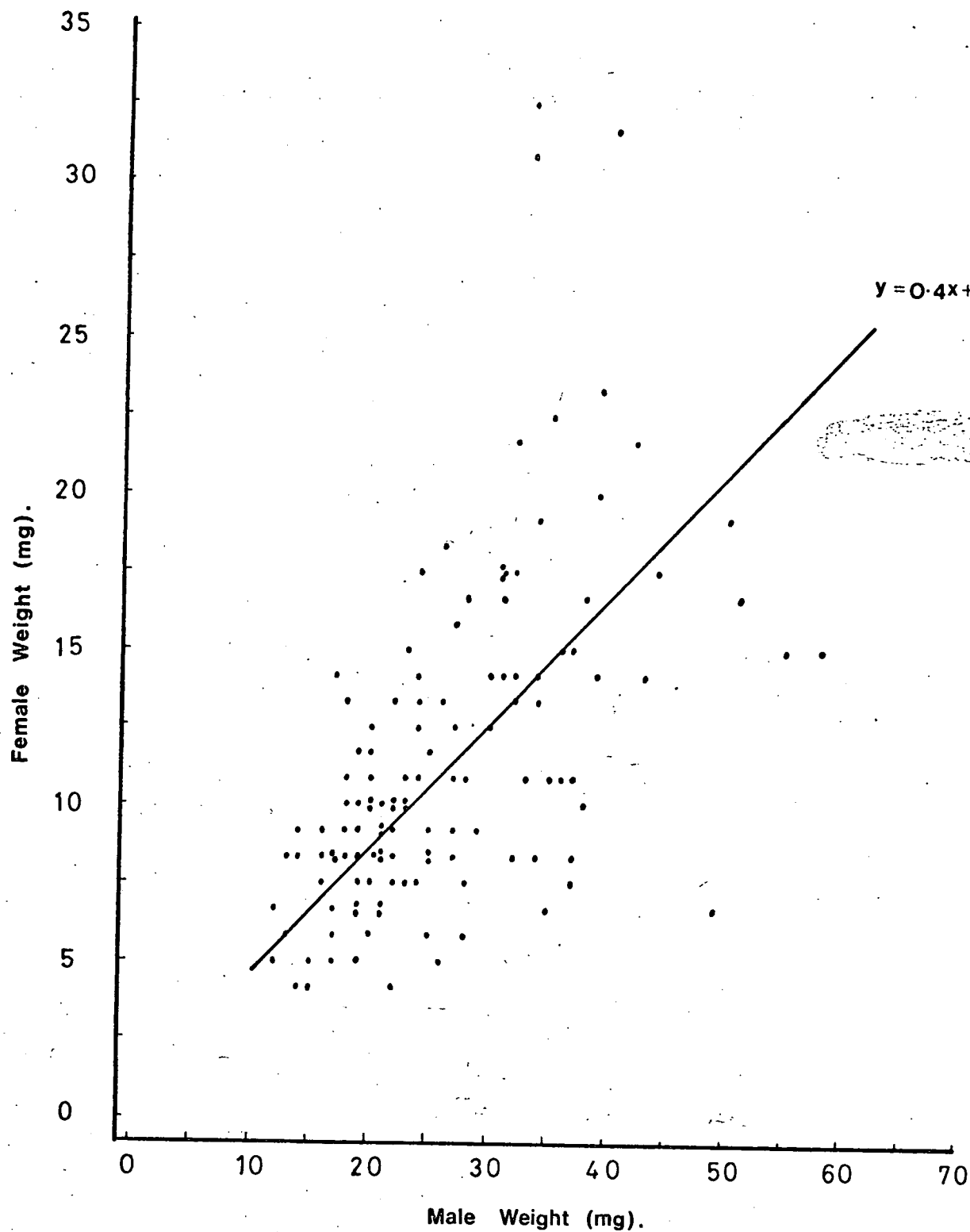| SAMPLE SITE	DATE	EXPT.	N	r	P
Laboratory	16/5	-	22	0.794	<0.001
Brasside	26/5	1	15	0.8234	<0.001
Jesmond Dene	30/5	1	16	0.4376	NS*
"	6/6	1	17	0.7452	<0.001
"	9/6	1	18	0.7316	<0.001
"	13/6	1	13	0.8483	<0.001
TOTAL		1	73	0.706	<0.001
Jesmond Dene	22/6	2	11	0.5165	NS*
"	11/7	2	21	0.6062	<0.01
"	19/7	2	20	0.1582	NS*
TOTAL		2	52	0.3741	<0.01
TOTAL		1+2	127	0.6297	<0.001

* NS = Not Significant.

Figure 7: The relationship between the weights of males and females in field-caught pre-copula pairs collected between 30/5 and 19/7 1983 .

$N = 127$, $r = 0.6297$, $P \leqslant 0.001$.

if not all of the effort for movement in the pre-copula pair. Viewed from the side through the perspex walls of the stream the female position in the pair could be seen, this position is described in the introduction (see Figure 1). Looking down on the pair (or single male) it was a straight-forward task to record the initiation and termination of pair movement by watching the male. Further considerations of male and female involvement in movement are given in the discussion.

Male performance was gauged by calculating the speed of movement either of the pre-copulatory pair or the male against a steady water current. Speed was calculated from two readings; the total distance moved against the current and the time spent in forward motion. So, speed is synonomous with performance and;

speed = distance moved ÷ time in motion

The response of males, paired or not, was not uniform. A majority of pairs (88% single and paired in Experiment 1 and between 89-95% of those paired in Experiment 2) remained orientated upstream and moved against the current. Those not following this pattern fell into three categories;

(i)   Pairs separating before measures of performance were taken.

(ii)   Pairs (or single males) remaining stationary for more than five minutes.

(iii)   Pairs (or single males) swept downstream.

Five minutes was the maximum time of any run, many were of shorter duration because the length of the channel had been covered. If during this time pairs fell into category (i) they were discarded. Categories (ii) and (iii) were recorded as zero distance (and, therefore no speed) but were retained where necessary.

3.3.1 Experiment 1: Male performance, loaded versus unloaded.

This experiment consisted of two parts; each part assessed male mobility or performance by calculating the speed of movement against the current. The first set of runs used paired males, the second used single males. Details of the results obtained are given in Tables 4-7, and Figure 8.

A males performance against the current was not related to the weight of that male regardless of whether the male was paired or not, see Table 4 for details. Speed it seems is a quality independent of the size of a male.

In general the speed of the male was greater when single than when paired. Females may, therefore, represent a load to males which reduces the efficiency of movement of the paired male relative to its performance when single.

The two readings of speed for each male are highly correlated which suggests that the two performances were not unrelated; (N = 62, r = 0.5288, P < 0.001; Figure 8).

No further assessment of the load a female represented to a male was possible from the data obtained in Experiment 1. These data were analysed to determine if female weight had a proportional effect in diminishing male speed when paired (i.e. female weight correlated with the speed ratio). Table 5 shows that female weight was not directly related to the reduction in speeds observed between the paired and single states; nor was female weight correlated with the male performance when paired (Table 6).

Male weight is not an indication of male performance (see above), however, the ratio of the weights in a pair (the proportional effect of the

Table 4: The correlation between male weight (mg) and;
(i) the speed (cms⁻¹) of single males, expt. 1,
and (ii) the speed (cms⁻¹) of paired males, expt. 1
and expt. 2 parts I&II.

(i) Single males.

CASE	N	r	P
Expt. 1	62	0.0143	NS*

(ii) Paired males.

CASE	N	r	P
Expt. 1	62	0.0743	NS*
Expt. 2. I	52	-0.3142	<0.05
Expt. 2.II	46	-0.0956	NS*

Table 5: The correlation between the speed (cms⁻¹) of
the pair and the weight of the female (mg) in the pair.

CASE	N	r	P
Expt. 1	62	0.2146	NS*
Expt. 2. I	52	-0.2095	NS*
Expt. 2.II	46	-0.2031	NS*

* NS = Not Significant.

Table 6: The correlation between the speed of the male
when in pre-copula pair and the speed of the male when
single.

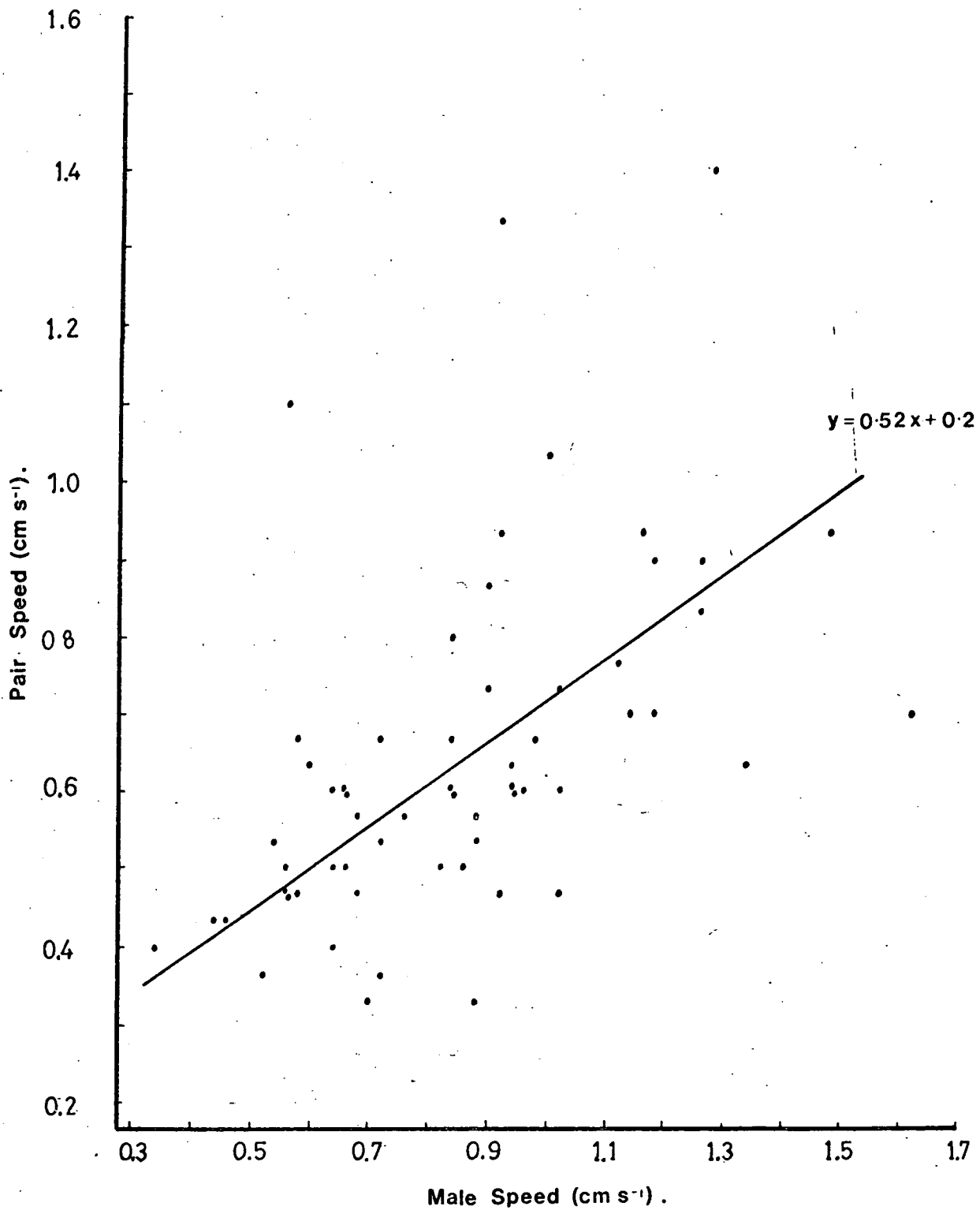| CASE	N	r	P
Expt. 1	62	0.5288	<0.001

Figure 8: The relationship between the speed males achieved when paired (y-axis) and single (x-axis).
N = 62 , r = 0.5288 , P <0.001 .

female with respect to the male weight) might be related to the ratio of the males two performances or the absolute difference between them. Table 7 gives the correlations relevant to such a postulation, no significant relationship was found.

Experiment 1 showed that pairs move more slowly than single males and that there was a relationship between the performance óf an individual male in the unpaired and paired states. Thus a distinct behavioural difference was detected but the experiment did not indicate that large male size relative to female size was of benefit to the male in terms of the males ability to move.

3.3.2 Experiment 2: Male performance with varying female weight

The second experiment was designed to assess the effect changes in the same loading factor (female weight) would have on male performance. Possible differences in male behaviour between single and paired states (see above) was controlled by keeping the male paired in both runs (see discussion). Yonow (1983) suggested an experiment of this type as a logical follow up to her preliminary study.

Changing the weight of the second female in relation to the weight of the first was controlled to give an even distribution of potential weight differences. This gave an even spread of weight changes either side of the zero weight change between part I and part II (see Figure 10 for the distribution of weight changes, negative values indicate females lighter in part II). This programme was adopted, in favour of a random swapping of females between the males, because unintentional bias would be introduced if the weights of the female in the second pair were generally heavier than the first, and there would be no way of distinguishing this from fatigue in males. If the range had been limited it would not correspond to the weight ratios found in field formed pairs.

Table 7: The correlation between paired speed (cms⁻¹) and the ratio of male to female weight in expt. 1 and expt. 2, parts I&II.

CASE	N	r	P
Expt. 1	62	-0.0178	NS*
Expt. 2.I	52	0.0517	NS*
Expt. 2.II	46	0.2537	NS*

* NS = Not Significant

Table 8: Pairwise 't' test between the mean speeds (cms⁻¹) of pairs in parts I&II of experiment 2.

VARIABLE	N	MEAN	STD DEV	't' STAT	SIGNIF
Speed part I	46	0.699	0.284	1.0976	0.2782 @
Speed part II		0.653			

@ denotes not significant.

Table 9: Spearman Rank Correlation between the difference in speeds (part I - part II) and the difference in female weights (part I - part II) in experiment 2.

CASE	N	r_s	P
Expt. 2	46	-0.5568	<0.001

The speed a male achieved in part 1 of Experiment 2, where it was in a field formed pair, correlated with the speed achieved in part II where the female size was predetermined (N = 46 , r = 0.3692; p < 0.05). This result is in accordance with Experiment 1 where males quick in pairs were also quick when single.

If an overall trend in speed differences existed then the assumption that conditions in part 1 and part II of Experiment 2 were the same would not hold. By observation (Figure 9) 27 pairs were faster in part 1 than in part II and 18 were faster in part II than in part 1. If most pairs were faster in part 1 then fatigue would be the probable cause given the known distribution of female weights between the two pairs. Were the speeds in part II significantly faster then males might have gained from experience in run conditions, such that their speed increased. A pairwise t-test testing the null hypothesis (that there was no difference between the mean of the speed in part 1 and the mean of the speed in part II) gave a none significant result (N = 46, t = 1.0976; p = 0.28, Table 8).

So the variation in between speeds recorded in parts 1 and II did not arise from fatigue or experience.

For each male there were values of speed and female weight for part 1 and part II of Experiment 2. From these data the relationship between female weight and male performance can be investigated. A test of the relationship was to calculate for each male the difference in weight between the female in part 1 and the female in part II and then to correlate that difference with the associated difference between the male's speed in part 1 and the males speed in part II. The difference in weight and the difference in speed correlate significantly (N = 46, r_s = 0.5568; p < 0.01, Table 9, Figure 10). The Spearman rank correlation was used because there was not a normal distribution of females in part II.
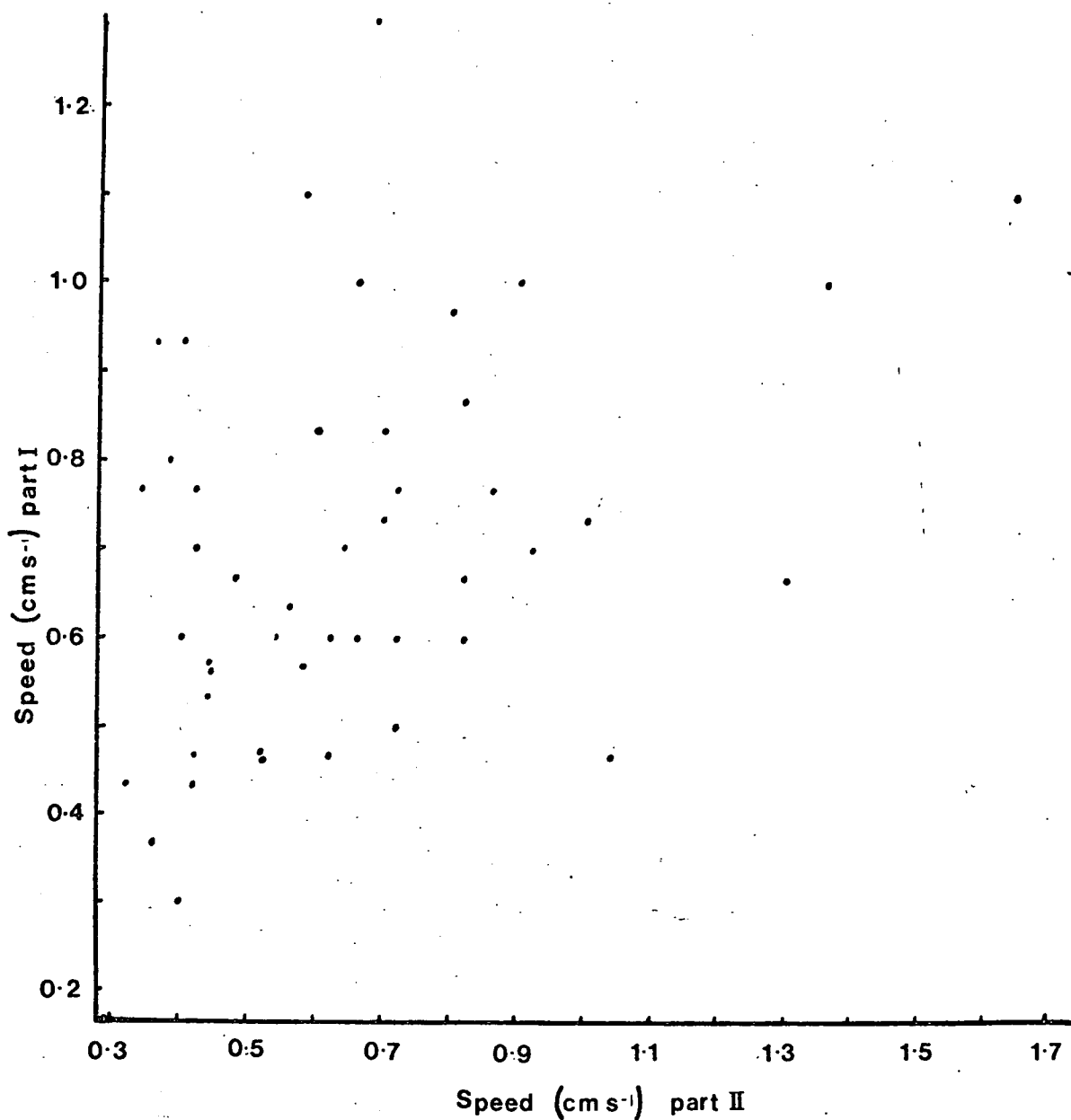
Figure 9: The relationship between the speed
males (in pre-copula pairs) achieved in the
channel, in part I (y-axis) and part II
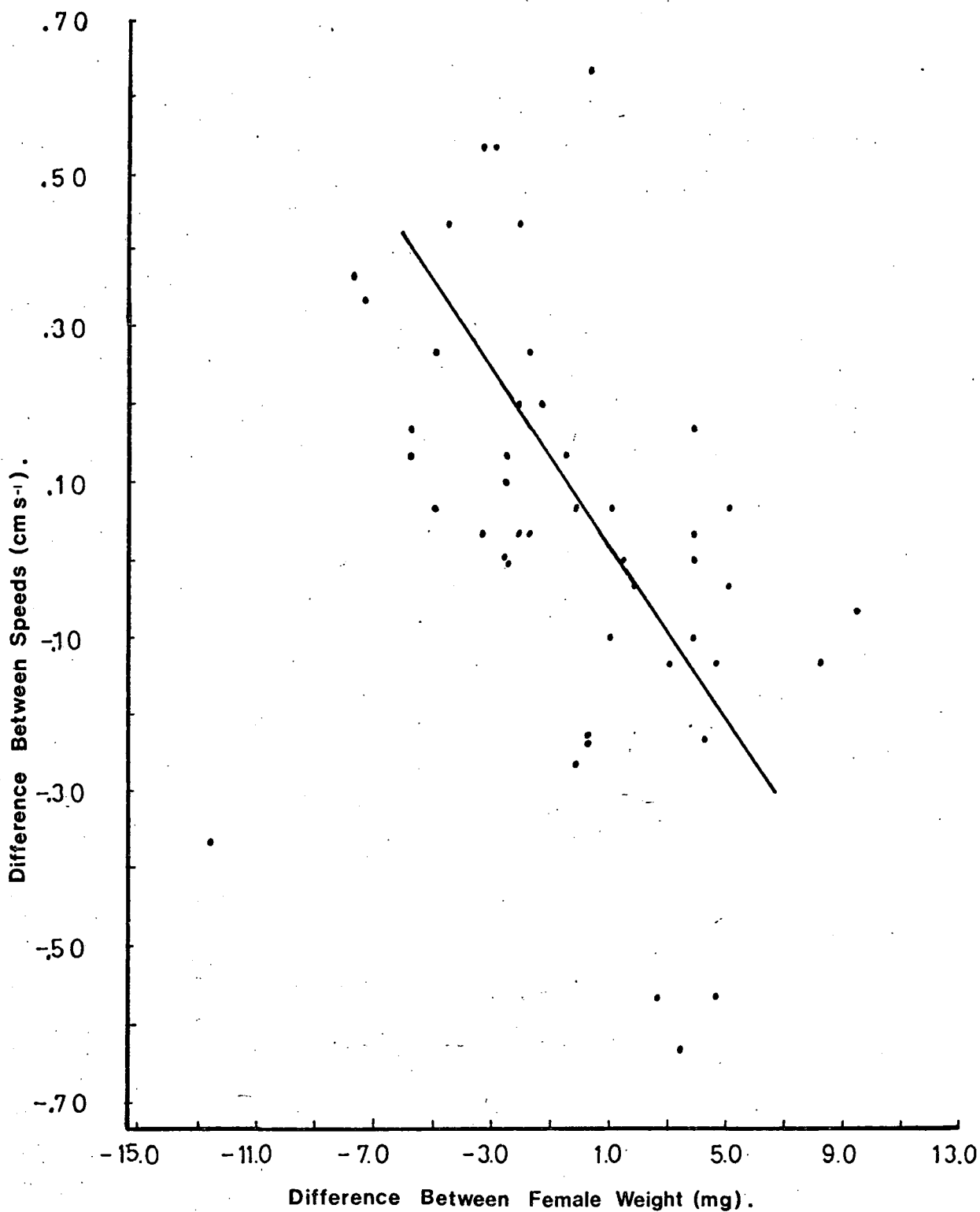(x-axis) of experiment 2.

N = 46, r = 0.3692, P < 0.01

Figure 10: The relationship between the difference in female
weight (part I - Part II) and the difference in speed
between the two runs (part I - part II) .

N = 45 , r_s = -0.5568 , P <0.001 .

The relationship is such that an increase in female weight between part 1 and part II will tend to produce a slower performance from the male (a decrease in speeds from part 1 to part II), the reverse situation also holds (Figure 10).

3.4   Brooding, Longevity and Mating Frequency

The experiments outlined in methods 2.2 and 2.3, were prematurely terminated by an engineering fault which allowed the temperature to reach 40°c. This did not allow analysis of the effects looked at. However, several males in pots with more than one female copulated more than once, no statistics are available but it is an observable fact that males are capable of mating with more than one female. This does not prove that males may pair consecutively in the field because no simulation of the costs involved were included but it shows they will mate with several females if the opportunity arises.

CHAPTER 4: DISCUSSION

4.1 Introduction

The discussion below follows the pattern established in the preceeding chapters. Attention is centred on the experimental work examining the loading constraint, mobility and implications for the existence of sexual size dimorphism in Asellus aquaticus.

4.2 Does Guarding Involve a Cost to Males

It is unlikely that any behaviour which might require the male to carry and defend the female for 5-11 days (Manning 1975) would be cost free. Of those pairs collected in this survey 67% (148) were still paired after the third day. The hypothesis examined is that the cost is related to the weight of the load (female) and that the ability of the male to bear the load is related to the weight of the male.

In the guarding phase the male Asellus will have to maintain itself to ensure survival to copulation. The female will require energy (in the form of food) to develop the eggs and survive through the brooding, which may last 40 days (Steel 1961); both will have a cost related to the female size because of size related fecundity.

In addition to feeding requirements the male will have to remove the pair from threats of predation (i.e. by trout, Bergland 1968) or from high densities of male Asellus searching for mates. As a deadweight load, female weight must be important in determining the work required by the male to move the pair.

4.3 Sexual Size Dimorphism

Asellus males are, at maturity, larger than the females, this is described by Unwin 1920 and in later works involving population sampling (Steel 1961, Ridley and Thompson 1979, and Yonow 1983). Male size in relation to female size varies enormously through the animal kingdom from dwarf males in deep sea fish (Ghiselin 1974) to elephant seals which may be eight times the size of the female (Cox and le Boeuf 1977). The Asellus male is two to three times heavier than the female.

Clearly this sexual size dimorphism will not arise through the higher cost to the female of producing eggs compared to the sperm production of males (Darwin 1871, Ghiselin 1974). The probable causes in evolutionary terms are male-male competition or some other selective force requiring males to be bigger than females, which in consideration of the behavioural ecology of the animal is postulated to be a loading factor on males determined chiefly by the size of females. The comparative evidence presented in the introduction (1.1) favours, in animals other than birds and mammals, an explanation which accommodates that part of the breeding behaviour where one sex moves or carries the other.

If guarding a female is taxing to a male it is plausible that the less impact a female has upon the male the greater the chances that the male will survive to fertilize the eggs of the female, but because selection for smaller (less fecund) females is improbable, the selective pressure should be exerted on the male to increase in size relative to the female.

4.4 Assortative Mating

If, as proposed, the female determines the size of the male which

can successfully guard her then because male and female size varies some degree of assortative mating would be expected. Asellus are repoted to mate assortatively in the field by Manning (1975), Ridley and Thompson (1979) and by Yonow (1983). In this study assortative mating was the general trend within samples. Figure 5(ii) shows that the mean size of males and females in each sample fell, but only slightly from the 5/6 to 19/7. So assortative mating was not wholly due to the change in size during the breeding season which is reported by Ridley and Thompson (1979). This study was carried out later in the season than the work by Ridley and Thompson. They sampled between January and May and discovered a drop of some 2mm between the means of male and female size around February/March. The assortative mating within the samples they took was attributed to random mating followed by takeover by the larger males of pairs held by small males. Larger females being more fecund attracted the larger males.

The hypothesis that males are limited to the female size they can accommodate would predict a similar outcome of pairing; that small males pair with small females and that whilst large males should pair with large females the selection of mates would be modified by availability. A variable relationship exists in Figure 6.7, and it could be explained by an interaction between an upper limit on female weight enforced by the effects of loading and a lower limit determined by fecundity availability and takeovers between males.

4.5   Female Size and Male Performance

Experiments 1 and 2 were designed to evaluate the cost for a male involved in guarding. Speed was used as an appraisal of the ability to avoid predators or competitors and was taken as a general representation of the males capacity to move.

In Experiment 1 an attempt was made to gauge the difficulties a male would face in pairing compared to its movement when single. Differences between this experiment and the work of Yonow (1983) were only in the techniques used to measure speed. She used a fixed distance to be covered, this study used a more flexible calculation of speed. The assumption made in both studies was that the behaviour of the male was essentially the same when paired and when single. This may not be the case because a single, recently displaced male may be searching for a mate whilst a paired male will not. However, this possibility is not supported by the comparison of the performances a male achieved under the two conditions. A male which was fast when single tended to be fast when paired (Figure 8). This is not definite proof but it does suggest that a relationship exists, this was exploited for experimental purposes.

The results of the present study were inconsistent with the work done by Yonow (1983). Male performance was impaired by the presence of the female, but where Yonow was able to relate the size of the female (or the ratio of male:female weights) to the diminution of male performance this study failed to reach similar conclusions. Pairing involves a cost but variation in the cost according to female size was not apparent.

Experiment 2 was able to dispense with the variable of male speed when single and a more accurate evaluation of the relationship between female size and performance was established. The size of the female a male pairs with is important; performance fell as female weight increased. This occurred in the majority of cases in such a way as to suggest that the smaller the female the more rapid the movement.

But males will be under pressure to mate with larger (more fecund) females, so that larger males capable of pairing more efficiently with the large females are likely to be favoured in subsequent generations.

4.6 Conclusions

The results obtained from Experiments I and II are consistent with the hypothesis outlined in the introduction, that female size dictates the male size capable of enduring potentially long and costly (time and energy) guarding sessions and so ultimately, the size of males in the population in relation to female size.

Sexual selection embraces many topics. In the case of Asellus it is likely that sexual selection (intra-male competition) favoured guarding in males as a means of obtaining and keeping a scarce resource: females. The females benefit from;

a) an increased probability of fertilization where an internal mechanism trying oviposition to the presence of a male is lacking;

b) guarding and takeover allows sorting of males prior to oviposition leading to a large mate;

c) avoiding repeated and costly interactions with searching males.

Against these benefits there are the costs of predation and the risk of a failure to find adequate food for the high energy requirements of brooding.

Males securing large females have to guard them, Ridley and Thompson (1979) suggest that smaller males i.e. those in a similar size range to females do not adopt guarding. Within the constraints that loading will impose, a range of factors will affect male mate choice. The larger the female size the more eggs she is likely to bear (Steel 1961) and the closer to oviposition she is likely to be (Manning 1975). Thompson and Manning (1981) found that males were capable of detecting the relative proximity to oviposition of two females and would on some occasions

choose smaller females where those females were closer to oviposition.

Large females will exert a load and may attract males larger than the one guarding, attempts to dislodge will involve costs to the defender and previous investment may be lost if the attacker succeeds. The density of males will, therefore, affect the pairing in two ways. First, by increasing the probability that a male will attack a paired male smaller than itself and second by increasing the duration of guarding (Manning 1980). Similarly abundant females should reduce the mean guarding time of males.

The benefit to males of a size difference in the pair outlined in 4.5 will favour the evolution of sexual size dimorphism. The nature of the selection, i.e. upon the sex bearing the load in those animals indulging in pre or post copulatory pairing, has implications upon the probable cause of sexual size dimorphism in these animals.

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