Some aspects of the evolution of sexual size dimorphism in the animal kingdom

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Hogan, Jacqueline Mary Catherine (1983) *Some aspects of the evolution of sexual size dimorphism in the animal kingdom*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/7886/

SOME ASPECTS OF THE EVOLUTION OF SEXUAL SIZE DIMORPHISM IN THE ANIMAL KINGDOM.

By

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A thesis submitted for the degree of Master of Science
at the
University of Durham.

August 1983

For Pete.

ABSTRACT

In most studies of sexually reproducing animals it is assumed that inter male competition results in selection of larger males. In higher vertebrates there appears to be a correlation between the type of mating system and the degree of sexual size dimorphism. Amongst the lower vertebrates and invertebrates, however, this correlation is less obvious; in these groups the females are usually larger than the male, despite considerable conflict between males for mates.

The hypothesis that differential loading or mechanical constraints, operating on males and females during mate guarding, are important factors influencing the relative sizes of sexes was investigated for two species; a pondskater, (Gerris sp.) and the common toad (Bufo bufo). In both species, the females carry the male prior to mating, the female being the larger sex.

Previous work on the common toad has shown that assortative mating is operating, this study, however, shows that the converse is true, ie that mating is random. Several suggestions have been proposed to explain these results.

In contrast, pondskaters show assortative mating, the females paired with males according to body size and possibly on midleg length. Both sexes, however, appear to be adapted to the loading constraints to which they are subjected during pairing.

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CHAPTER 1 .....

Introduction

Sexual reproduction entails gamete formation by meiosis and the fusion of genetic material from individuals. It almost always, but not invariably, involves two sexes called male and female. In higher animals the sexes are often most readily distinguished by features such as genitalia, plumage, size or colour, but these are not fundamental differences. In all plants and animals the basic difference between the sexes is the size of their gametes; females produce large immobile food-rich gametes called eggs, while male gametes, or sperm, are tiny, mobile and consist of little more than a piece of self propelled DNA. The fusion of two gametes of unequal size, (one large and one small) occurs in virtually all sexually reproducing multicellular plants and animals and is called anisogamous sex. This fundamental asymmtery in gamete size leads to significant effects on sexual behaviour. Male courtship behaviour is largely directed towards competing for and exploiting the high female investment, males, by virtue of their relatively lower investment in each gamete, having the potential to mate with a large number of females. Thus, potential mating opportunities are not equal for the two sexes. There is a basic conflict of interests because each sex is pursuing a different strategy. Females will select males whose genes will contribute most to the survival and viability of her offspring (ie the fittest male to be found) whilst males may attempt to mate with as many females as possible. In effect, females represent a limiting resource for which males must compete amongst themselves. This competition amongst males imposes a powerful selection pressure that favours those males who make the most effective mating effort. This selection pressure is called sexual selection.

1.1 Sexual Selection

Many differences between the sexes are related particularly to the competition that characteristically occurs between males, either for territory or for possession of a female or several females. When an individual attains sexual maturity secondary sexual characteristics appear and these may be important for the purpose of competition. Darwin (1871) gave considerable thought to the nature of sexual selection and its consequences for sexual dimorphism and mating patterns. He introduced the theory of sexual selection to account for those characters and patterns of variation which did not appear to be explicable in terms of natural selection for adaptations promoting success in the ´struggle for existence´ (Selander 1972). He proposed two major forces in the evolution of sexual differences. First, that the fighting and display among animals for the possession of females, which is especially prominent among mammals, accounted for the evolution of secondary sexual characteristics such as antlers and horns which are useful in battle. This form of selection, called Intrasexual Selection by Huxley (1938b), has generally been accepted as an explanation for the evolution of special male weapons. Darwin's second category proposed that the extreme development of plumage characters amongst some birds, such as birds of paradise and peacocks, features which did not appear to be of use in inter-male combat, could be explained as being due to cumulative effects of sexual preference exerted by the females at the time of mating. This aspect of his theory of sexual selection, called Epigamic Selection by Huxley and Intrasexual Selection by many other authors, depends on the assumption that females show a sexual preference for the males ornamented or behaving in a particular way. This assumption has been the subject of much discussion and disagreement since Darwin first proposed it. Darwin simply assumed that females have preferences for certain types of males, without suggesting how such preferences may have arisen or how they might be maintained in a population by selection. For this reason this part of his theory was widely challenged by a number of workers but Fisher (1930) clearly showed that the notion of female choice is reasonable, not withstanding the fact that direct evidence was then scarce for species other than man (Orians 1969).

In practice the two aspects cannot always be separated. Fisher (1930) pointed out that when a selective advantage is linked to a secondary sexual characteristic there will be simultaneous selection on the opposite sex in favour of those who prefer the advantageous type.

1.2 Sexual Dimorphism

Sexual selection as envisaged by Darwin usually results in sexual dimorphism i.e. in a difference between males and females. Sexual dimorphism is of interest in that it shows that there is a class of characters (morphological, behavioural and others) differentially expressed in the sexes because of sexual variation in ways of maximising fitness (Fisher 1930). With regard to both survival and reproduction, adaptations may or may not be similar in the sexes. Thus males and females may exploit an identical food niche and as a consequence be monomorphic in trophic features; or they may be differentially adapted for niche exploitation or other activities affecting survival. Similarly, displays and other adaptations for reproduction (including displays functioning in the maintenance of breeding territories and in courtship) may or may not be similar in the sexes. The central problem is to analyse the environmental and other conditions responsible for the variable combinations of survival, and reproduction, enhancing adaptations occurring in different species. Although particular attention has been given to sexual variation in these combinations, this aspect is, in a sense, secondary to the larger problem (Selander 1972).

Although Darwin was concerned with sexual dimorphism almost exclusively, he was aware that with regard to a given character sexual selection may act uniformly on males and females thus producing sexually selected monomorphism. Mayr (1972) suggested that most of the differences between sexes are clearly a result of natural selection (e.g. claspers) which facilitate copulation and fertilization, as well as a wide range of characters concerned with parental care.

1.3 Sexual Size Dimorphism

It is often assumed in studies of sexually reproducing animals that, when males are larger than females, the size difference is the result of sexual selection in the form of male:male competition. This leads to the generalisation that there is a strict association between body size and aggression, the larger sex being the more aggressive (Trivers 1972). The argument that larger males have an advantage over smaller males when competing for resources or mates, leads to the possibility that males could then evolve to be the larger sex.

In some groups, particularly the higher vertebrates, there does appear to be an association between the type of mating system and the degree of sexual size dimorphism. In birds and mammals males are generally larger than females and often more aggressive, where females are known to be more dominant as in birds of prey, they are often larger than males. In polygynous birds and mammals in which male-male competition for mates is likely to be intense, sexual dimorphism tends to be greater than in monogamous species (Clutton-Brock & Harvey 1977, Alexander & Borgia 1979). Amongst invertebrates and the lower vertebrates associations between sexual size dimorphism and the degree of male-male competition is less obvious. Females are usually the larger sex in these groups even when there is considerable conflict between males for mates. In fact there appears to be no a priori reason for assuming that male conflict should result in the evolution of males as the larger sex.

1.4 Aims

Post or pre-copular mate guarding is a widespread reproductive tactic in the animal kingdom. There are numerous examples of mate-guarding in animals, in a passive phase the male remains mounted or otherwise attached to the female but without genital contact (Parker 1974). In amphipods the males of several species carry the females around for a considerable time in precopula (Birkhead and Clarkson 1980, Hynes 1955, Adams and Greenwood in press). Anurans and pondskaters, the subjects of this study, often show precopulatory passive phases for considerable time before fertilization (Noble 1937, Andersen & Polhemus 1976). In almost all these examples the passive phase terminates on (or more rarely without) insemination; when it continues after insemination it probably then functions to reduce the chances of sperm competition by restricting subsequent matings, as do other post-copulatory passive phases. Parker (1974) suggests that guarding will be favourable where the male can predict an encounter that the female is close to mating ie where the probable gain rate due to guarding is potentially greater than that due to withdrawal for further searching.

Recent work (Wheeler & Greenwood 1983, Adams & Greenwood in press) suggests that an important but ignored influence on the relative sizes of the sexes is the differential loading or mechanical constraints on males and females which operate during mate guarding. When considering loading constraints one has to bear in mind the interaction between mates during this period. In this study an invertebrate and a vertebrate were used to investigate whether loading and mechanical costs might be important factors in determining the optimal reproductive size of the sexes. In both species the female is the load bearing partner and despite intense male-male competition it is suggested that selection has operated on the size of the female to accomodate the male load. In both toads and pondskaters females are the larger sex.

Direct measurements of loading constraints on the female are difficult but by looking at sex differences in the morphometric characters ie their body weight and length, and limb lengths, it may be possible to gain an insight into the mechanical problems through indirect means. The aims of this research were:

a) to estimate the size of males and females in natural populations of Bufo bufo and some species of the Gerrid family and establish the relationship between male and female sizes in paired individuals.

b) to investigate the scaling relationships between body length, weight and limb length and weight loading in both sexes.

From (b) predictions on male and female size may be made. In Gerris where males are carried around by females it is predicted that the scaling relationships between body length and limb length will differ for males and females. Within each sex, where the front legs are used for feeding, the mid-pair which are load bearing and the hind pair used for steering, it would be expected that the load bearing female would have relatively long mid-legs and that the male, who appears to steer the female when paired, to have relatively longer hind legs. In both sexes no effect is predicted for the front legs.

In Bufo bufo, males are again carried by females, and hence females would be expected to have relatively short back legs in order to cope with the extra loading. Males, however, would be selected for mobility and fighting and consequently should have relatively longer back legs and since they need to clasp the female, relatively longer front legs.

The thesis is organized along the following lines;
Chapter 2 introduces the first study animal, the common European Toad _Bufo bufo_ giving a brief life history and outlines the capture techniques used.
Chapter 3 analyses the data obtained from the study, concentrating mainly on the general observations made at the pond over the three week period and deals with the mating strategies of the males in view of the biased sex ratio.
Chapter 4 concentrates on the morphometric characters of the toads in the light of the predictions made previously.
Chapter 5 introduces the next study animals, pondskaters and outlines the various adaptations they have to life on the water surface. A brief outline of the life histories of species captured is also included
Chapter 6 briefly describes the study sites used and the methods adopted for the capture and subsequent treatment of the data. The paired material is dealt with here although some of the unpaired data are discussed.
Chapter 7 compares the species found throughout the study and discusses their various adaptations and morphometric characters.
Finally chapter 8 discusses the overall findings of this investigation.

CHAPTER 2 ....

2.1 General Description of the Common Toad

The common European toad, Bufo bufo, is an Anuran in the family Bufonidae which have been described as the ´true toads´ (Goin & Goin 1955). It spends most of the year on land and hibernates in dry holes or clefts from October to March, reappearing at ponds for the breeding season. It is known as an explosive breeder (Smith 1969) which means that all sexually mature individuals of the district migrate from their hibernation quarters within a few days of one another and all the years reproductive activity occurs within a span of a few weeks in early spring. The same pond is returned to every year, toads sometimes travelling considerable distances to reach the spawning site.

Male toads do not develop courtship colours in the breeding season like newts, however they do develop swellings on the inner tubercle and inner finger which are known as nuptial pads (Plate 2.1) and these are believed to assist in clasping the female.

The first arrivals at the breeding site are the single males, some go straight to the water and others remain on the bank. It has been suggested that the croaking of the early arrivals leads the rest of the assembly to the breeding site (Frazer 1966), alternately the croaking will frequently attract

Plate.2.1 Left forelimbs of male and female common toads, the male on the left. Although out of breeding season, the nuptial pads of the male can be clearly seen on the thumb and the first two fingers.

the females to the right part of the pond. However, the male of the common toad is normally sufficiently alert to spot a nearby female and climb on her back, thus when the main colony arrives a few days later many have already paired. Toads pair in axillary amplexus, ie the male clasps the female with his arms around her body behind her forelimbs. The position of the male is always such that his hind legs are always near her cloaca (Plate 2.2). The males grip is very strong and the tenacity with which he holds on to the female is remarkable, considerable force is required to separate them. Occasionally two males may try to clasp lhe same female or one may attempt to dislodge the male of a pair already formed, this takeover occurs on the passive female (Davies & Halliday 1979). On rare occasions a whole series of males may be found struggling in a mass centred on an unfortunate female which is usually drowned by her suitors in the struggle. Males are carried around like this for several days before the female eventually lays her eggs. Numbers of eggs laid varies from 2000-7000 and are small, 1.5-2.0mm in diameter. They are expelled in double rows or strings one coming from each oviduct. These strings consist of a soft gelatinous mass in which the double rows of black eggs are embedded. On laying these eggs the male moves his legs in certain characteristic movements (these vary according to species), while at the same time exuding his sperm over the eggs as these pass over his toes. The effect of the movements of the male is to deposit the fertilized eggs in strings around the water weed.

Plate.2.2 Axillary amplexus in the European toad, _Bufo bufo_.

Once the female has finished spawning and no eggs emerge, the male releases her from his clasp. She leaves the breeding ground almost immediately and if intercepted by any other males on the way to the bank will at once be liberated as they appreciate her struggles and thinness. The male stays behind and waits for another female. Thus while individual females only spend one or two nights at the pond, the individual males may be present over two to three weeks. At any one time there will be more males than females. Only when no more females come to the water for several nights do the males abandon the spawn site, though it is not known whether this is directly due to the absence of females or to environmental factors that all the males depart. Variations in local temperature are known to affect the spawning process either by speeding it up or slowing it down (Frazer 1973).

2.2 Materials and Methods

Toads were collected from Brasside ponds in Durham (NZ 288 460). The ponds are derived from former brickworks derelict since the 1930's. Their main use now is by the local angling club although this is restricted to the larger stretches of water.

The pond shelves deeply in parts and is surrounded on all sides by vegetation comprising of willow, hawthorn shrubs, brambles and nettles (see Appendix I for analysis of the vegetation). Visibility in the pond was restricted due to rotting vegetation and debris on the surface, and a thick layer of detritus and bricks on the bottom.

Access was by means of a cinder path leading from a metal road and this footpath lay to the east of the road providing access to the lakeside. The pond is surrounded by undulating farmland on the west and north which probably forms an extended catchment area for the toads (Fig.2.1)

Observations at the pond were made from mid March to early April 1982. Every other evening the pond was checked for signs of toads until their arrival was noted. Once this had occurred the pond was visited each night and toads were collected.

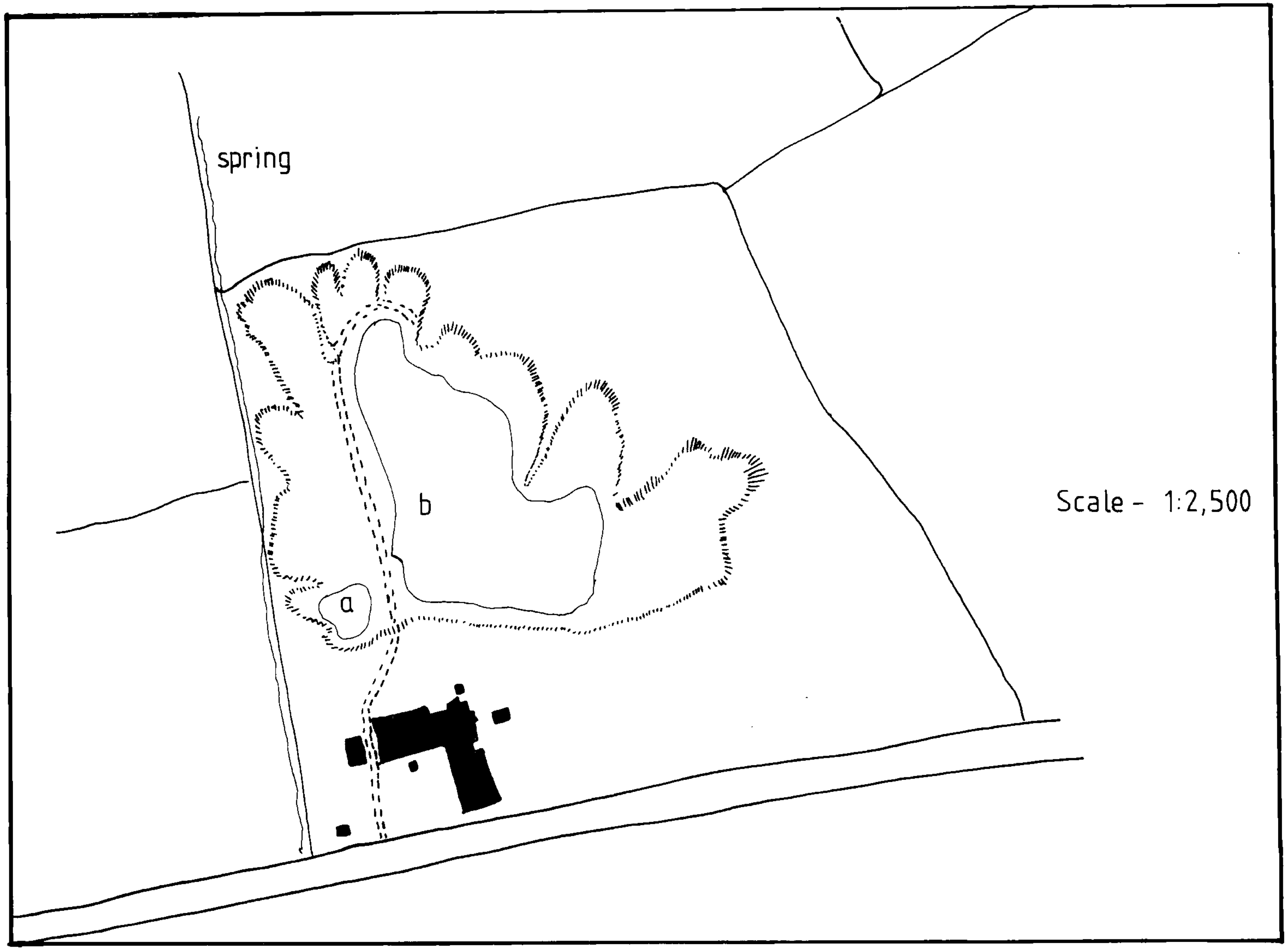
Two methods of capture were employed. On arrival at the pond one or two observers would follow the circuit of the lake path and using powerful torches collect as many toads as seen. These were processed and released at the margin of the pond after the final collecting round.

Toads were also caught whilst in the pond using thigh waders, a pond net and a headlamp attached to a car battery. On cold nights the reduction in numbers was marked by the lack of toads on the path and in the pond, but on mild nights the toads were very active and collecting would continue until after midnight.

Each individual toad was permanently marked by toe clipping with its own unique code, thumbs in both males and females were not clipped as it was feared that this might interfere with breeding success.

All toads were weighed using Pesola balances, those toads under 50g were weighed to the nearest 0.5g while the few females

Fig. 2.1 Study site showing clay pits and ponds. Pond (a) contained the toad population investigated.


spring
b
a
Scale - 1:2,500

over 50g were taken to the nearest gram. In addition, measurements of snout-vent, leg and arm lengths were read to the nearest mm. Snout-vent length was measured by flattening the spinal curvature against a blunt edged ruler with light pressure from the hand.

Weather records for the period were obtained from the University's Meteorological Station and each night was classified on the basis of the amount of cloud cover and precipitation (if any) into wet, dry, cloudy or clear.

CHAPTER 3........

3.1 Period of Activity

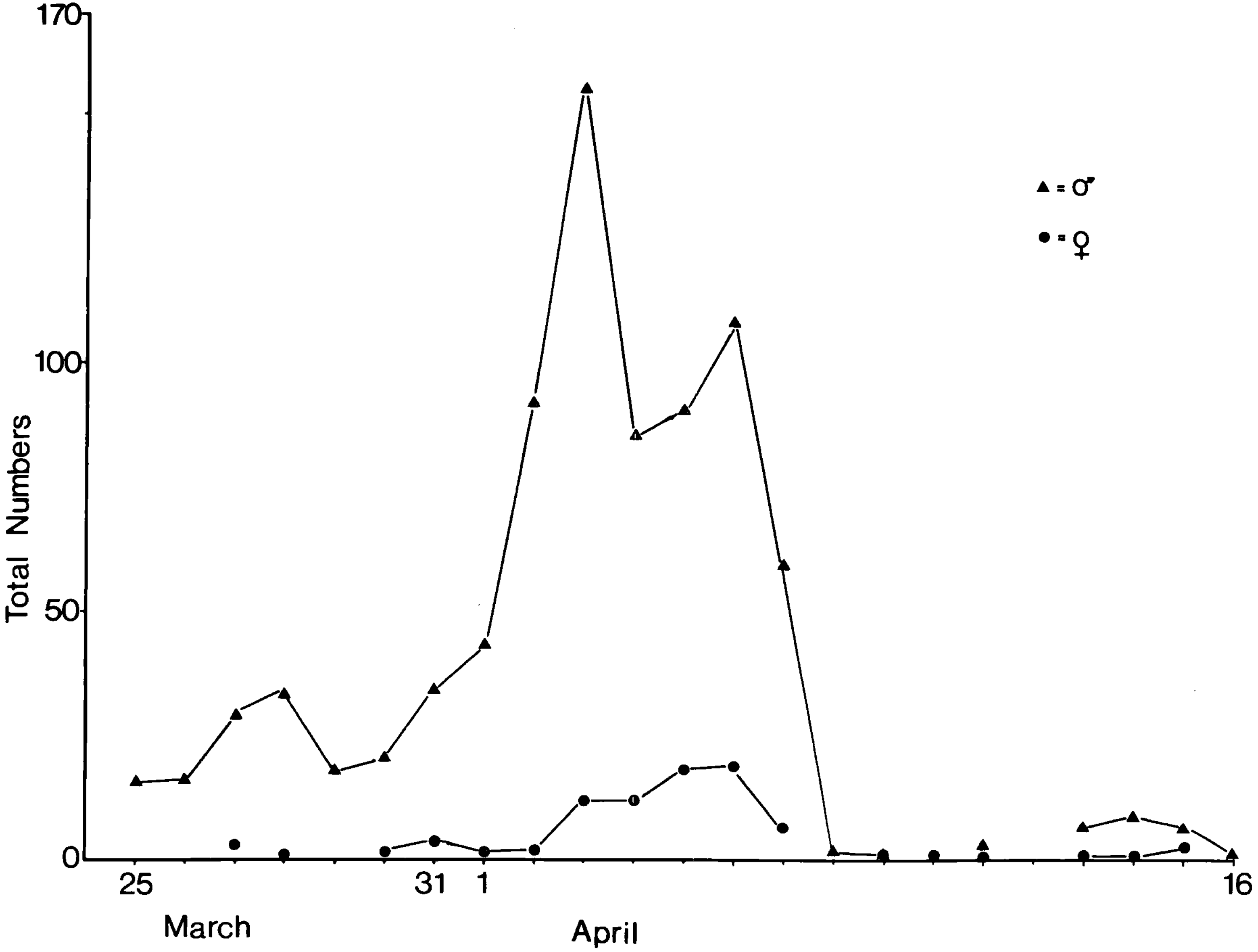
The toad migration to the ponds commenced on the 25 of March and effectively ended on the 7th of April, the breeding season lasting approximately two weeks. During this period there was only one main peak of activity which corresponded to a period of mild weather, Fig.3.1. Previous work (Gittins et al 1980a, Davies & Halliday 1979) has indicated that the main movement of toads is usually recorded towards the end of the March and lasts approximately three weeks. In this study the main movement was later, probably as a result of the extremely harsh winter and the number of nights when toads were active (ie when more than 15 toads were captured) was cut short by a cold spell.

3.2 Length of stay at the pond

Males marked during the first peak of activity re-appeared in collections right through the migration. The highest recapture rate for males occurred on the day after initial capture. This may be explained in behavioural terms as several workers (Savage 1934, Frazer 1966, Smith 1969) have remarked upon the tendency of males to wait at the margins of the breeding grounds, presumably awaiting the arrival of females.

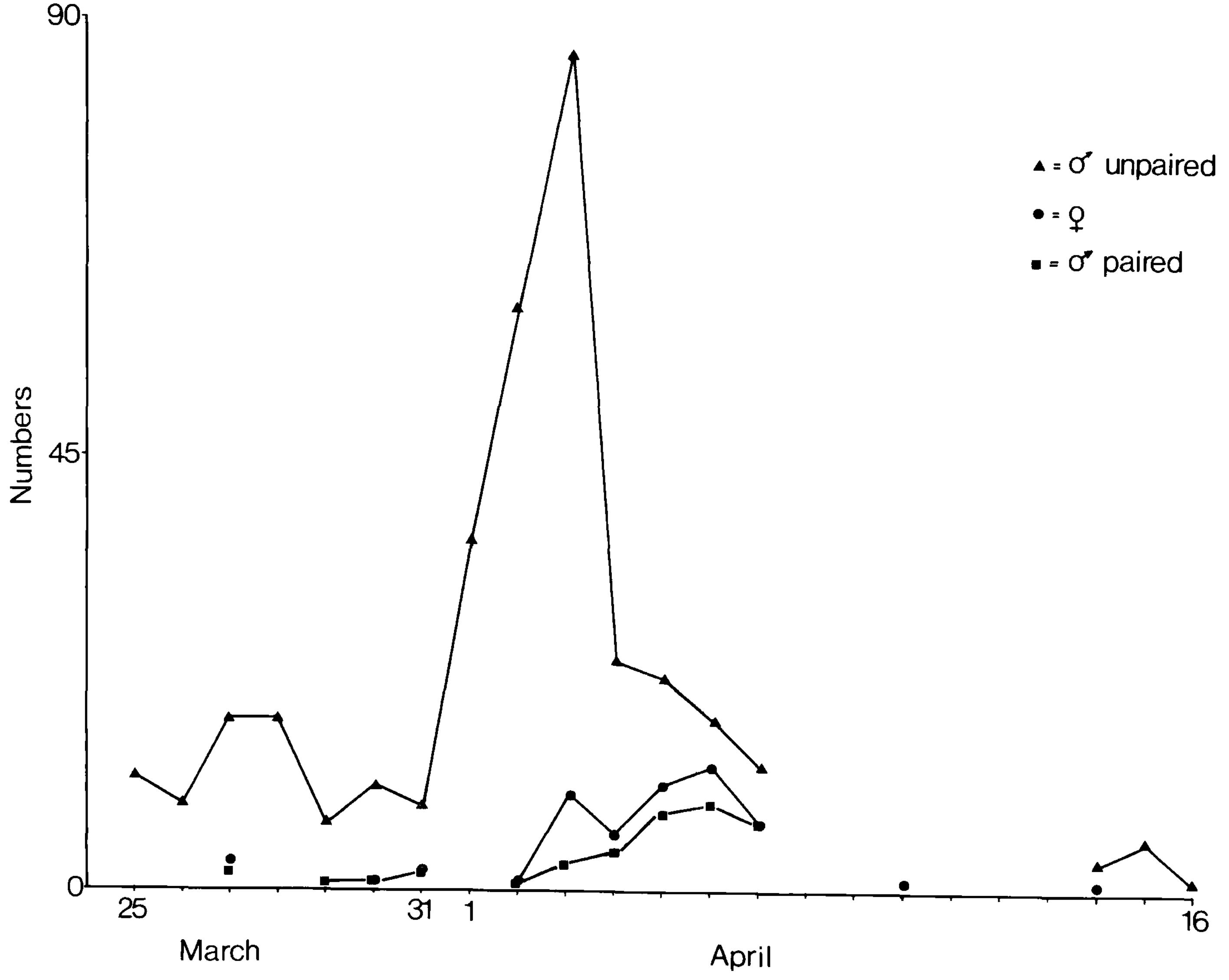
Looking at Figs.3.1a,b the unpaired males can be seen to

Fig.3.1a Total number of toads of both sexes active on different nights throughout the migration.



170
100
50
0
Total Numbers
25
31
1
16
March
April
▲ = ♂
● = ♀

Fig.3.1b Variation in the number of unpaired toads (male) and paired males and females compared to female arrival times.


90
45
0
Numbers
25
31
1
16
March
April
▲ = ♂ unpaired
● = ♀
■ = ♂ paired

peak just before the arrival of the females, however for those males that paired the peak occurred within the second peak of female arrivals. The number of females marked was much lower than the number of males and only a few were subsequently recaptured. A few spent females were recaptured leaving the pond side two days after marking and some still gravid females were captured several days after marking. The data for the females, although sparse, suggest that they remain in the pond for a few days at least, though not as long as the males. This behavioural difference may also explain some of the disparity between the proportion of each sex recaptured since the longer the males remain in the vicinity of the pond, the greater their chance of recapture. The peaks may indicate that all the females in the pond had paired and spare males returned to the pond to await more females.

Cold spells undoubtedly prolong the breeding season (Frazer 1966, Smith 1969), the cold snap after spawning may explain the prolonged capture of males well after the females had left the pond.

During the migration period 53% of the male population was recaptured, the greatest number of recaptures were found to be on the first day after initial capture, toads marked later in the migration period stayed for a shorter length of time. This suggests that the migration is physiologically synchronized towards meeting a certain deadline, presumably spawning, which occured around the 4-5th April.

3.3 Sex Ratio

Captures of toads over the breeding season revealed that males greatly outnumbered the females (Figs.3.1a,b), so that although all of the females were paired there was always a large excess of unpaired males. Two factors contribute to the excess of males at the pond:

a) the length of stay of the toads, and

b) the absolute numbers.

The asynchrony in female arrival partly explains the excess of males at the breeding pond, males prolonging their stay in order to await the arrival of all the females. Over the entire breeding season males far outnumbered the females, a total of 412 individuals were recorded over the migration period most of the population being present from day to day. The females, however only numbered in total 56 individuals, and only a fraction of their total was present on any one day. Similar behaviour has been noted in other anurans. The sex ratio was approximately seven males to every female, all of the females acquiring mates but only one eigth of the males did so.

3.4 Methods by which males obtain females

The biased sex ratio gives rise to a situation which provokes fierce inter-male rivalry for the female. Consequently males must adopt different methods in order to obtain a female. This they do in two distinct ways:

i) By encountering a single female and pairing up with her, or

ii) by fighting and dislodging a paired male, thereby achieving a ´takeover´.

Most of the females were already paired before they reached the pond. Of those seen on land at night within 30m of the pond, 95% had a male clasped on their backs in amplexus whereas only 17% of the males were paired before they entered the water.

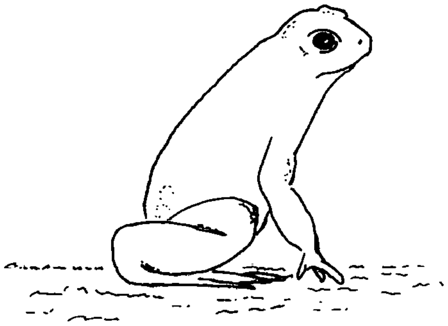
Unpaired males searched for females and pairs with characteristic postures on the land and in the water (Figs.3.2a,b). On detecting any movement they would attempt to grasp it with their forearms. They appeared to be quite indiscriminate and often momentarily grabbed other males, or even the handle of the net, before realising their mistake, relaxing their grip and going off to search elsewhere.

Having entered the pond almost all of the unpaired males remained in the pond. As dusk approached, many of the unpaired males lined up around the edge of the pond and sat there with their heads poking above the water surface, facing towards the land and apparently waiting for the newly arriving females and pairs to enter the pond. Unpaired females were found as they entered the water or within a few hours of doing so. Pairs were approached by single males as soon as they reached the edge of

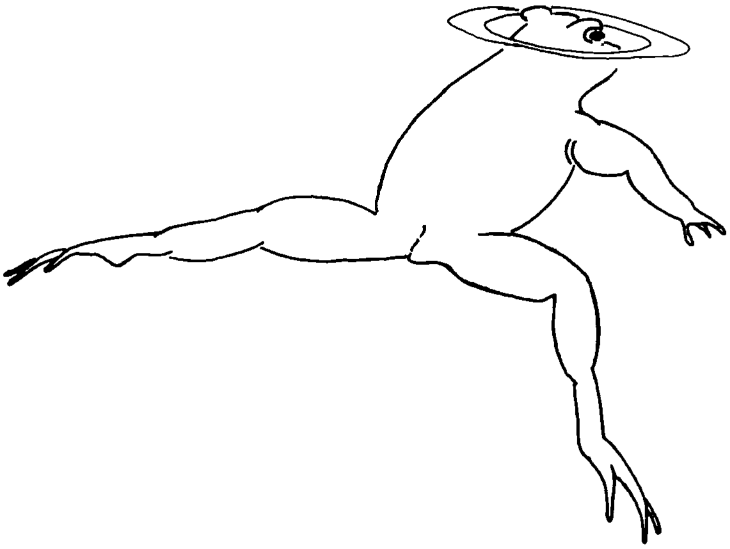
Fig.3.2 Postures adopted by unpaired male toads when searching for females.

(a) on land,

(b) in the pond.



a



b

the pond. From the moment they entered the pond until spawning took place a few days later, pairs were continuously bombarded by unpaired males. On encountering a pair, a single male often launched a vigorous attack and attempted to dislodge the rival from the females back (Fig.3.3). The paired male defended by lashing out with his hind legs, but once the attacker took hold an intense wrestling match would ensue which could continue for several hours.

The struggles by competing males resulted occasionally in the death of the female, who found it difficult to come up to the water surface to breathe because of the increased weight on her. In one case up to eight males, a total weight of 205g, were observed clasping, to the female who was close to death. The female, it has been suggested, dives or swims away to prevent attacks.

Fig.3.3 How one male attempts to oust another (after Davies & Halliday 1978).

Where the interloper is rejected,

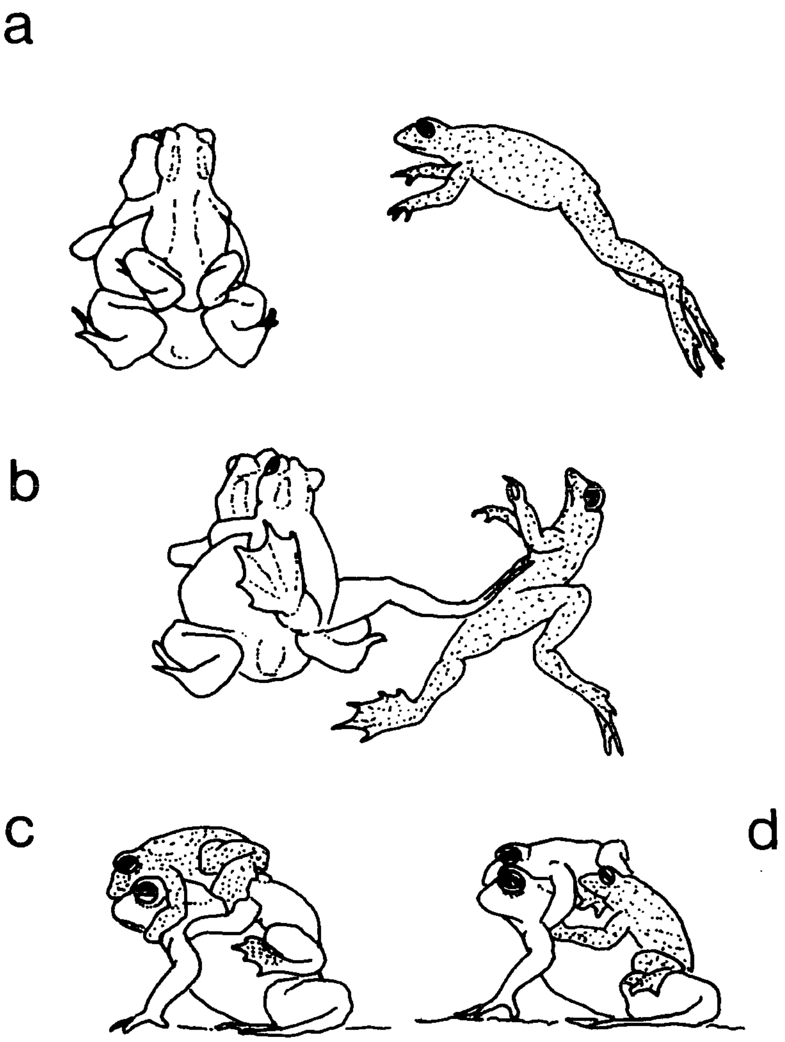
a) an unpaired male launches an attack on the pair,

b) the paired male kicks him away.

Where the male succeeds either by:

c) holding onto the front of the female and pushing the paired male off her backwards with his hind legs, or

d) squeezing in between the pair from behind and pushing forward so as to force the paired male out of amplexus.


a
b
c
d

3.5 Discussion

Numerous studies indicate that anuran breeding aggregations tend either to endure over a prolonged period or to last for a short time of explosive activity (Wells 1977). As predicted by Emlen and Oring (1977) and subsequently demonstrated by Davies and Halliday (1979), Wells (1977) and Howard (1980,1981), the duration of the breeding period can play a significant role in determining the species mating system. For example, prolonged breeding anurans are often characterized by male-skewed operational sex ratios and territorial males who defend oviposition or calling sites. Although male territoriality and aggressive behaviour within breeding aggregations has been reported for several anuran families, it has not yet been described for a bufonid.

Many workers (Moore 1954, Reed 1963, Frazer 1966, Collier 1970, Gittins et al 1980a) have drawn attention to the imbalance in the sex ratio at the breeding ponds. Gittins et al (1980) stated that this might result if the females did not breed every year. Davies and Halliday (1977) found that at any one time there were about six males to every female in their pond in Oxford; Moore (1954) working in Dorset, found an instantaneous sex ratio of two males to every female and Gittins et al (1980a) found a sex ratio of 3:1 for toads coming to their site in Llandrindod Wells. The imbalance in this ratio can be partly explained by the fact that males arrive earlier and remain throughout the spawning period, whereas females only stay for a few days yet Frazer (1966) found that only 11% of the males returned to breed the following year and that some females reappeared at the breeding ground for two consecutive seasons. Marked toads were not found at nearby ponds in subsequent years rather suggesting that the low recapture is a result of mortality. A study at Llandrindod Wells over 1978-79 found that 27% of the males captured in 1979 appeared to bear a mark from 1978 and similarly 16% of the females. The lower percentage of returns for female toads may indicate that some females do not breed every year or may be indicative of a disparity in ´catchability´ for each sex, reflecting behavioural differences (Wisniewski et al 1980).

There is some evidence that male toads reach sexual maturity a year earlier than females (Smith 1969). If toads are long-lived in the wild this would not greatly effect the sex ratio, but if they are short-lived breeding only once or twice upon reaching maturity, then the differential maturation rate would have an important effect on the sex ratio. More data are required on the life expectancy, age of maturation and frequency of breeding in the toad before one can be clear about the reasons for the skewed sex ratio.

The arrival of the male toads at the spawn site before females has been noted previously (Smith 1969). In this investigation the number of females increased relative to the number of males as the migration proceeded. There was no significant change in the sizes of male or female arriving at the pond although Gittins et al (1980a) noted that the average size of the males increased, suggesting that small males arrive at the pond first with the larger males arriving with the main body of females.

Very few small males succeeded in mating, Gittins et al (1980a) noted at Llandrindod Wells that small males were sometimes displaced by larger males in fights for female possession, however they point out that this process is complicated by the difficulty in displacing small males from small females than from larger females. That small males come to the lake before the larger males and the main body of females could be a behavioural response to effectively increase their ´season´ and thus marginally increase their chances of mating. Large males, who are more likely to be successful in mating can afford to wait until female numbers are higher when the chance of encounter will also be higher.

Chapter 4 ......

Introduction

This chapter deals with the predictions made in the opening chapter, investigating the length and weight distributions of both sexes before analysing the scaling relationships for both paired and unpaired animals.

4.1 Length and Weight Distributions

The mean body length of migrating males was 63.1mm (SD=4.1, Range 50-77mm), and for females 77.36mm (SD=4.8, Range 68-88mm). A test for skewness and kurtosis showed that both male and female length distributions differed from normal. The moment statisics showed that there was tendency to skewness in the two distributions, Table 4.1a,b.

Arm

The mean arm length of males was 29.98mm (SD=3.46, Range 22-37mm) and for females was 36.88mm (SD=2.5, Range 31-42mm). Tests showed that there were differences from normal with a tendency to negative skewness in the two distributions (Tables 4.1a,b, Fig.4.1a,d, Appendix II).

Leg

The mean leg length of males was 62.04mm (SD=7.4, Range 59-79mm) and for females was 66.21mm (SD=4.04, Range 50-76mm). Again there was a tendency to negative skewness in both

Table 4.1a

Mean Size + 1 S.D. of measured body parameters for female Bufo bufo, lengths in mm.

	Mean	SD	N
Arm	36.38	2.48	56
Leg	66.36	4.04	56
Body	77.36	4.76	56
Wt	44.77	9.79	56

Table 4.1b

Mean size + 1 S.D. of measured body parameters for paired and unpaired male Bufo, lengths in mm, weights in mg.

Paired

	Mean	SD	N
Armlength	30.24	1.94	353
Leglength	63.23	4.07	353
Bodylength	63.05	4.06	353
Bodyweight	21.94	3.91	353

Unpaired

	Mean	SD	N
Armlength	30.12	2.03	59
Leglength	62.52	3.77	59
Bodylength	62.85	4.15	59
Bodyweight	21.83	4.30	59

distributions. There is a large overlap in the ranges of the sexes.

4.2 Changes in mean length during migration

Length measurements were taken for all males and females arriving during the course of the migration, there were no significant between day differences in the sizes of animal arriving for either sex, except for males on days six and seven ($t=11.02$, $P<0.001$).

4.3 Inter-relationships

Body length and Body Weight

Regression lines relating body length to body weight for both sexes are shown in Fig 4.2c. Correlation coefficients for each relationship were similar ($z=-0.1$ ns) but the gradients for each were significantly different ($d=2.22$, $P<0.05$) indicating that for a given length females were significantly heavier than males (Tables 4.2a,b).

Arm

Regression lines relating arm length to body weight are shown in Fig. 4.2b. There were no significant differences in the relationship between arm length and body weight for males and females.

Table 4.2a

Correlation relating body size and limb length for male and female toads.

	Male			Female		
	Leg	Body	Wt.	Leg	Body	Wt.
Arm	0.70*	0.74*	0.72*	0.74*	0.73*	0.67*
Leg		0.79*	0.75*		0.82*	0.90**
Bodylth			0.80*			0.81*

* r significant at P<0.01

** r significant at P<0.001

Table 4.2b

Comparison of calculated regression and correlation coefficients relating various body size parameters between male and female toads.

	z			d		
Variable	Leg	Body	Wt	Leg	Body	Wt
Arm	0.58	0.36	0.68	1.62	0.09	1.84
Leg		0.27	3.39*		1.60	2.43*
Body			0.10			2.22*

* r significant at P<0.001

Fig.4.2a-c. Relationships between various body size measurements for Bufo bufo, both sexes shown seperately.

a) Log. arm length v Log. body (length & weight)

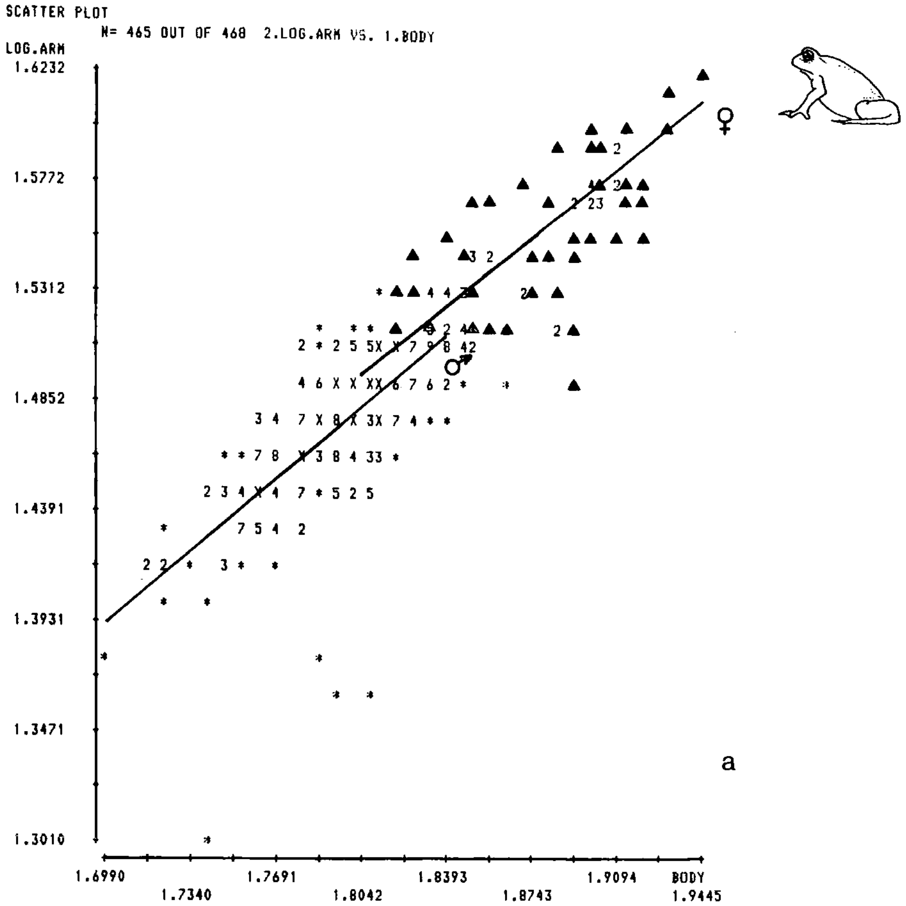
b) Log. leg length v Log. body (length & weight)

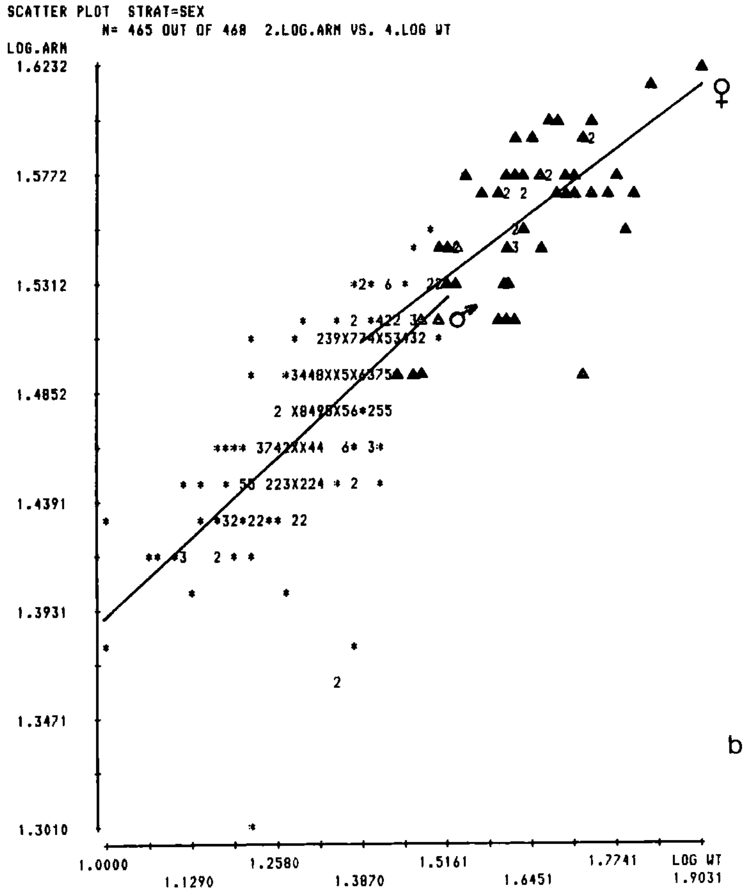
c) Log. body length v Log. body weight

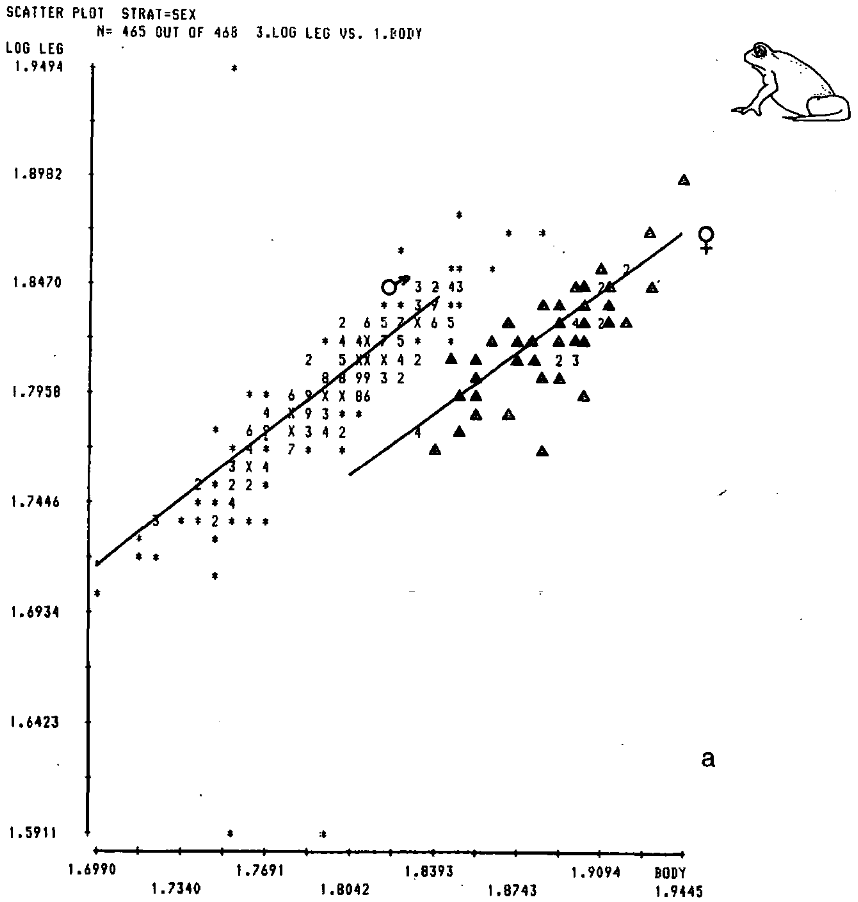
Key

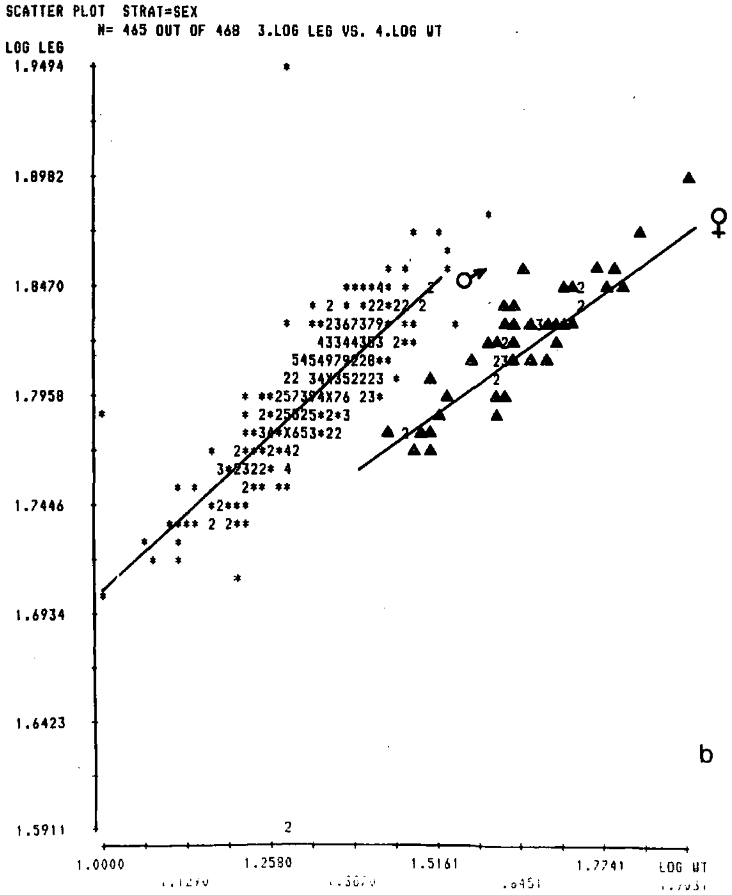
▲ =Females

✳ =Males

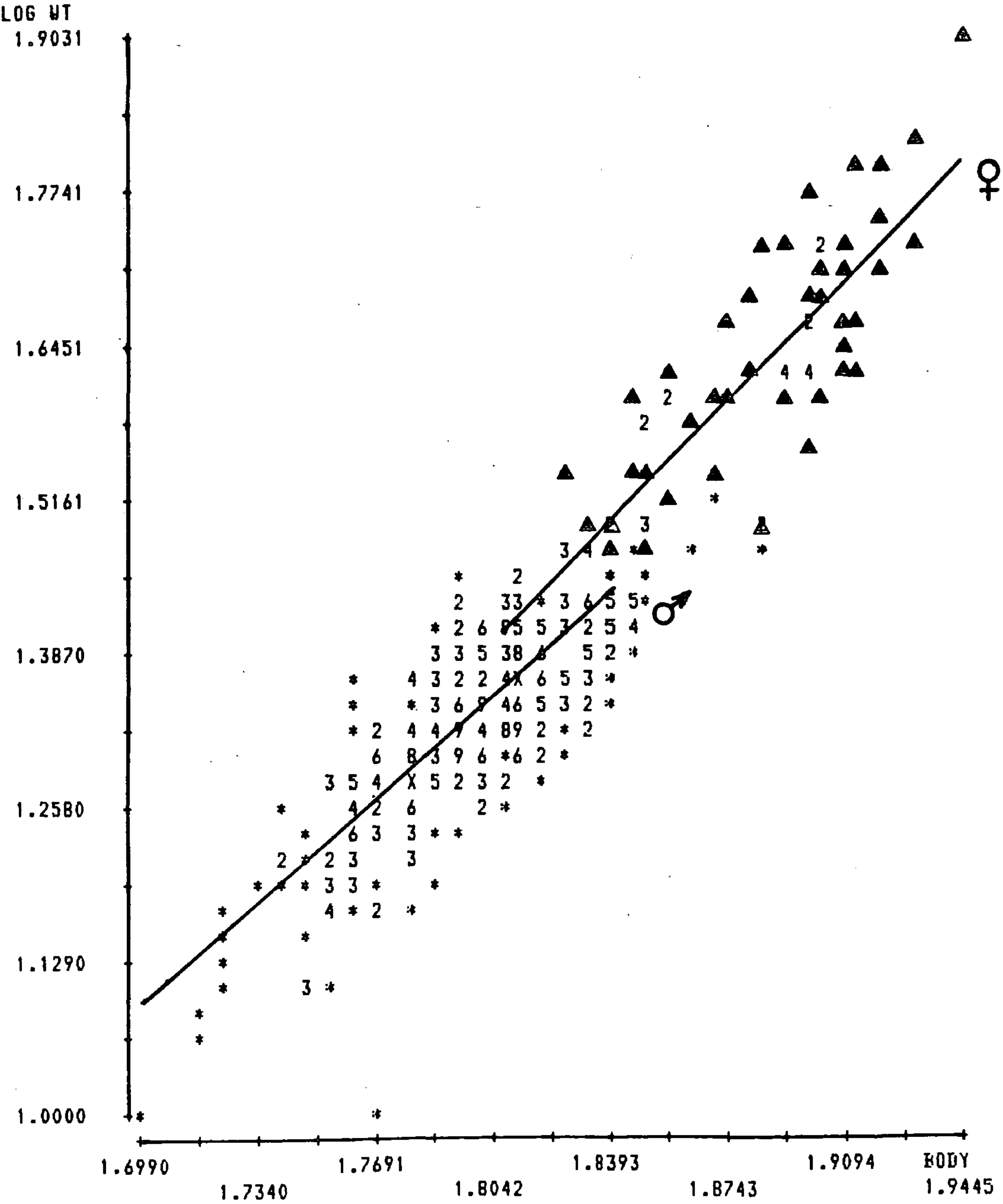

SCATTER PLOT
N= 465 OUT OF 468 2.LOG.ARM VS. 1.BODY
LOG.ARM
1.6232
1.5772
1.5312
1.4852
1.4391
1.3931
1.3471
1.3010
1.6990
1.7340
1.7691
1.8042
1.8393
1.8743
1.9094
BODY
1.9445
♀
♂
a


SCATTER PLOT STRAT=SEX
N= 465 OUT OF 468 2.LOG.ARM VS. 4.LOG WT
LOG.ARM
1.6232
1.5772
1.5312
1.4852
1.4391
1.3931
1.3471
1.3010
1.0000
1.1290
1.2580
1.3870
1.5161
1.6451
1.7741
LOG WT
1.9031
♀
♂
b


SCATTER PLOT STRAT=SEX
N= 465 OUT OF 468 3.LOG LEG VS. 1.BODY
LOG LEG
1.9494
1.8982
1.8470
1.7958
1.7446
1.6934
1.6423
1.5911
1.6990
1.7340
1.7691
1.8042
1.8393
1.8743
1.9094
BODY
1.9445
♂
♀
a


SCATTER PLOT STRAT=SEX
N= 465 OUT OF 468 3.LOG LEG VS. 4.LOG WT
LOG LEG
1.9494
1.8982
1.8470
1.7958
1.7446
1.6934
1.6423
1.5911
1.0000
1.2580
1.5161
1.7741
LOG WT
♂
♀
b

SCATTER PLOT STRAT=SEX
N= 468 OUT OF 468 4.LOG WT VS. 1.BODY



Leg

Regression lines relating leg length to body length for both sexes are shown in Fig. 4.2a. Gradients for these lines were significantly different ($t=2.43$, $P<0.05$) as were the correlation coefficients ($z=-3.39$, $P<0.01$) indicating that for a given weight females have shorter legs than males, which might be expected in view of the fact that females are gravid and thus heavier when compared to males of the same length during the breeding season.

4.4 Relationships between pairs

Since individual weights alter during the migration it was considered that body length was a more accurate measure of body size. In addition arm and leg lengths were taken for comparison of scaling in the two sexes.

The individual sizes of males and females taken in copula were compared by a paired t test. The results in Table 4.3 show that the sexual dimorphism between pairs is marked especially for body length, leg lengths having the smallest t value.

The data were further analysed to determine whether large females tended to pair with large males (positive assortative mating) or with small males (negative assortative mating) independent of any sexual dimorphism in body size. This assortative mating was tested by a product moment correlation coefficient between the size of the male and female in each pair (Figs.4.3a-g, Table 4.4). The results show that there was no assortative mating among pairs. T tests comparing the size of

Table 4.3

T Tests comparing body size and length parameters for male and female toads taken in copula

	T	Sig.	Ratio
Bodylength	19.29	P<0.001	0.82
Armlength	14.26	P<0.001	0.82
Leglength	4.77	P<0.001	0.95
Bodyweight	16.90	P<0.001	0.50

Table 4.4

Between sex comparison of body size parameters for paired toads.

	Correlation Values, r			
Males	Females			
Variable	Arm	Leg	Body	Bodywt
Arm	0.01		0.05	
Leg		0.06	0.04	
Body			0.07	
Wt			0.05	0.14

All r values non significant at P>0.05

Figs.4.3a-g Scatter diagrams comparing various body size parameters for male and female Bufo taken in copula.

a) arm length

b) leg length

c) body length

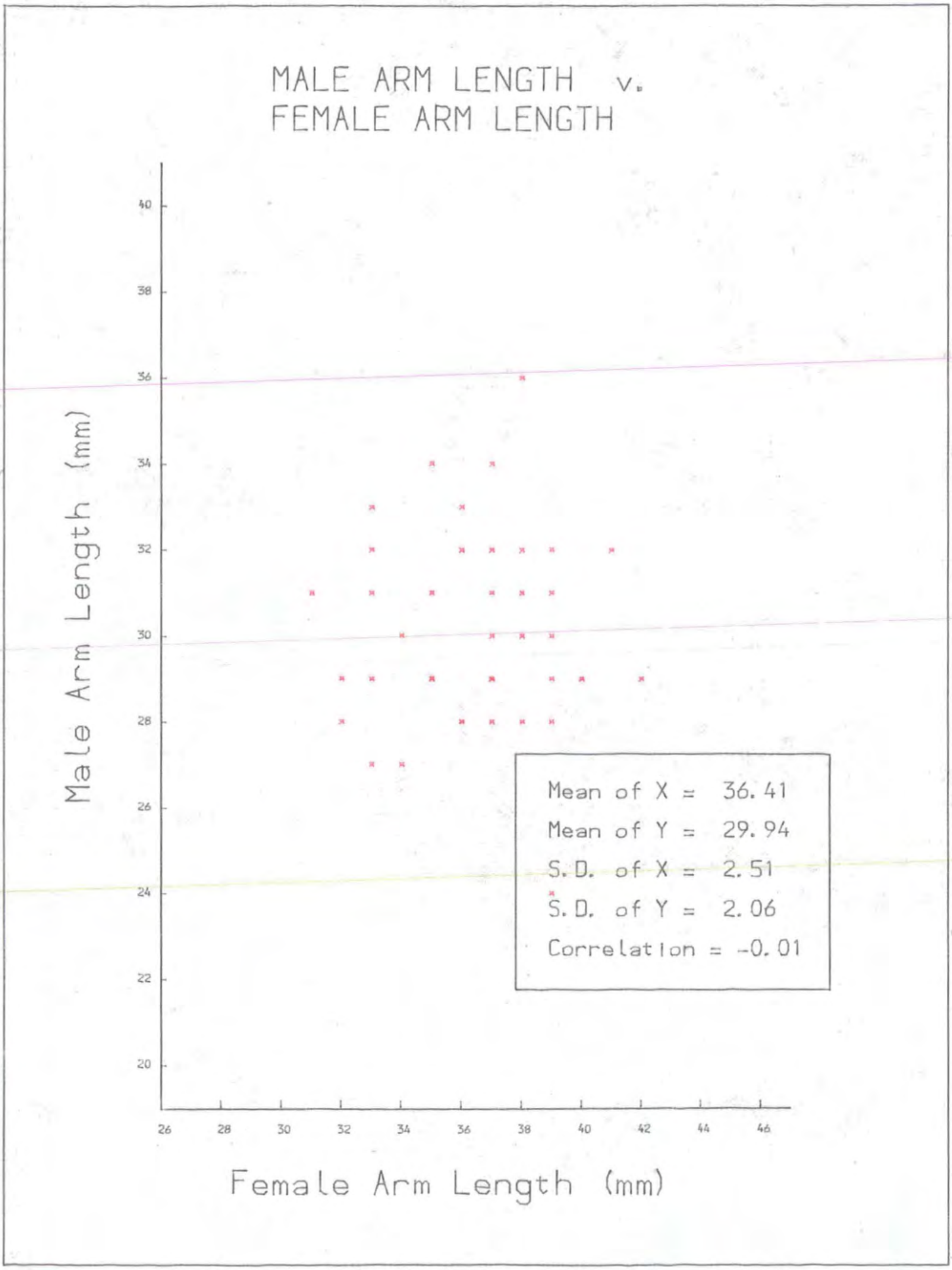
d) body weight

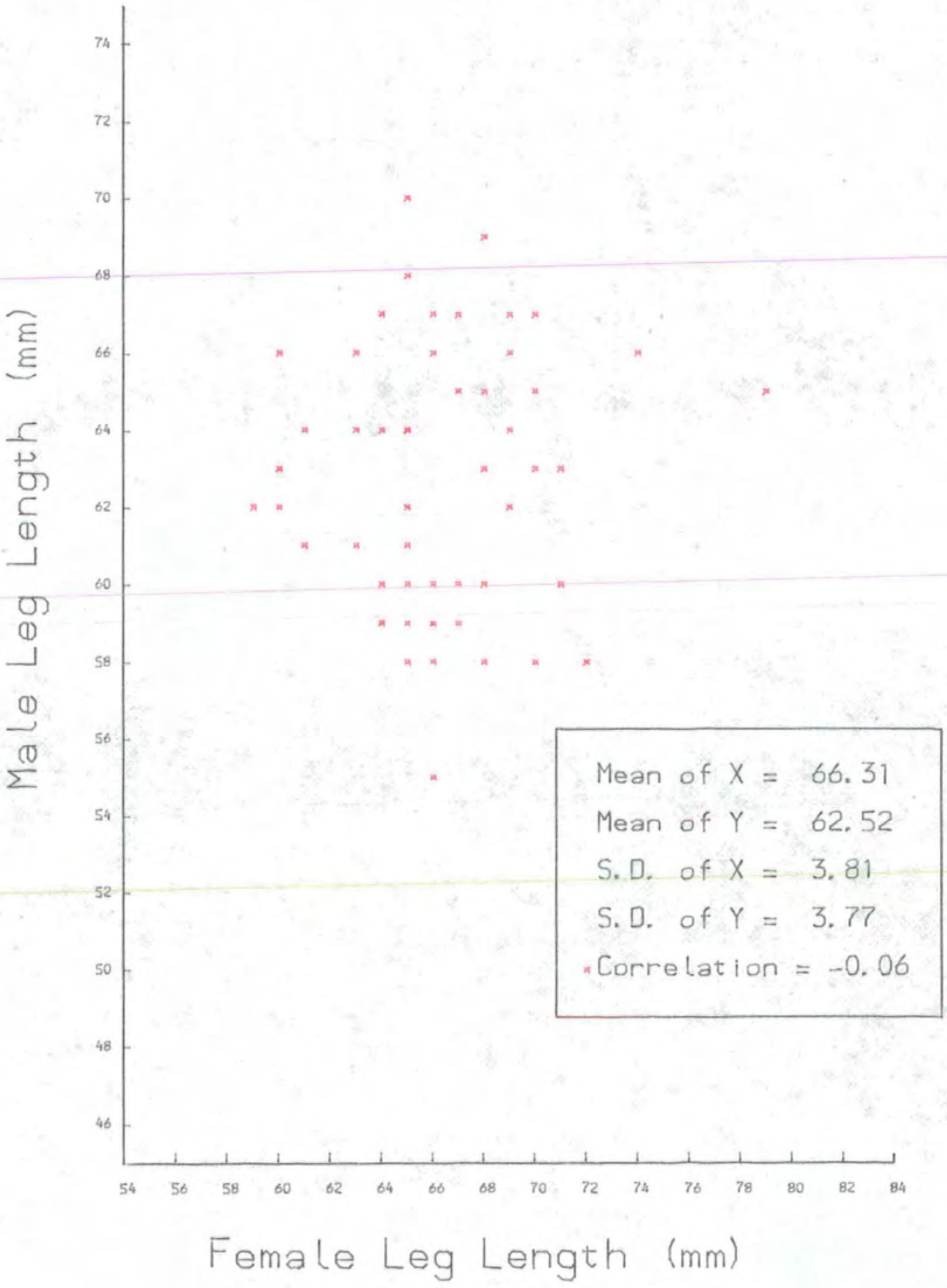
e) male arm length v female body length

f) male body weight v female body length

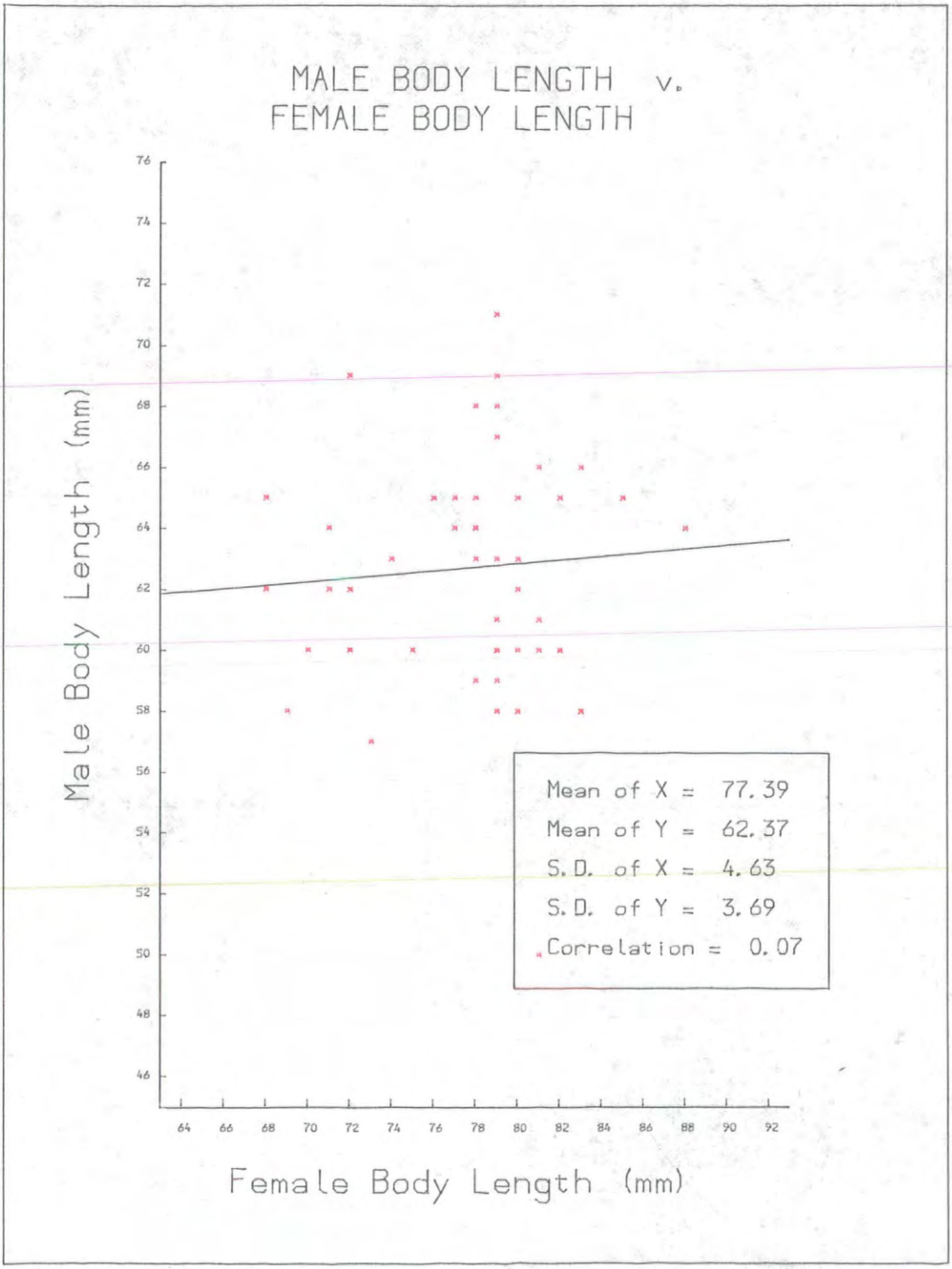
g) male leg length v female body length

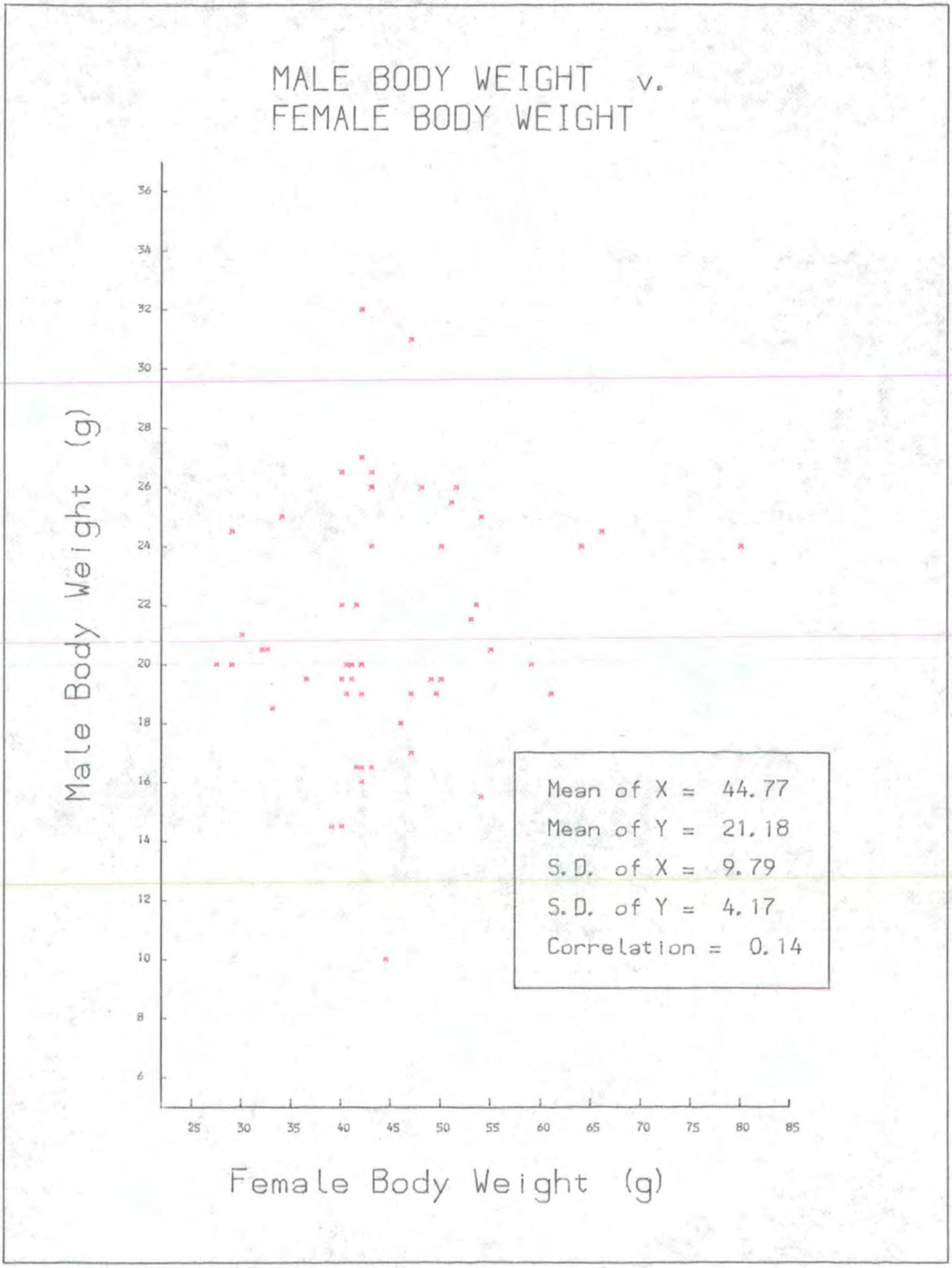
All lengths in mm, weights in mg.


MALE ARM LENGTH v.
FEMALE ARM LENGTH
Male Arm Length (mm)
40
38
36
34
32
30
28
26
24
22
20
Female Arm Length (mm)
26
28
30
32
34
36
38
40
42
44
46
Mean of X = 36.41
Mean of Y = 29.94
S.D. of X = 2.51
S.D. of Y = 2.06
Correlation = -0.01



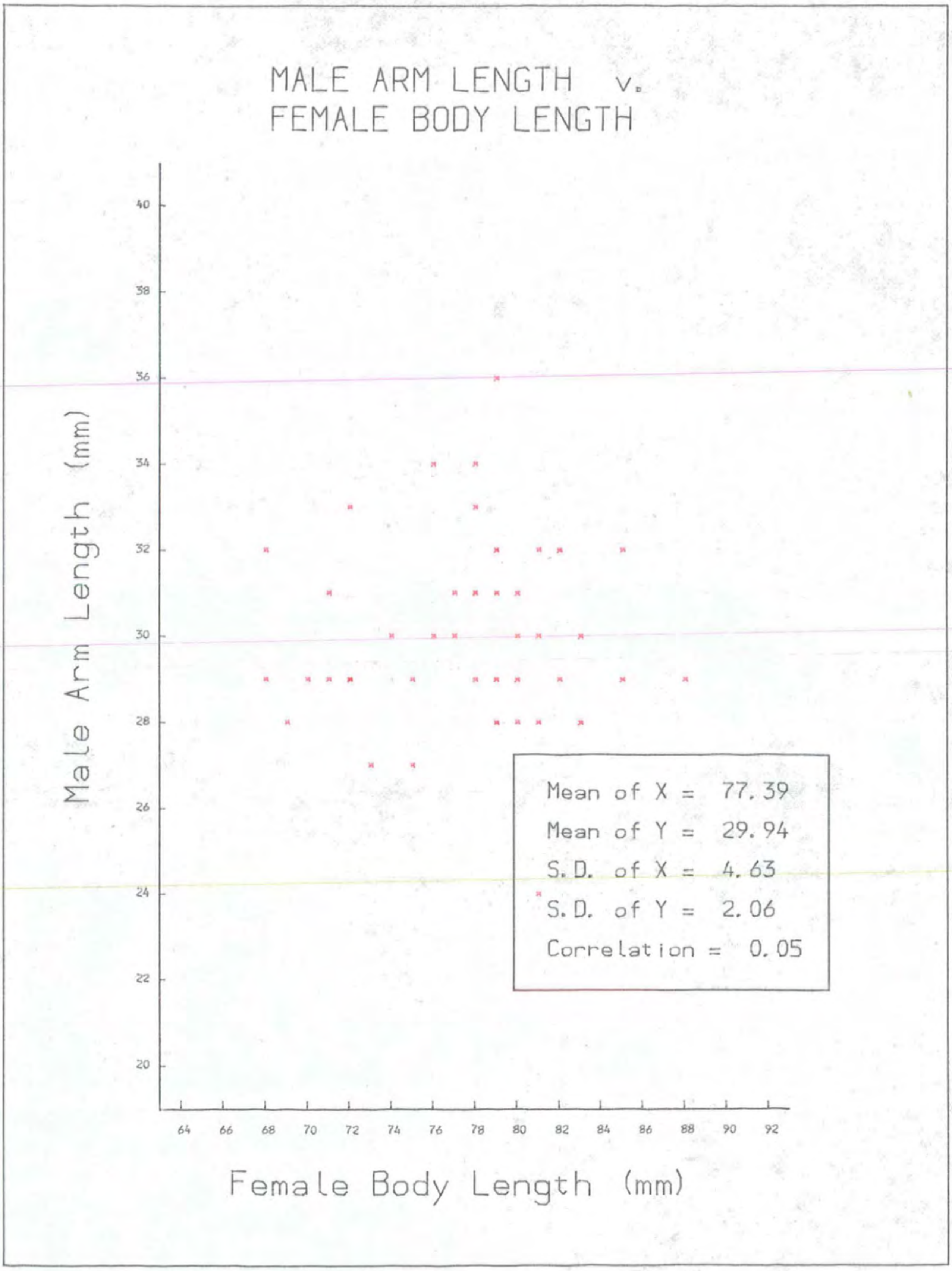
MALE LEG LENGTH v.
FEMALE LEG LENGTH


MALE BODY LENGTH v.
FEMALE BODY LENGTH
Male Body Length (mm)
76
74
72
70
68
66
64
62
60
58
56
54
52
50
48
46
64
66
68
70
72
74
76
78
80
82
84
86
88
90
92
Female Body Length (mm)
Mean of X = 77.39
Mean of Y = 62.37
S.D. of X = 4.63
S.D. of Y = 3.69
Correlation = 0.07

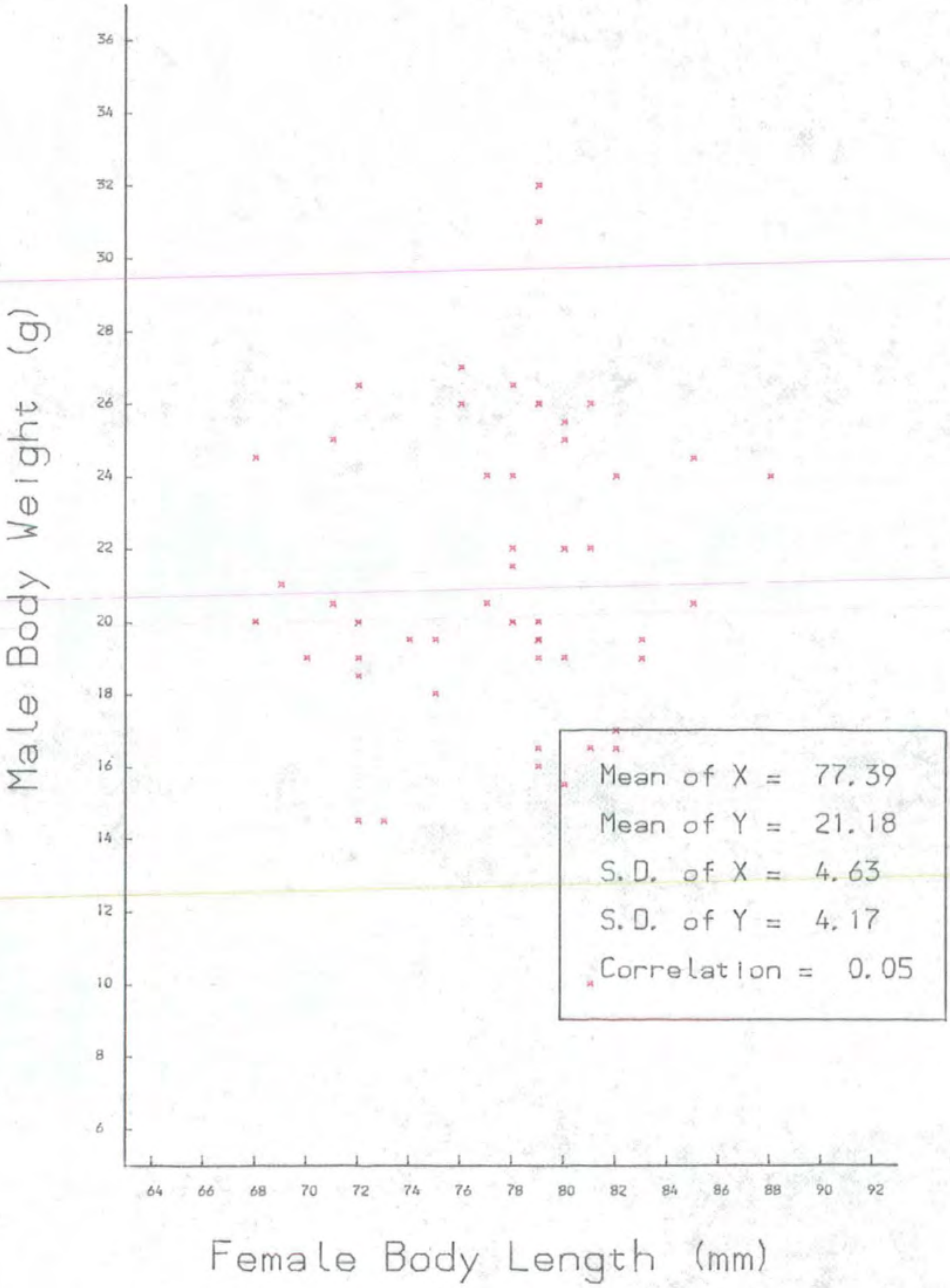


MALE BODY WEIGHT v.
FEMALE BODY WEIGHT

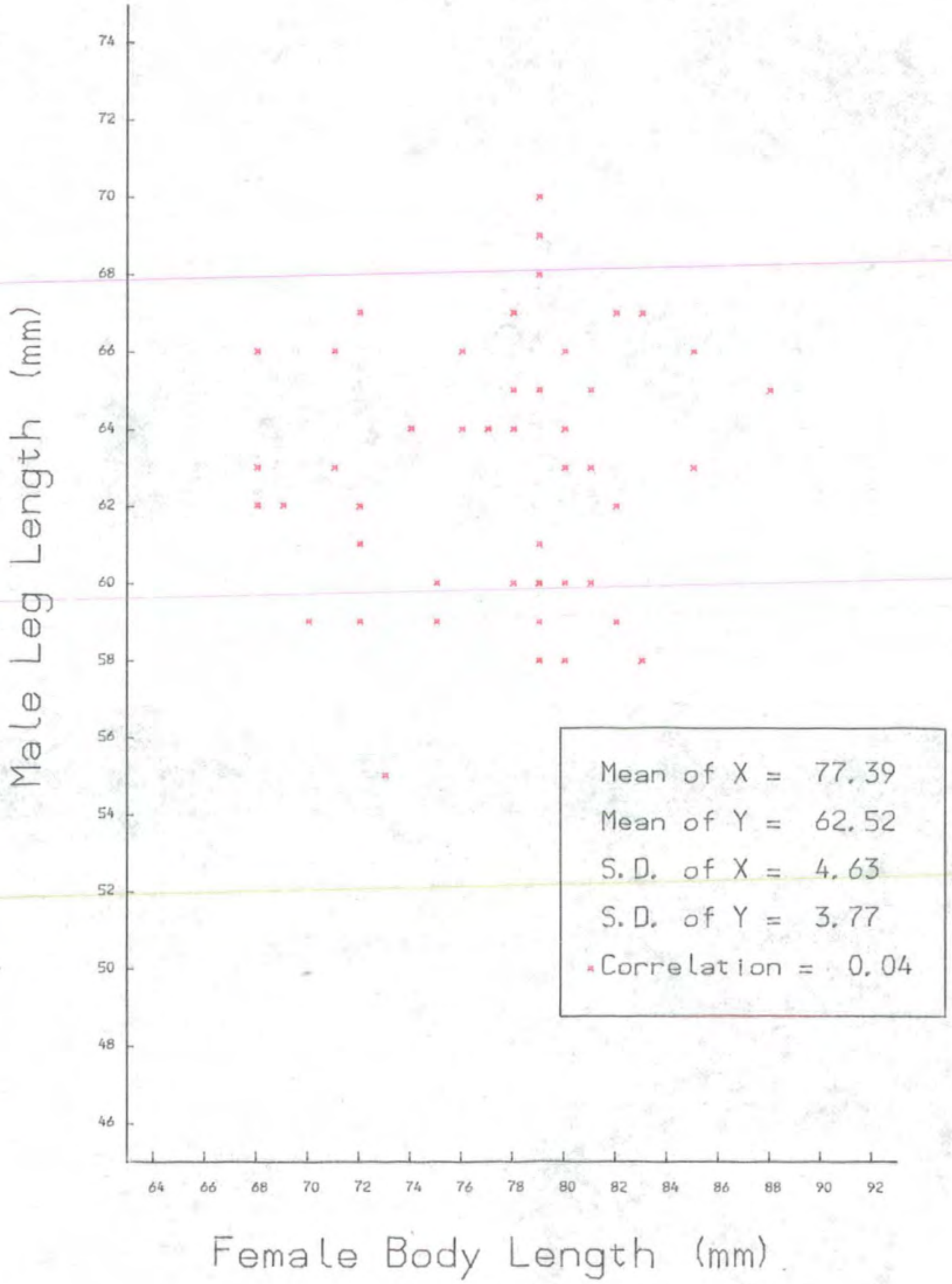
Mean of X = 44.77
Mean of Y = 21.18
S.D. of X = 9.79
S.D. of Y = 4.17
Correlation = 0.14


MALE ARM LENGTH v.
FEMALE BODY LENGTH
Male Arm Length (mm)
40
38
36
34
32
30
28
26
24
22
20
64
66
68
70
72
74
76
78
80
82
84
86
88
90
92
Female Body Length (mm)
Mean of X = 77.39
Mean of Y = 29.94
S.D. of X = 4.63
S.D. of Y = 2.06
Correlation = 0.05

MALE BODY WEIGHT v.
FEMALE BODY LENGTH



MALE LEG LENGTH v. FEMALE BODY LENGTH



males found in amplexus with females with unpaired males were non significant indicating that females did not select males on the basis of size, rather that mating was random (Table 4.5).

4.4 Effect of Male Size

Mean snout:vent lengths of males observed in amplexus (62.9mm) was not significantly greater (t=0.25, P>0.05, N=353) than the mean SVL of unmated males (63.1mm), suggesting that females did not preferentially select large males as mates (Table 4.5). However, when each variable was correlated for paired and unpaired males, d tests showed paired males to have relatively longer arms to leg length (d=3.27, P<0.002) than unpaired individuals, see Table 4.6, Figs.4.4a-c.

Table 4.5

T tests comparing body size parameters for paired and unpaired males.

Variable	Body length	Arm length	Leg length	Body weight
Bodylength	0.25			
Arm length		0.49		
Leg length			0.42	
Body weight				0.70

All non significant at $P<0.05$.

Table 4.6 a

Correlations between limb length and measures of body size for paired and unpaired male toads (all r values significant at P<0.001).

	Correlation coefficients	
Variable	Bodylth	Bodywt
Leg a	0.94	0.88
b	0.79	0.73
Arm a	0.84	0.80
b	0.74	0.71
Body a		0.87
b		0.79

a=paired b=unpaired

Table 4.6b

Comparison of calculated regression coefficients relating various body size parameters between paired and unpaired male toads

	z			d		
	Leg	Body	Wt	Leg	Body	Wt
Armlth	3.71*	1.90	1.50	3.27*	0.84	0.03
Leglth		4.74*	3.05*		0.74	
Bodylth			1.86			0.08

* r significant at P<0.002

Fig.4.4 Relationships between various body size measurements for <u>Bufo</u> males.

(a) Log. arm length v Log. body (length & weight)

(b) Log. leg length v Log. body (length & weight)

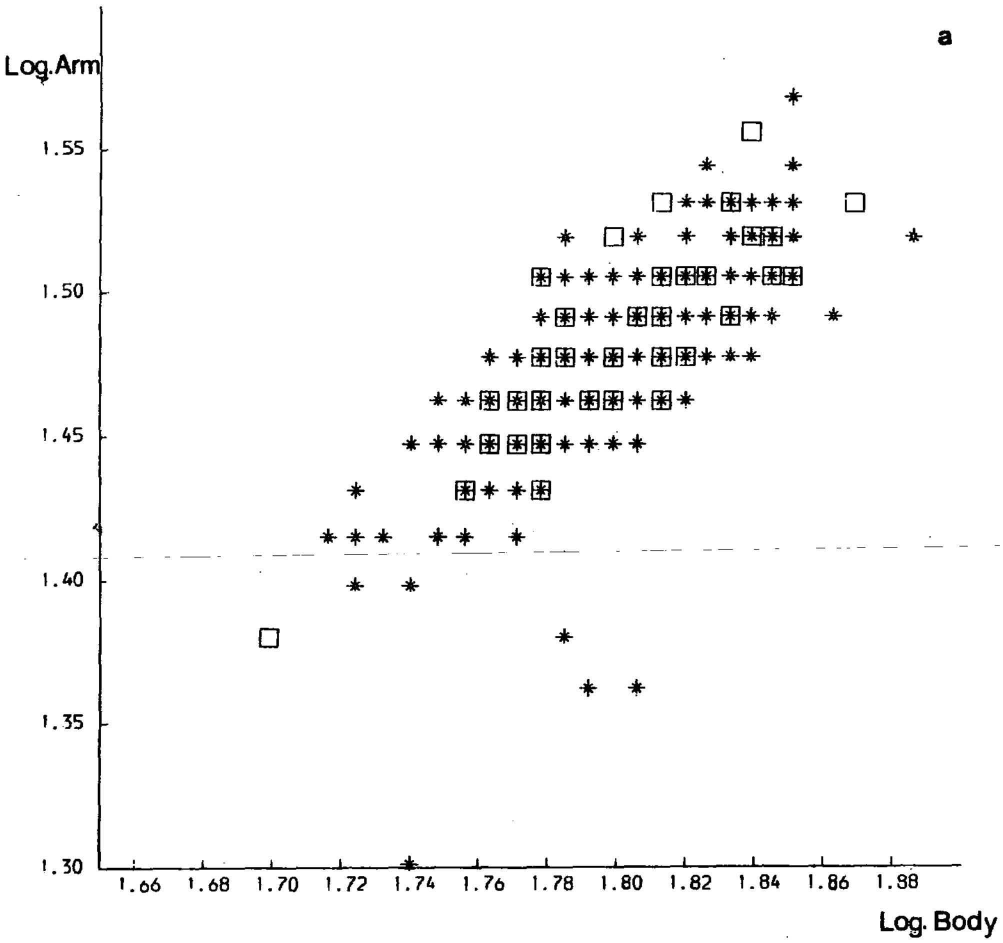
(c) Log. body length v Log. body weight.

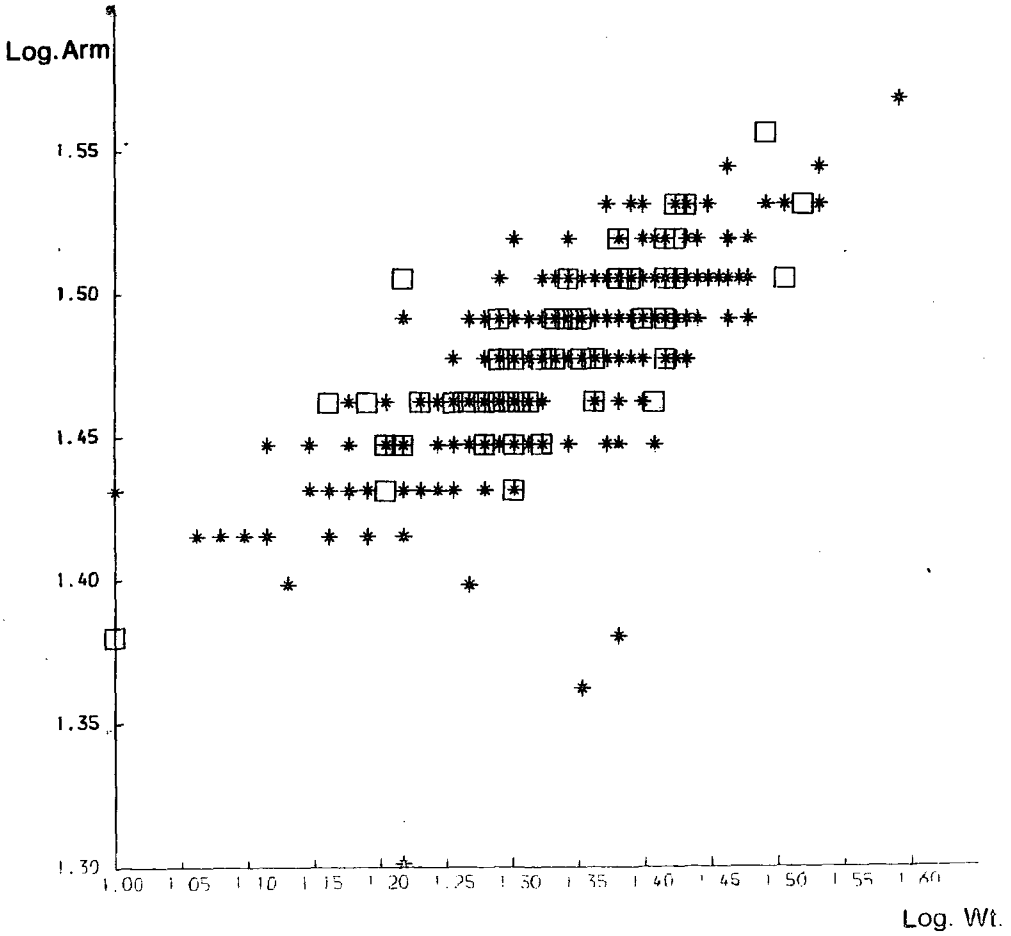
Log. Arm length v Log. Leg length.

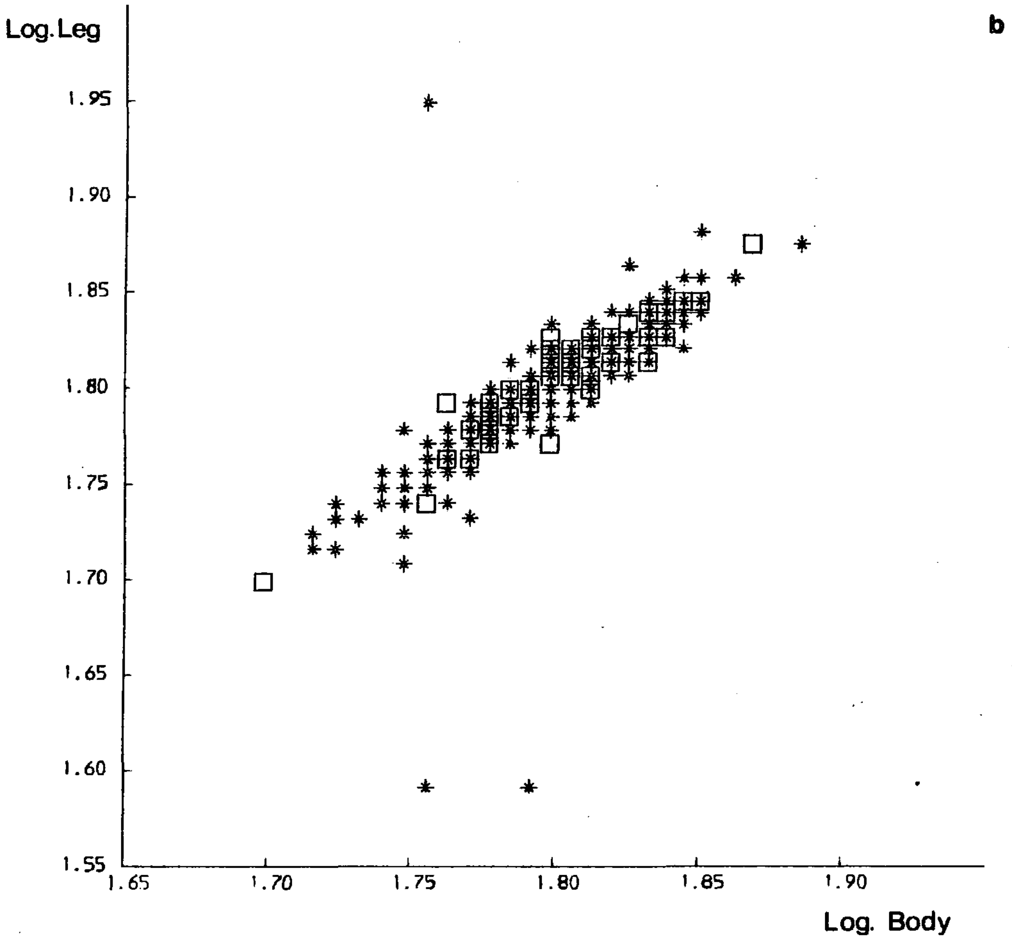
<u>KEY</u>

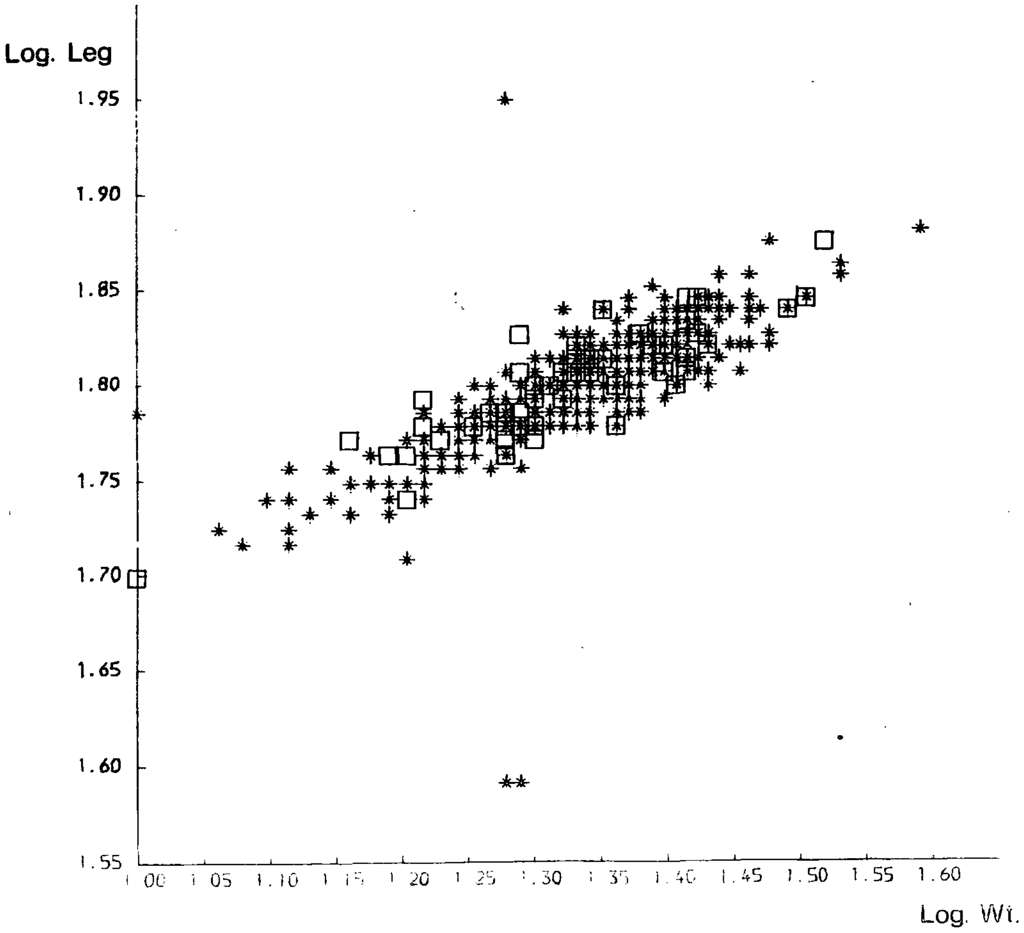
□ = paired

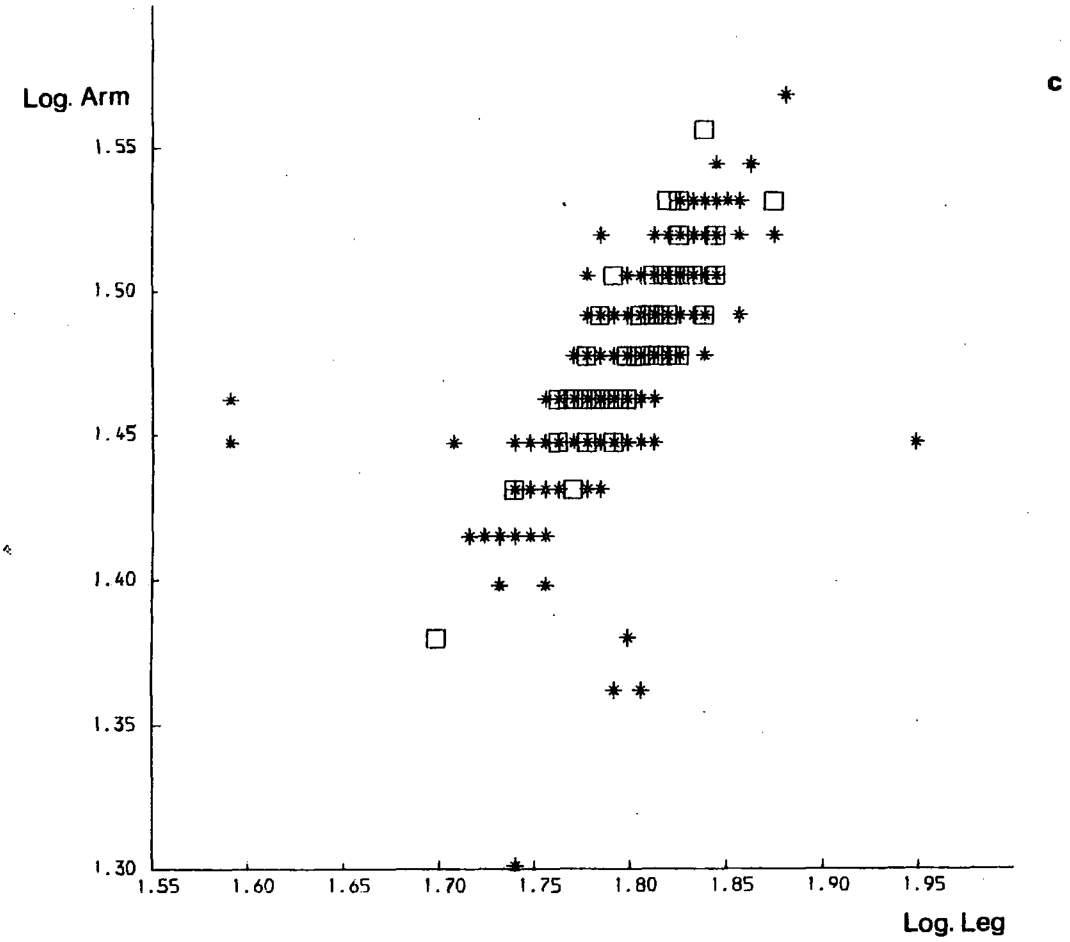
* = unpaired

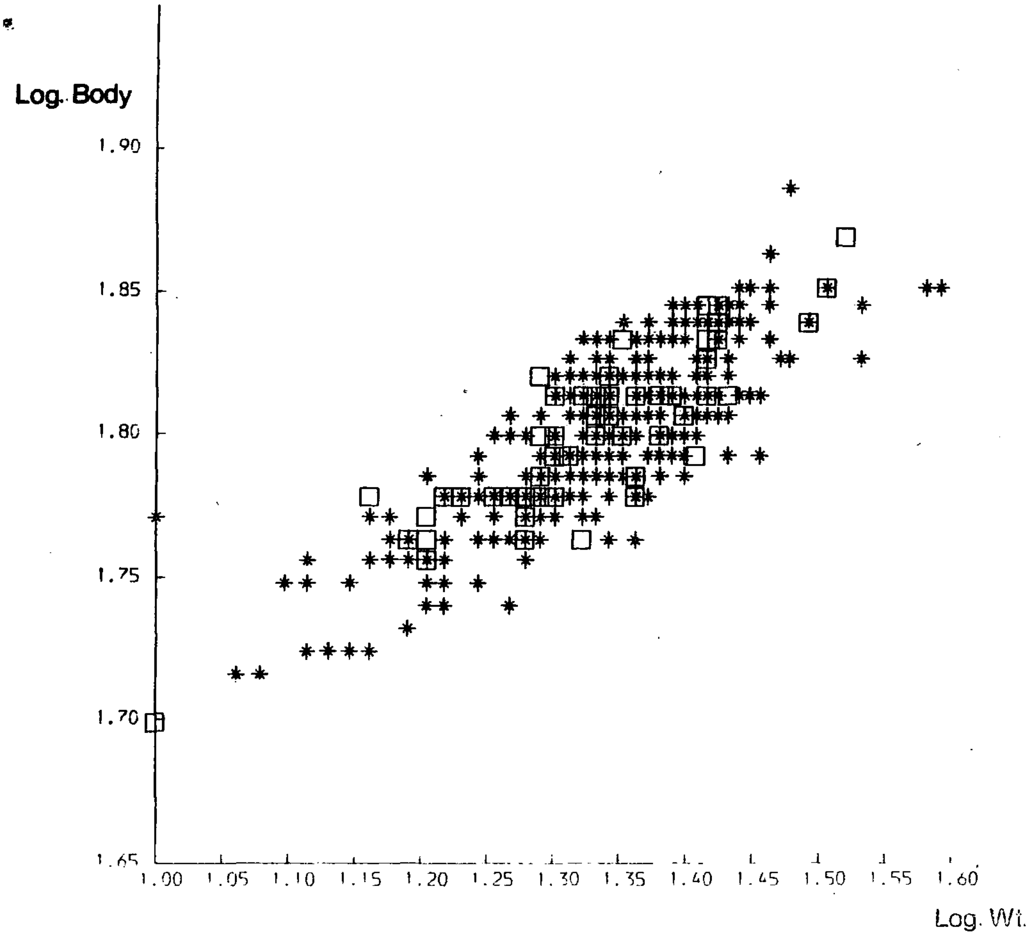

a
Log.Arm
1.55
1.50
1.45
1.40
1.35
1.30
1.66
1.68
1.70
1.72
1.74
1.76
1.78
1.80
1.82
1.84
1.86
1.88
Log. Body


Log.Arm
1.55
1.50
1.45
1.40
1.35
1.30
1.00
1.05
1.10
1.15
1.20
1.25
1.30
1.35
1.40
1.45
1.50
1.55
1.60
Log. Wt.


Log.Leg
b
1.95
1.90
1.85
1.80
1.75
1.70
1.65
1.60
1.55
1.65
1.70
1.75
1.80
1.85
1.90
Log. Body


Log. Leg
1.95
1.90
1.85
1.80
1.75
1.70
1.65
1.60
1.55
1.00
1.05
1.10
1.15
1.20
1.25
1.30
1.35
1.40
1.45
1.50
1.55
1.60
Log. Wt.


c
Log. Arm
1.55
1.50
1.45
1.40
1.35
1.30
1.55
1.60
1.65
1.70
1.75
1.80
1.85
1.90
1.95
Log. Leg


Log. Body
1.90
1.85
1.80
1.75
1.70
1.65
1.00
1.05
1.10
1.15
1.20
1.25
1.30
1.35
1.40
1.45
1.50
1.55
1.60
Log. Wt.

4.5 Discussion

At the pond male toads were significantly smaller than the females (Figs.4.1 a-d). As noted by Davies and Halliday (1976) in other animal species where males fight for the possession of females sexual selection results in larger body size in males (e.g. Scatophaga, Parker 1978; Asellus, Ridley and Thompson 1979) and consequently they assumed that in toads that there is stronger selection for large female body size because of the increased success ie they can lay more eggs.

The scaling relationship analyses carried out reveal that each morphological character is strongly inter-dependant upon the other. The egg loading constraints placed upon the female are such that the increased weight is placed over a greater surface area resulting in a corresponding increase in body length as well as limb length, hence a larger female, dispelling the assumption above made by Davies & Halliday (1979). Significance tests showed that females are heavier than males of comparative body length, similarly for arm and leg lengths. Males on the other hand, require relatively longer legs and arms in order to remain clasped to the female during pre-copular and more importantly fighting, where not only the firmest clasp retains the female but also the longer the legs, the better they are for fending off rival males. From the scatter plots, males for their body size possess relatively longer legs than females, and from the histograms (Figs.4.1a-d) it can be seen that there is a large overlap in leg size which is not apparent for the other measurements. Females appear to have relativly shorter front legs, which would imply that the weight load may be pushed onto the forward limbs during this period.

There was no evidence of assortative mating, this may be due to the particular mating strategies adopted by the toads. In animals where egg investment in females is greater than in males the female would be expected to show greater selectivity in mate choice than the male. This, however, does not appear to be the case for toads, insofar as there is no evidence for such deliberate behaviour on the part of the female.

Although there may be an optimal size of female for any particular sized male, intense male-male competition will mitigate against males being too selective. In a situation where mating is uncertain, it is suggested that males are more successful if they remain with a sub-optimal sized partner, rather than trying to find more suitable ones. The relative sizes of males and females that achieve amplexus have much significance on several aspects of toad breeding success. The optimum size of the male relative to the female is that which allows him to clasp her shoulder with his snout behind her orbits and his cloaca juxtaposed with hers (Plate 2.1).

If the female is 5-10mm larger than the male, this position is achieved by the clasping male. In this fashion, the males grip is exceedingly tight and firm, making them difficult to remove from the female. Also, the head of the female is left free to remain above water and the males cloaca is in position to release sperm directly on the extruding eggs.

Problems arise if the male is the same size or larger than the female. In both cases it covers the entire body and head of the female and restricts movements and respiration. If the male is larger than the female, the entire body is covered and the cloaca extends posterior to that of the female, in which case sperm are likely to be shed beyond the extruding eggs. If the male is too small (more than 20mm smaller) his grip may become supra-axillary, which is less firm than a grip in the axillary position. Licht (1976) quotes Anderson (1944) who noted that in very small males the grip is easily loosened and there is a high probability that they can be dislodged by a rival male whilst paired. If a small male is clasping too far anterior on the back of a female and his cloaca is too far anterior to the females cloaca, then fertilization is likely to be less successful and the percentage of fertilized ova is reduced. Moreover if the male is too small and the head and part of the females dorsum are exposed, then these parts will be clasped by rival males and if a rival gets a good hold on any part of the females body he is likely to stay on.

When a pair is continually molested by rivals the female seeks escape in deep water, if clasped by a small male with another male trying to clasp the female is in danger of drowning because it cannot easily keep its head above water. Often the rival male tries to clasp the female head and inadvertently keeps it under.

There is also the probability of a female being unable to ovulate if she is disturbed by males for a lengthy time. If males are competing for clasping then the eggs may not be fertilized at all.

Previous investigators have suggested that female anurans should select males similar in size to themselves in order to maximise fertilization efficiency (Davies & Halliday 1979, Licht 1976). No positive assortative mating with respect to body size was found in this study or in a similar study on _B. cognatus_ (Sullivan 1983) thus refuting the hypothesis. Other workers have predicted that when afforded the opportunity to select mates, female anurans should prefer large males (Wilbur et al 1978). The results here show that mating males are not significantly larger than unsuccessful males.

CHAPTER 5 .....

5.1 Pondskaters:Amphibicorisae

The surface living bugs are members of 33 families in the Hemiptera . These families form a very distinct ecological group specially adapted for life on the water surface. One of the main features is the coating of fine water repelling hairs that clothe at least the undersides of the insects and prevent them getting wet. All are predatory insects, finding food by sight and or by sensing vibrations in the surface film.

The family Gerridae contains 56 genera with about 450 species in eight sub-families. The major works on higher classification are by Hungerford and Matsuda 1960, Matsuda 1960 and Andersen 1975.

The Gerridae, typified by the common pondskater, Gerris lacustris, are the most advanced of the surface bugs. These are the true pondskaters or water-striders, which are found on almost all stretches of still, fresh water. The insects 'row' themselves across the surface at high speed by means of the long middle legs. The hind legs trail behind and act as a (sort of) rudder. This arrangement leaves the short front legs free to catch food in the form of small insects that fall on to the water. The claws, like those of the Veliidae, are situated just before the apex of the tarsi and the apical position is occupied by a pad of water-repellent hairs. This makes movement over the surface more efficient. Gerris is usually fully winged and a good flier but short winged individuals are often found. The front wings are always homogenous in texture, there being no distinct membrane.

The Gerrids are elongate or oval bodied bugs. The antennae are four segmented and long. The eyes are large, globular, with a multitude of facets, ocelli are absent. The middle thoracic segment is greatly lengthened and the points of insertion of the long, slender middle and hind legs widely separated from those of the front legs (Fig.5.1a,b). The middle and hind coxae are inserted laterally on the body and rotated to an almost horizontal position. The claws are inserted pre-apically on the last tarsal segment. Most gerrids have a single, median scent gland opening on the metasternum.

5.2 Life History and Seasonality

As in other Heteroptera, the life history of water striders includes an egg, five (rarely four) nymphal instars, and an adult stage. The water striders prefer to deposit their eggs at or slightly above the water-level on vegetation but some gerrid species submerge completely to place their eggs below water. The stucture of the egg shell and the gross embryology in a great number of bugs has been studied thoroughly by Cobben (1968).

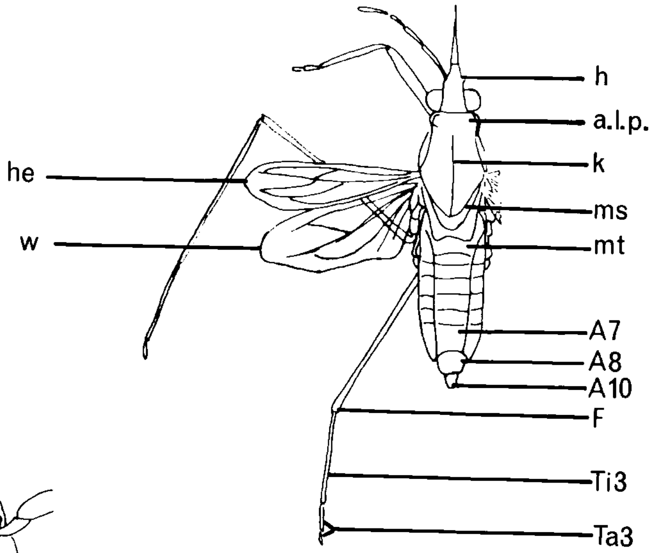
The newly hatched nymph is very feeble, but after it has stretched out its legs and become tanned (about 30 minutes after hatching) it becomes very active. The nymphs are rather similar

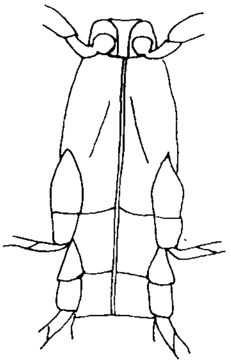
Fig.5.1a,b

(a) Structural features of Gerris of taxonomic importance a.l.p. anterior lobe of pronotum, cv. connexivum, d. disk of pronotum, h. head, he. hemielytron, k. keel, ms. mesonotum, mt. metanotum, w. wing, A7, seventh (sixth visible) abdominal tergum; A8, eigth (first genital) segment; A10, tenth segment or anal tip; F3, femur, Ti3, tibia, Ta3, tarsus of hindleg.

(b) The underside of the thorax of Gerris showing insertion of the legs.

a





b

to the adult in structure except for size, proportions of the body parts and lack of segmental differentiation of the tarsi. The post-embryonic development includes five moults during which the old cuticle splits open along a dorsal Y-shaped suture on the thorax (Cheng 1966b). The newly moulted adult is pale and soft. The teneral development of the adult may last for a few days or even longer (Andersen 1973).

In most water striders the male is slighlty smaller than the female but in some cases this size difference is rather pronounced (as in the genera Trochopus and Halovelia). Mating is usually initiated by the male which lies upon the back of the female, grasping her with his front legs only, although other legs may be used in other families particularly the Veliidae. The male then attaches its genitalia to the female. In many water striders the males remain in the riding position for quite a long time even though not engaged directly in copulation and are reluctant to release their hold even when roughly handled.

5.3 Feeding and Food Preferences

All known water striders are predacious fluid feeders. Their mouth-parts are of the same piercing and sucking type found in other hemipterous insects. The rostrum or beak consists of a four-segmented sheath like labium enclosing two long stylets, the outer mandibular and the inner maxillary pair (Cranston & Sprague 1961, Cheng 1966a). The rostrum is usually held in a horizontal position but when the insect is feeding it is swung forward. The tip of the rostrum is equipped with sensory hairs which aid in the localisation of suitable spots for the penetration of prey (Cheng 1974a). The mandibular stylets with their serrated apices are used for piercing the integument of the prey and also serve to anchor the mouthparts. The tissue of the prey is then liquified by salivary enzymes and sucked up the food tube formed by the highly extensible maxillary stylets held together by hairs (Cheng 1966a, 1974a). The general structure of the salivary glands and the alimentary canal of water striders have been described by Miyamoto (1961) and Cheng (1966a).

Water striders are very sensitive to disturbances of the water surface and may locate potential prey as well as mates by the different ripples created by their movements (Murphey 1971, Wilcox 1972).

Water striders have very few known predators. The metasternal scent glands which discharge through a single mid ventral opening produce a volatile and in some cases rather unpleasant smelling fluid. These insects are therefore believed by many authors to be repugnant to potential predators. However, scent glands are absent in the nymphs and in some adult water striders eg Rheumatobates (Andersen & Polhemus 1976).

5.4 Adaptations

When one is investigating the allometric properties of any insect it is important to consider the insects adaptations especially when life is on the water surface.

The overall structure of water striders deviates from the generalized insect plan. Most of these modifications are adaptations towards a life at the water-air interface and especially towards locomotion on the water surface, involving specialization in the thoracic skeleton and musclature, leg structure and surface fine structure of body and legs (Andersen & Polhemus 1976).

In order that one might fully appreciate the various adaptations to surface-dwelling life, the properties of the water surface must first be considered. The most important property is that of surface tension which is approximately 70.8 dynes per cm at 20°C, since the water surface tends to minimize its energy by making its area as small as possible it behaves like a stretched elastic membrane. When water is in contact with the surface of a solid, the water-air interface meets the solid-air interface at a definite angle which is constant for the substances concerned. This angle, measured in the water, is known as the contact angle. A high contact angle indicates that the surface of the solid is only wetted with difficulty such a surface is then a hydrofuge.

When a water strider is submerged in water it carries with it a large bubble of gas entangled in the hair coat of its body and its appendages. This gas store makes the insect highly buoyant and it will rise rapidly to the surface when released. Once on the surface, the water falls away leaving the insect dry. The causes of this resistance have been much discussed but the most likely explanation is that the hairs of the insect have hydrofuge surfaces, either on account of their innate structure or due to a waxy layer (Holdgate 1955).

The hydrofuge property of the coat hair is not permanent, upon prolonged exposure to water the hairs will finally become wetted and the submerged insect will experience great difficulty in regaining an above water position. Grooming and thorough drying in the air however allows the water strider to resume a hair coat with its former unwettable condition. Grooming of the hair coat of the body and legs is effected by specialized hair structures on the front tibiae (Andersen & Polhemus 1976).

The middle and hind legs are constructed to allow extremely wide movements. When resting, the body of the water strider is elevated above water, and only the distal segments are in contact with the water film. A water strider weighing 10mg requires a total line of contact of about 0.4cm with the water surface just in order to be supported.

Since many water striders are able to make vertical jumps from the water surface to a height of several centimetres (Hadden 1931, Cheng 1974a) the thrust produced by the legs may reach a magnitude of more than 10 times the weight of the insect. The specialized long hairs on the legs of the water strider ensure a corresponding increase in the area of contact (Andersen 1976b).

Locomotion on the water surface is quite diversified within the semi-aquatic Hemiptera (Andersen 1976b). Some species run along the surface using all three pairs of legs but in the more specialized water striders the legs are adapted for different functions. The forelegs are raptorial and are used in feeding. They are shorter than the other two pairs of limbs and differ from them in that they are inserted apically. These limbs are normally used as supports and do not participate in the rowing movements. As in all three pairs of limbs, the claws lie at the base of a sub-apical notch, into which they can be withdrawn when on the water surface. These claws are employed when the insect walks or climbs emergent vegetation.

The mid- and hind-limbs are long and are used in the normal mode of progression as well as in leaping, both of the water and also when on land. As the fulcrum of the limb is very close to its base, its elongation increases the leverage produced by the limb and thus its rowing efficiency. Both mid- and hind-limbs are set close to the centre of gravity of the insect, in the optimal position for steering, and they are rotated so that the coxae and the limbs are horizontally inclined. An analysis of rowing movements (Brinkhurst 1960) has shown that this is an adaptation towards life on the water surface which leads to a loss of efficiency on the land. When placed on a solid substratum these insects either progress by a series of uncontrolled leaps, or walk slowly and awkwardly by the normal ´tripod´ method of most terrestrial insects.

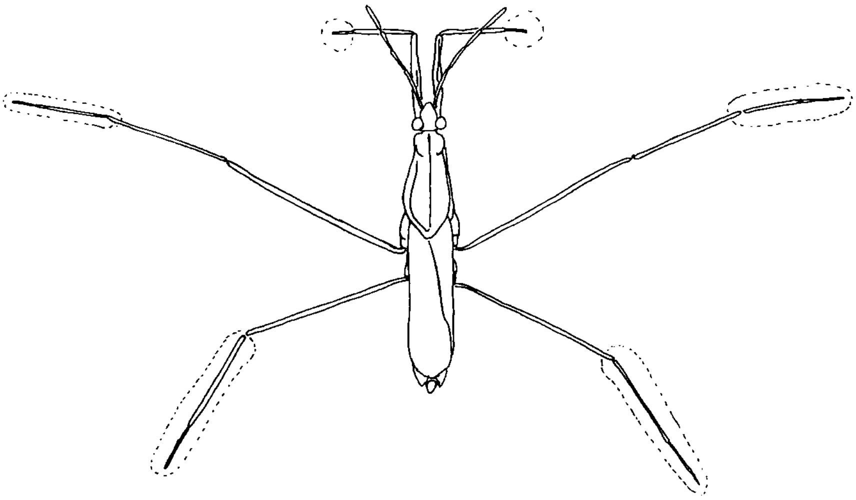
The elongation of the limbs is an adaptation to rowing and not to the distribution of the insects weight over a larger area of the surface (China 1955) as each limb bears one sixth of the total body weight wherever it is placed so long as the depressions made in the surface film do not also co-alesce (Fig.5.2a,b). Increased surface area of the tarsus, however, probably compensates for the increased weight of the larger species as the relationship between weight and ´limiting value´ of the surface tension is constant (see Brinkhurst 1959 for fuller explanation).

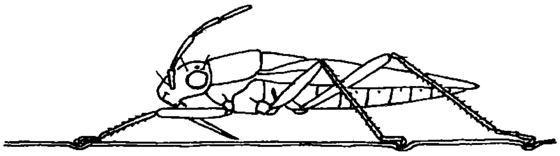
These insects would be unable to maintain their position on the surface if the tarsal claws were not modified as these would penetrate the surface immediately. It has been shown that for Aquarius najas the females deposit their eggs below the water surface, laboratory observations suggesting that the initial penetration of the film is carried out by the front tarsal claws (Brinkhurst 1960).

Fig.5.2a,b

a) G.lacustris, brachypterous female, resting on water surface. Broken lines show the menisci around the leg segments in contact with the water.

b) Diagram illustrating the conjectural ancestral form of all surface bugs on surface film at the time when, as terrestrial forms, they were first taking to an aquatic life.





5.5 Subject Description

Three species were mainly caught at the sites:

Gerris lacustris

Gerris gibbifer

Aquarius najas

5.51 Gerris lacustris

This is the most widely distributed British bug and it is found virtually everywhere bar the Outer Hebrides and Shetlands. It tolerates a lower surface tension than some other species and tends to occur at the oligotrophic but permanent end of the habitat range (Vepsalainen 1973).

The most typical habitat of the species is a semi-open pond or small lake with moderate vegetation cover on the shores and water surface and deep water. Such waters are brown and often have a high humus content (Southwood & Leston 1959). The shores are usually firm and raised well above the water level so that there are many sheltering cavities in the bank.

This species typically occurs in large schools, gathering under tall trees (often birches),whose branches hang far out over the water. The individuals often anchor themselves to floating leaves with the legs of one side. The species is also often met in small streams with a slow or even fast current and moderate to dense shade. It avoids springs entirely and is very rare in brackish water.

Overwintered bugs appear in late April or early May. Short-winged forms first (micropters). Oviposition occurs in

May At 12-14°C eggs develop in 12-14 days and larvae in 24 days for micropters, but 30 days for macropters. During each instar, as well as each of the moults, increase in size is generally by elongation of the abdomen.

The first generation are adult and mature from late June onwards and the second generation from mid August onwards. Adults which are retarded, ie, whose final moult occurs in late September or October, show a tendency to be small and dark. Some may still be found active in early November.

G. lacustris exhibits a great range of form, but these can be grouped as apters, micropters, subbrachypters, brachypters; and macropters.

Observations on a pond over some months showed that the differences in make-up of a population could be explained by the greater mobility of the macropters which fly freely. Flight direction, both in late autumnal migrations to overwinter ing sites and at other times, is dependant upon the wind. Behaviour is influenced in Gerrids, by light and the presence of anchoring points, thus water plants developing in summer modify the overall population behaviour.

5.52 Gerris gibbifer

This species occurs in lowlands on somewhat acid waters also frequenting peat pools and extends up to 1,000 feet or so. In Britain, shallow Sphagnum pools, stone-built artificial ponds, shallows on clay and moorland ditches are amongst its habitats but on streams it is confined to back waters.

There are two generations per year, the first maturing late in July and the second in late September. The overwintering adults may appear on warm days in January but the bulk leave the hibernation sites between late March and early May. The females appear, on the whole before the males.

A pale variety exists (var. flaventris) but whether this is produced by higher temperatures or is merely a developmental phase is unknown (Southwood & Leston 1959). The bugs feed on living prey and are often, as other Gerrids, cannibals.

5.53 Aquarius najas

Aquarius are highly evolved species of somewhat more open and flowing waters than Gerris. Aquarius najas usually inhabits rivers and stony margins. It overwinters as an adult and has one generation each year. The adults pair in the Spring and row about in a pre-copular pairing during the day, but when they separate in the dark the females lay the eggs beneath the water, usually in close packed batches on flat stones. The eggs are laid in two batches and recruitment to the first of the larval instars is continued form the beginning of the breeding season (i.e. mid June) until most of the nymphs have become adult (in late September).

They are catholic in their feeding, taking a wide variety of soft bodied insects that become trapped on the surface film (Lumsden 1949) and are quite often cannibals, larger nymphs preying particularly on smaller nymphs during ecdysis. Otherwise they seem to have no natural enemies, a fact which may be connected to their unusual habitat, thick exoskeleton and long legs, the presence of a ventral thoracic gland , their rapid locomotion with sudden directional changes and their well developed sensory system which includes huge almost globular eyes and ripple detecting hairs.

Gerrids tend to orientate towards light but in flowing water species this is overridden by a ripple sense causing orientation upstream. In A.najas the long sense hairs of the trochanter and the femur of the hind and mid-legs are sensitive ripple detectors; they control balance and sense ripples sent out by struggling insects caught in the surface film towards which they will move. These reactions cause A.najas to be gregarious. The 'mutual attraction' is a response to external stimuli but probably internal factors (e.g. the state of the gonads) may modify its extent; gregariousness is less marked in Spring (Southwood & Leston 1959).

Surface bugs have a finely pilose abdomen and if this is scratched or dirtied the bug wets and drowns. An elaborate cleaning routine using the legs is practised by A.najas. Eggs are laid beneath the surface, the female descending with the male attached. Eggs take 19 days for development at 18°C, but this period is extended at lower temperatures. There is a cruciform eggburster on the embryonic membrane, and the eggs split lengthways on hatching; the new-born larvae soon swim to the surface.

All adult specimens are unable to fly (Brinkhurst, 1966 has noted wings without wing muscles in two of the many insects he has handled) and so migration is reduced to a minimum.

Chapter 6.......

6.1 Introduction

Complimentary to the toad work a similar investigation was carried out with the pondskaters which were collected during the summer months of 1982. Two aspects of the pondskater population were investigated:

(i) the degrees of sexual size dimorphism in the three species of pondskaters caught,

(ii) the scaling and degree of assortative mating between pairs of one species, A. najas.

The following predictions made in Chapter 1, were tested:

(a) the scaling relationships - i.e. are males and females different?

(b) assortative mating - is selection for size operating at the pre- copular stage?

From these and knowledge of pondskater anatomy as outlined in Chapter 5, the following would be expected:

a) that for the ratio of body weight to body length males would be relatively larger than females.

b) that no relative difference between the sexes would be observed for the front limb length.

c) that for females the mid-legs, those that bear the weight load, would be relatively longer than males, and

d) for males, that the backlegs, those that steer, would be relatively longer than in females.

If these predictions are fulfilled it would be expected that assortative mating between pairs is operating.

6.2 Methods

The surface of the small pond at Brasside was found to be rather overgrown with duckweed and Potamogeton plants and so capture of the beasts was made difficult by weed entangling the nets.

Insects were collected with a small pond net, 15mm x 15mm, by placing the net over the insect and submerging it briefly to entrap it in the net. Once caught they were placed in a dry screw-top jar, if water was included in the jar the animals became wetted and survival was lowered. Pairs were kept seperately in petri dishes to ensure that partners were not exchanged. The insects were returned to the laboratory where they were processed before release.

The majority of specimens caught were Gerris lacustris (either nymph or adult), however G.odontogaster and G.lateralis were also found to be present in small numbers.

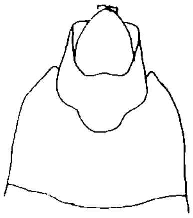
The insects were identified and then sexed under a low-power binocular microscope before linear measurements were taken. The sex is readily determined by the shape of the aedegas plates on the underside of the abdomen (Fig 6.1). The linear measurements were made from photographs of each animal in order to minimise error.

Fig. 6.1 G.lacustris, tip of abdomen from below.

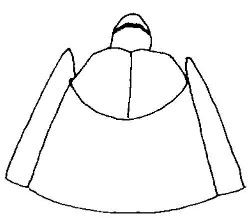
a) male x27

b) female x27

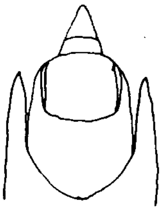
c) A.najas, tip of the male abdomen from beneath x27



A



B



C

Numbered petri dishes were prepared for each individual specimen and these were placed in the freezer compartment of the fridge to reduce activity.

The petri dish was then placed on a sheet of millimetre square graph paper which served as a linear scale, directly beneath a tripod mounted camera. The camera, an Olympus OM1, was fitted with a 135mm macro-photography lens and bellows. The aperture of the lens and focus were adjusted to ensure both specimen and scale were in sharp definition.

After the exposure had been taken the specimen was weighed to the nearest milligram using an electric microbalance (Griffin & George 201 series).

The specimens were enlarged to three times life size, thus facilitating accurate measurement. Linear measurements were taken directly from the prints using a pair of dividers, the back ground graph paper providing a consistent scale.

The collected material from Brasside ponds were nearly all unpaired (only three pairs were caught) and so tests to investigate the type of mating selection operating could not be used. Further additional material was obtained from the South of France in order to complete the investigation for Gerrid species.

6.21 French Study Site

Paired specimens were collected from the area surrounding of the village of Les Mayons, situated in the Massif des Maures in the South of France.

The Maures are a range of low, forested hills north east of the town of Toulon. The village of Les Mayons lies at an altitude of 180m above sea level on the northern fringe of the Massif. To the north of the village lies a plain dominated by open oak-pine woods with an ericaceaous shrub layer.

Two riverine sites were selected, the Aille, situated on the plain and the river Mourrefrey located at the foot of the village of Les Mayons.

The paired material was handled in the same way as for the English specimens except that both sexes were photographed together on the same petri dish in order to prevent separation of the paired data.

6.3 Results

As previously all data collected were processed using the statistical facilities on the Durham M.T.S. system, histograms of the resulting distributions may be found in Appendix II, Figs.6.2a-f. Tables of the means and standard deviations are shown for each species (Tables 6.1-6.3).

6.31 Sexual Size Dimorphism

From the Tables and histograms (Figs.6.2a-f), it is obvious that A.najas is by far the largest of the captured specimens, the females appearing to be proportionately larger inAnajas than for G.gibbifer. The two populations of lacustris are the smallest of the three species, the English population appearing

Table 6.1a

Gerris lacustris

English population (unpaired)

Limb length and body size parameters for male and female G.lacustris + 1 S.D. Lengths in mm, weights in mg. Relative differences between sexes for each parameter shown as a ratio.

	Male		Female	
	Mean	SD	Mean	SD
Foreleg	4.68	0.44	5.08	0.39
Midleg	12.74	0.66	13.95	0.96
Hindleg	9.24	0.83	10.15	0.56
Bodylth	9.01	0.35	9.86	0.49
Antennae	3.41	0.95	3.66	0.89
Bodywt	5.00	0.25	6.80	0.35

Sample size=106

Males=45 Females=61

Table 6.1b

French population (unpaired)

Limb length and body size parameters for male and female G.lacustris (Fr.) ± 1 S.D. Lengths in mm, weights in mg. Relative differences between sexes for each parameter shown as a ratio.

	Male		Female		
	Mean	SD	Mean	SD	Ratio
Foreleg	4.95	0.23	5.58	0.44	0.88
Midleg	13.57	0.83	15.12	0.52	0.89
Hindleg	10.25	0.60	11.06	0.50	0.92
Bodylth	9.24	0.29	10.12	0.34	0.91
Antennae	3.04	1.74	3.90	1.08	0.78
Bodywt	5.90	0.11	12.20	0.21	0.49

Sample size=25

Males=9 Females=16

Table 6.1c

English Population

Limb length and body size parameters for paired male female G.lacustris + 1 S.D. Lengths in mm, weights in mg. Relative differences between sexes for each parameter shown as a ratio.

	Male		Female		
	Mean	SD	Mean	SD	Ratio
Foreleg	5.00	0.50	5.58	0.44	0.91
Midleg	13.99	0.61	15.30	0.74	0.92
Hindleg	10.45	0.44	11.31	0.65	0.89
Bodylth	9.04	0.23	10.11	0.37	0.56
Antenn	3.88	0.35	4.11	0.36	0.94
Bodywt	9.60	0.19	17.00	0.22	0.56

Sample size=14 pairs

Table 6.2a

Limb length and body size parameters for unpaired male and female G.gibbifer + 1 S.D. Lengths in mm, weights in mg. Relative differences between sexes for each parameter shown as a ratio.

	Male		Female		
	Mean	SD	Mean	SD	Ratio
Foreleg	6.28	0.62	6.50	1.45	0.93
Midleg	16.30	1.21	17.44	1.28	0.96
Hindleg	13.08	1.13	13.69	1.20	0.93
Bodylth	12.34	0.91	13.25	0.78	0.68
Antenn	3.00	2.01	3.51	2.04	0.85
Bodywt	19.00	0.64	28.00	0.80	0.68

Sample size=49

Males=24 Females=25

Table 6.2b

Limb length and body size parameters for paired male and female G.gibbifer + 1 S.D. Lengths in mm, weights in mg. Relative differences between each parameter shown as a ratio.

	Male		Female		
	Mean	SD	Mean	SD	Ratio
Foreleg	6.45	0.93	7.04	0.85	0.92
Midleg	16.47	1.97	17.98	2.23	0.91
Hindleg	13.07	1.70	14.38	2.01	0.90
Bodylth	11.66	1.42	12.95	1.37	0.65
Antenn	2.03	2.02	3.06	2.11	0.66
Bodywt	20.00	0.60	31.00	0.90	0.65

Sample size=7 pairs

Table 6.3a

Limb length and body size parameters for unpaired male and female A.najas + 1 S.D. Lengths in mm, weights in mg. Relative differences between sexes for each parameter shown as a ratio.

	Male		Female		
	Mean	SD	Mean	SD	Ratio
Foreleg	5.82	3.38	7.38	2.07	0.79
Midleg	22.09	2.45	25.28	0.99	0.87
Hindleg	19.05	2.06	22.08	0.66	0.86
Bodylth	13.78	1.80	16.82	0.56	0.82
Antenn	5.31	2.02	4.79	3.70	1.11
Bodywt	21.00	0.60	42.00	0.63	0.50

Sample size=25

Males=19 Females=6

Table 6.3b

Limb length and body size parameters for paired male and female A. najas + 1 SD. Lengths in mm, weights in mg. Relative differences between sexes for each parameter shown as a ratio.

	Male		Female		
	Mean	SD	Mean	SD	Ratio
Foreleg	7.83	0.92	11.55	0.96	0.68
Midleg	21.03	1.50	26.26	1.17	0.80
Hindleg	17.94	1.19	22.99	1.77	0.78
Bodylth	12.71	0.88	17.38	0.63	0.73
Antenn	5.59	0.55	7.01	0.60	0.80
Bodywt	19.00	0.40	53.00	0.70	0.36

Sample size=36 pairs

to be slightly smaller than the French and although their ranges overlap they are regarded as seperate data sources in the following analyses.

By computing the ratios of male:female size the degrees of sexual size dimorphism are put into perspective (Fig.6.3). For all species a similar trend was noted in leg lengths. Body length and body weight showed a greater degree of dimorphism the extent of which differed between species (Tables 6.1-6.3).

6.32 Paired Insects

Statistical analysis of paired data was only undertaken for one species. This was due to the low sample sizes for the other two species which were too small for analysis, although the trends found in A.najas were echoed in both of the other species, though to a lesser extent.

Females are larger than males (see Table 6.3a). On a weight basis alone they are approximately twice as heavy. On average, females are approximately 3mm larger on each appendage than the male. The differences in the paired material (see Table 6.3b) are more marked, females being up to 5mm greater in appendage size than the males. From the histograms, Figs.6.2a-f, it can be seen that the unpaired material have a greater range of size than the pairs. By plotting the means with their standard deviations for each measurement (Fig 6.4) this overlap can be seen more clearly. T tests for body length showed that paired females were significantly larger than unpaired females (t=-2.04, P<0.05) and paired males were

Fig 6.3 Extent of sexual size dimorphism in <u>Gerris</u> species expressed as a male:female ratio of measures of various body size parameters.

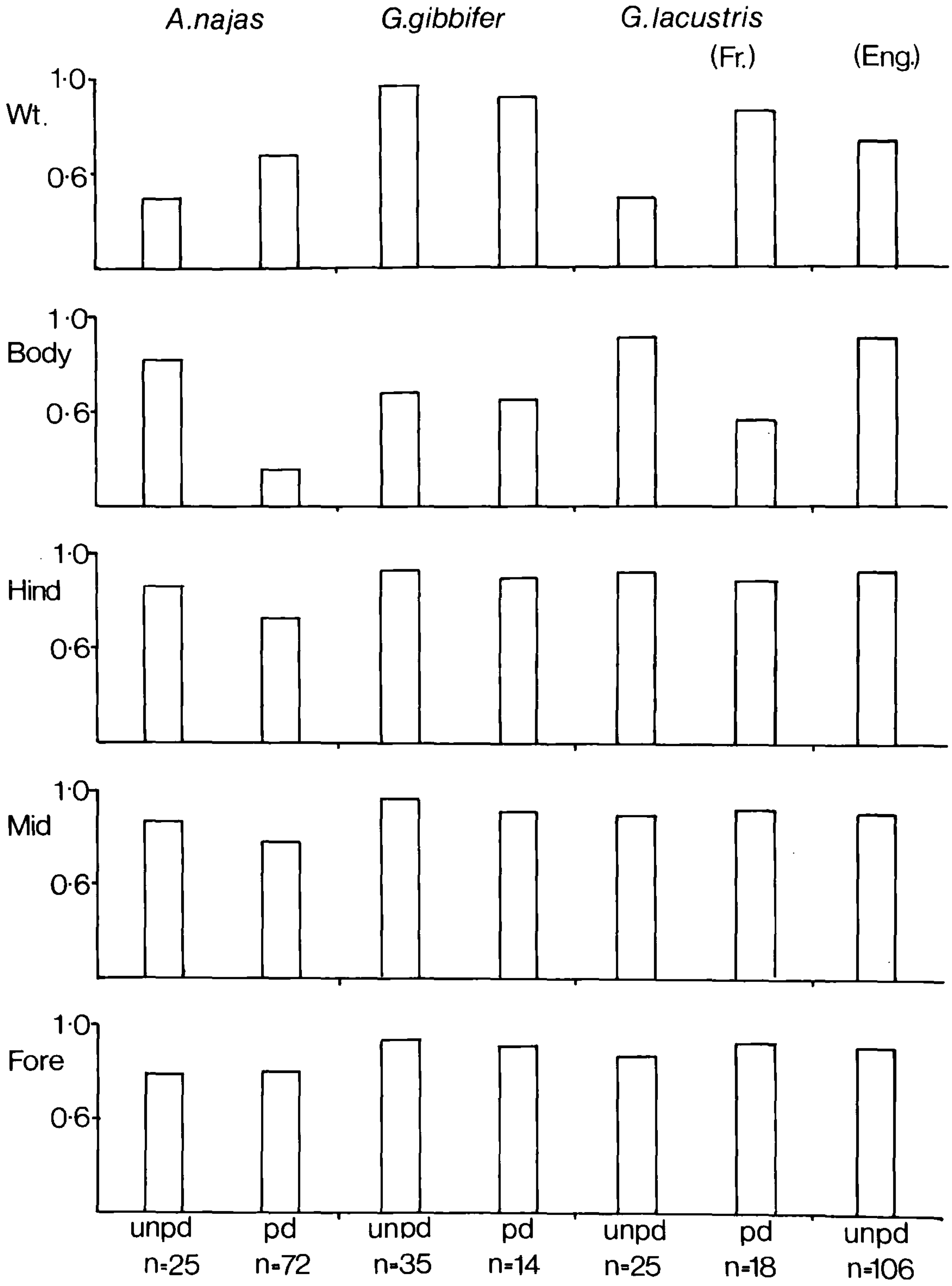
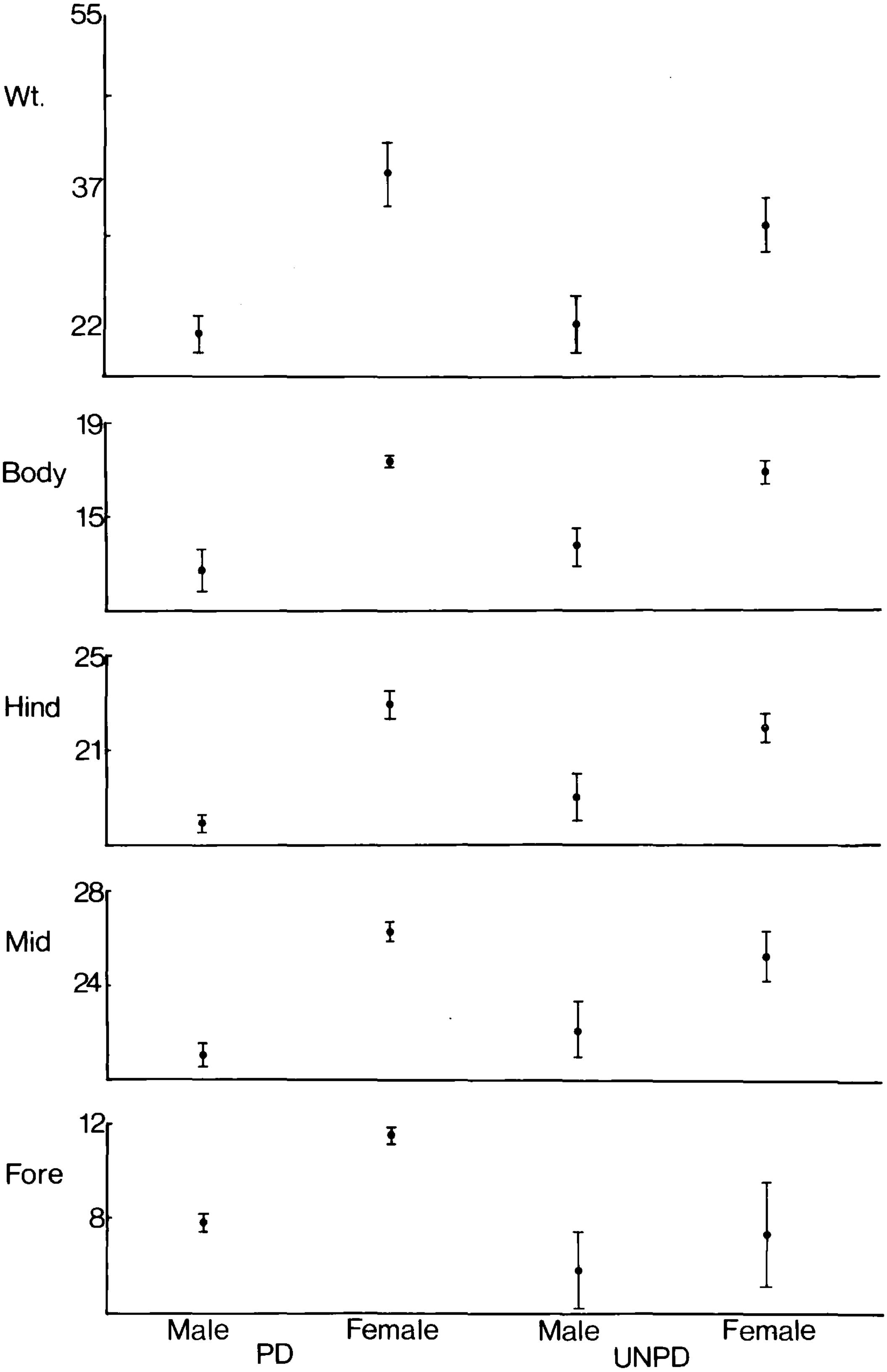

A.najas
G.gibbifer
G.lacustris
(Fr.)
(Eng.)
Wt.
Body
Hind
Mid
Fore
1·0
0·6
unpd
pd
n=25
n=72
n=35
n=14
n=25
n=18
n=106

Fig 6.4 Means and 95% confidence limits for various body size parameters for each sex for *A. najas* taken in copula and collected individually.

All lengths in mm, weights in mg.


55
Wt.
37
22
19
Body
15
25
Hind
21
28
Mid
24
12
Fore
8
Male
Female
PD
Male
Female
UNPD

significantly smaller than unpaired ($t=2.99$, $P<0.004$), see Table 6.4.

6.4 Scaling Relationships

Length of appendage was correlated with both body length and body weight using both normal and log transformed data for each sex and the calculated regression lines were plotted onto each scatter diagram (Figs.6.5a-d). The strength of association was assessed from the size of r, the correlation coefficient, Table 6.4.

Females showed a significant correlation when foreleg was correlated with body length ($r=0.32$, $P<0.05$). No other correlations were found which was as predicted.

Males showed the strongest correlation when midleg length was correlated with both body variables (Males $r=0.74$, $P<0.001$, females $r=0.61$, $P<0.001$). However d tests used to compare the slopes and z tests used to compare r values indicated that there were no significant differences between the two sexes.

Males (as predicted) were shown to have relatively longer hind legs than females ($r=0.83$ for males, $P<0.001$, $r=0.38$ for females, $P<0.02$). D tests showed that there was no significant difference between the slopes even though a z test showed that there was a significant difference between the r values ($z=3.34$, $P<0.01$).

When midleg length was correlated with hindleg length there were significant relationships for both sexes ($r=0.74$, $P<0.001$) and $r=0.45$, $P<0.01$, for males and females repectively). Z tests

Table 6.4

Correlations between limb length and measures of body size for paired and unpaired A.najas.

	Correlation Coefficients			
	Male		Female	
Variable	Body length	Body weight	Body length	Body weight
Fore.a	0.79***	0.68***	0.83***	0.72***
b	0.27	0.23	0.32*	0.24
Mid. a	0.93***	0.73***	0.74**	0.63***
b	0.74***	0.69***	0.61**	0.22
Hind.a	0.90***	0.76***	0.67**	0.83***
b	0.83***	0.76***	0.38**	0.22
Body a		0.77***		0.74***
b		0.80***		0.26

* r significant at P<0.05

** P<0.02

*** P<0.001

a=unpaired b=paired

Figs.6.5a-d Relationships between various body size measurements for A.najas taken in copula, both sexes shown seperately.(All a data Log. transformed).

(a) Log. foreleg v Log. body (length & weight)

(b) Log. midleg v Log. body (length & weight)

(c) Log. hindleg v Log. body (length & weight)

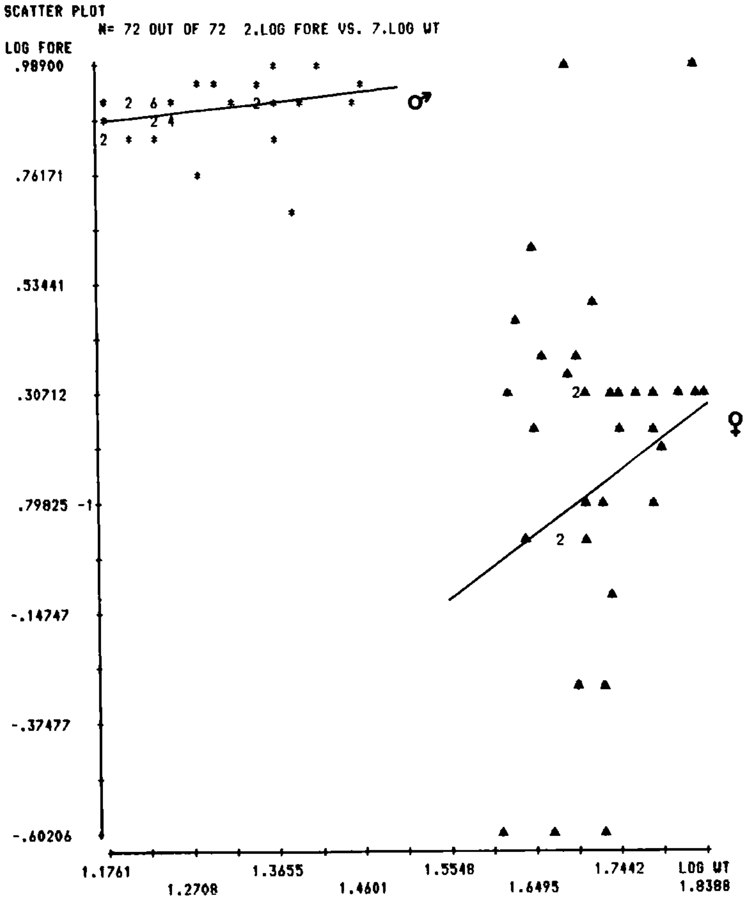
(d) Log. midleg v Log. hindleg.

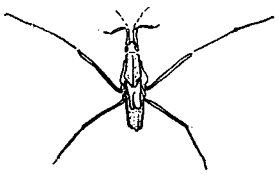
Log. body length v Log. body weight

Key

▲ =Females

✳ =Males


SCATTER PLOT
N= 72 OUT OF 72 2.LOG FORE VS. 7.LOG WT
LOG FORE
.98900
.76171
.53441
.30712
.79825 -1
-.14747
-.37477
-.60206
1.1761
1.2708
1.3655
1.4601
1.5548
1.6495
1.7442
LOG WT
1.8388
♂
♀



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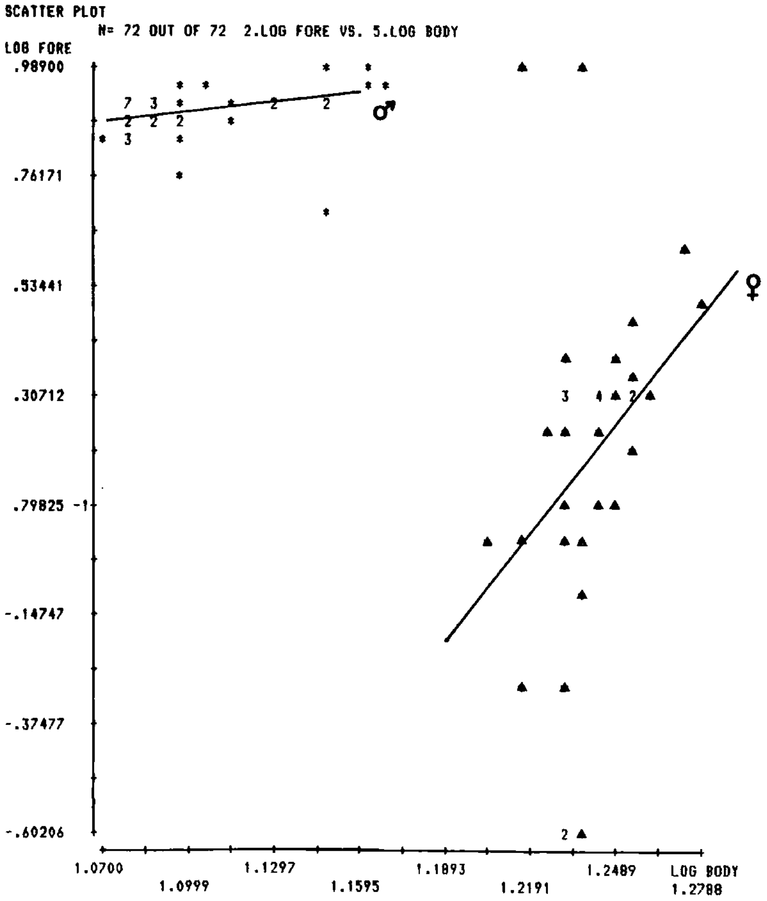
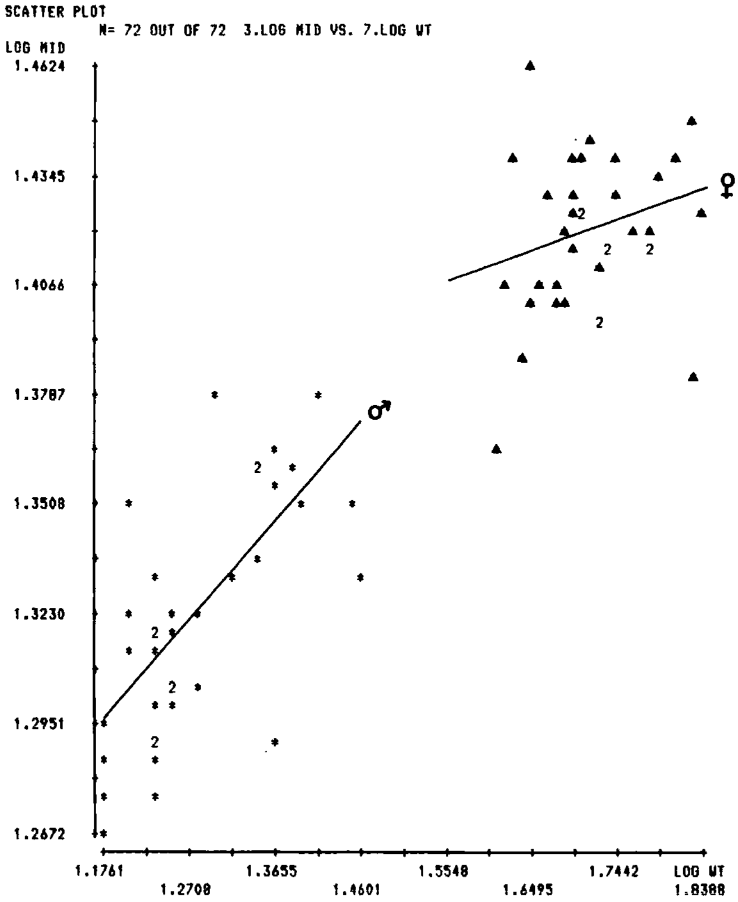
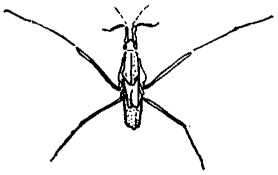

SCATTER PLOT
N= 72 OUT OF 72 2.LOG FORE VS. 5.LOG BODY
LOG FORE
.98900
.76171
.53441
.30712
.79825 -1
-.14747
-.37477
-.60206
1.0700
1.0999
1.1297
1.1595
1.1893
1.2191
1.2489
LOG BODY
1.2788
♂
♀

b


SCATTER PLOT
N= 72 OUT OF 72 3.LOG MID VS. 7.LOG WT
LOG MID
1.4624
1.4345
1.4066
1.3787
1.3508
1.3230
1.2951
1.2672
1.1761
1.2708
1.3655
1.4601
1.5548
1.6495
1.7442
LOG WT
1.8388
♀
♂



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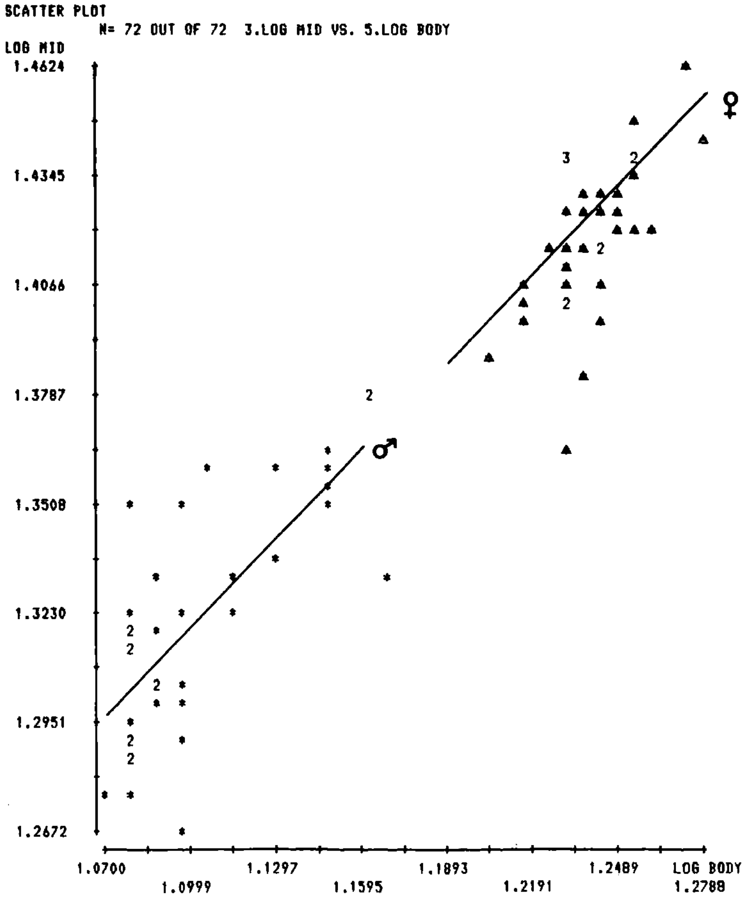
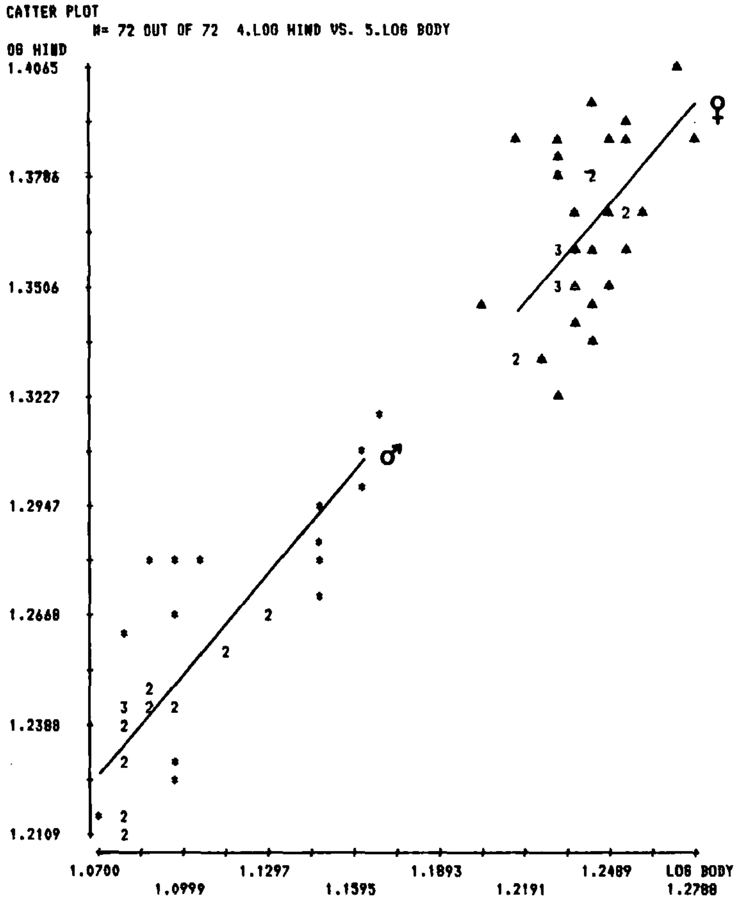
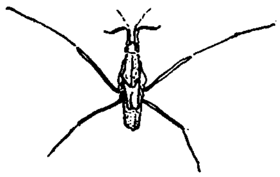

SCATTER PLOT
N= 72 OUT OF 72 3.LOG MID VS. 5.LOG BODY
LOG MID
1.4624
1.4345
1.4066
1.3787
1.3508
1.3230
1.2951
1.2672
1.0700
1.0999
1.1297
1.1595
1.1893
1.2191
1.2489
LOG BODY
1.2788
♀
♂

b


CATTER PLOT
N= 72 OUT OF 72 4.LOG HIND VS. 5.LOG BODY
OG HIND
1.4065
1.3786
1.3506
1.3227
1.2947
1.2668
1.2388
1.2109
♀
♂
1.0700
1.0999
1.1297
1.1595
1.1893
1.2191
1.2489
1.2788
LOG BODY



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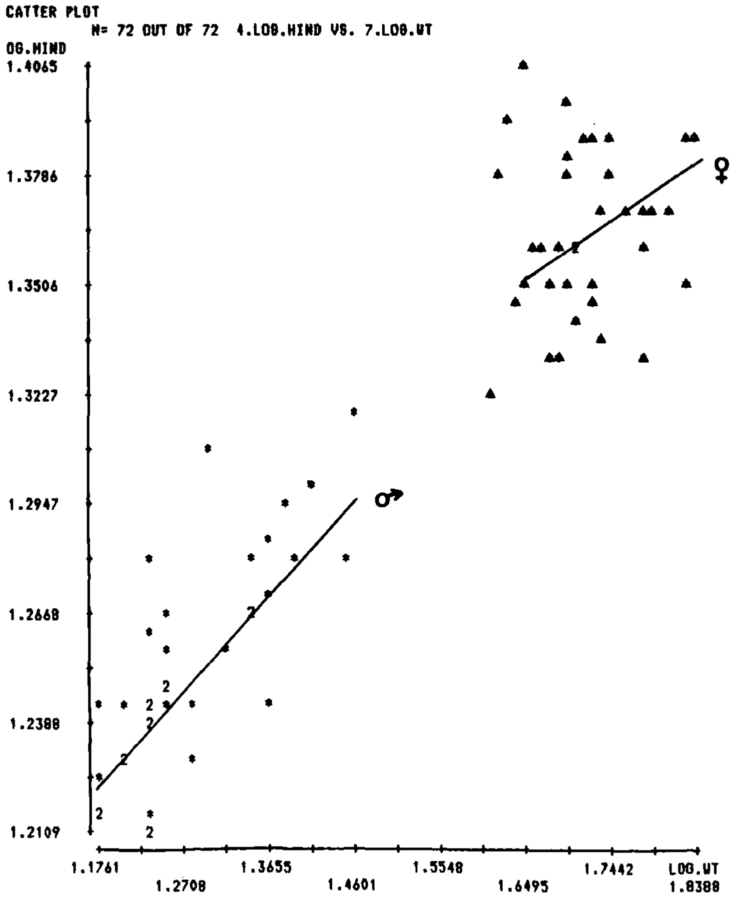
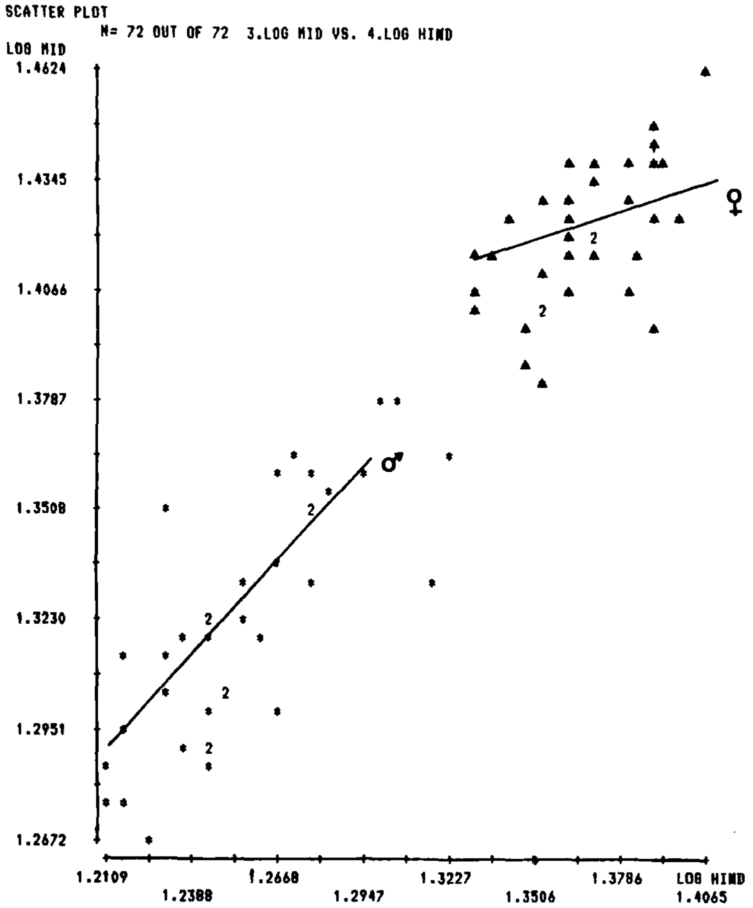
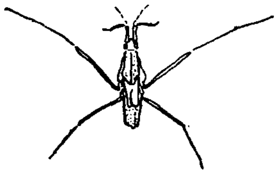
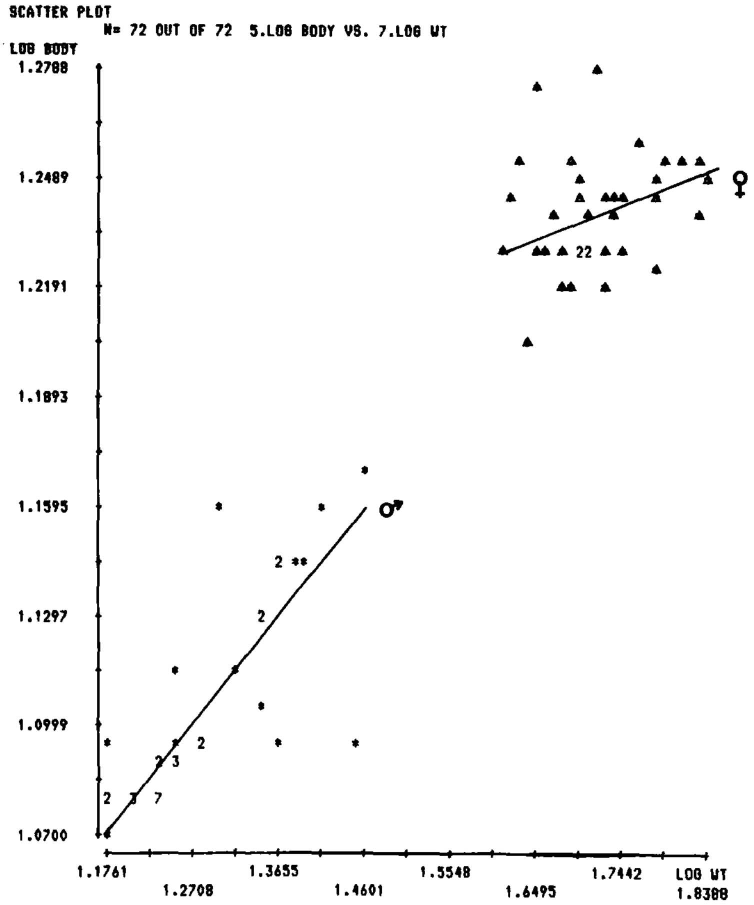

CATTER PLOT
N= 72 OUT OF 72 4.LOG.HIND VS. 7.LOG.WT
OG.HIND
1.4065
1.3786
1.3506
1.3227
1.2947
1.2668
1.2388
1.2109
♀
♂
1.1761
1.2708
1.3655
1.4601
1.5548
1.6495
1.7442
1.8388
LOG.WT

b

SCATTER PLOT
N= 72 OUT OF 72 3.LOG MID VS. 4.LOG HIND
LOG MID
1.4624
1.4345
1.4066
1.3787
1.3508
1.3230
1.2951
1.2672
1.2109
1.2388
1.2668
1.2947
1.3227
1.3506
1.3786
1.4065
LOG HIND
♀
♂
2



a

SCATTER PLOT
N= 72 OUT OF 72 5.LOG BODY VS. 7.LOG WT
LOG BODY
1.2788
1.2489
1.2191
1.1893
1.1595
1.1297
1.0999
1.0700
1.1761
1.2708
1.3655
1.4601
1.5548
1.6495
1.7442
1.8388
LOG WT
♀
♂
22
2
3
7

b

and d tests showed that there was a significant difference between correlation values ($z=2.38$, $P<0.05$) and slopes ($d=4.35$, $P<0.001$).

Males also showed a greater degree of association than females when body length was correlated with weight (For males $r=0.80$, $P<0.001$, females $r=0.26$ ns).

6.5 Assortative Mating

Scatter plots of male against female were made for all of the measured variables in order to determine if the mating was random or assortative.

The plots (Figs.6.6a-f) indicated that all the variables were positively related and that the relationships were rectilinear. To permit comparison with relationships between other pairs an assessment of the closeness of the relationships was needed. Correlation methods were used to calculate the correlation coefficient r, the degrees of association between each parameter being obtained from statistical tables (Bailey 1959) and the significance being noted (Table 6.5). There was a strong correlation between male and female body length ($r=0.91$, $P<0.001$) suggesting that mating is assortative. The relationship between midleg lengths was also significant ($r=0.33$, $P<0.05$). The remaining relationships reveal no significant correlations indicating that there is a tendency for selection on the basis of body length and probably also midlength.

Figs. 6.6a-f Scatter diagrams comparing various body size parameters for male and female _Aquarius najas_ taken in copula.

a) antennae length

b) foreleg length

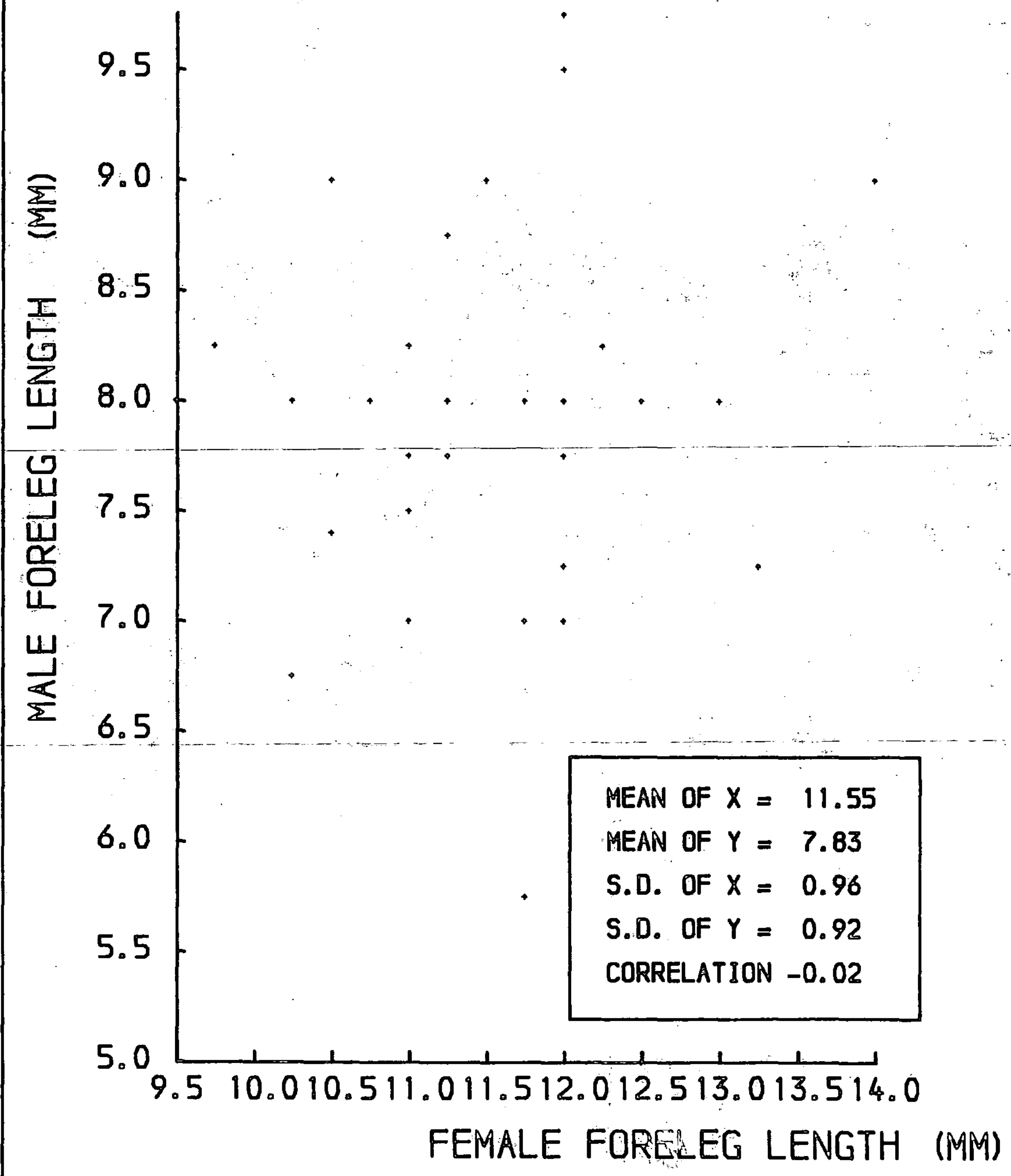
c) midleg length

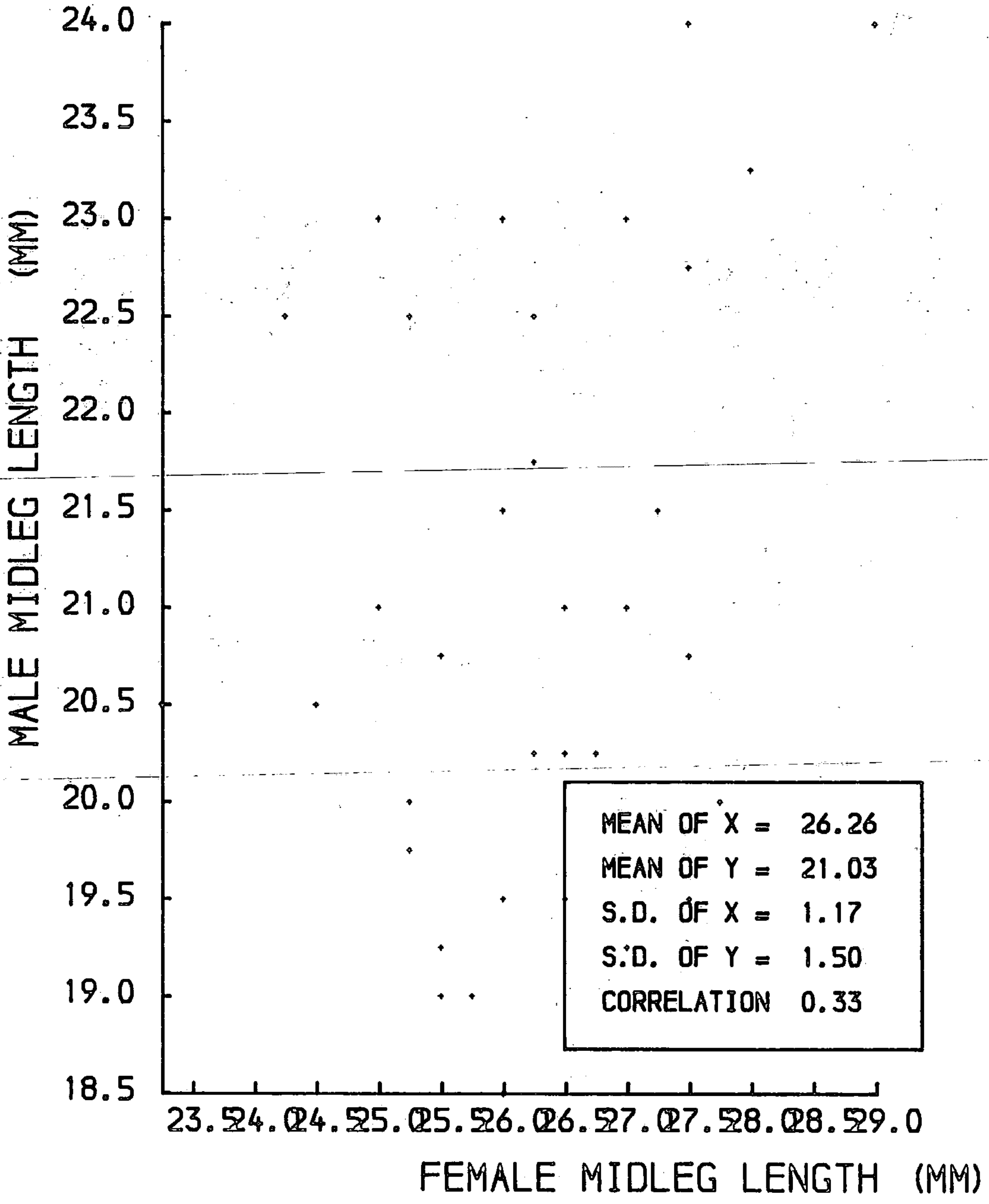
d) hindleg length

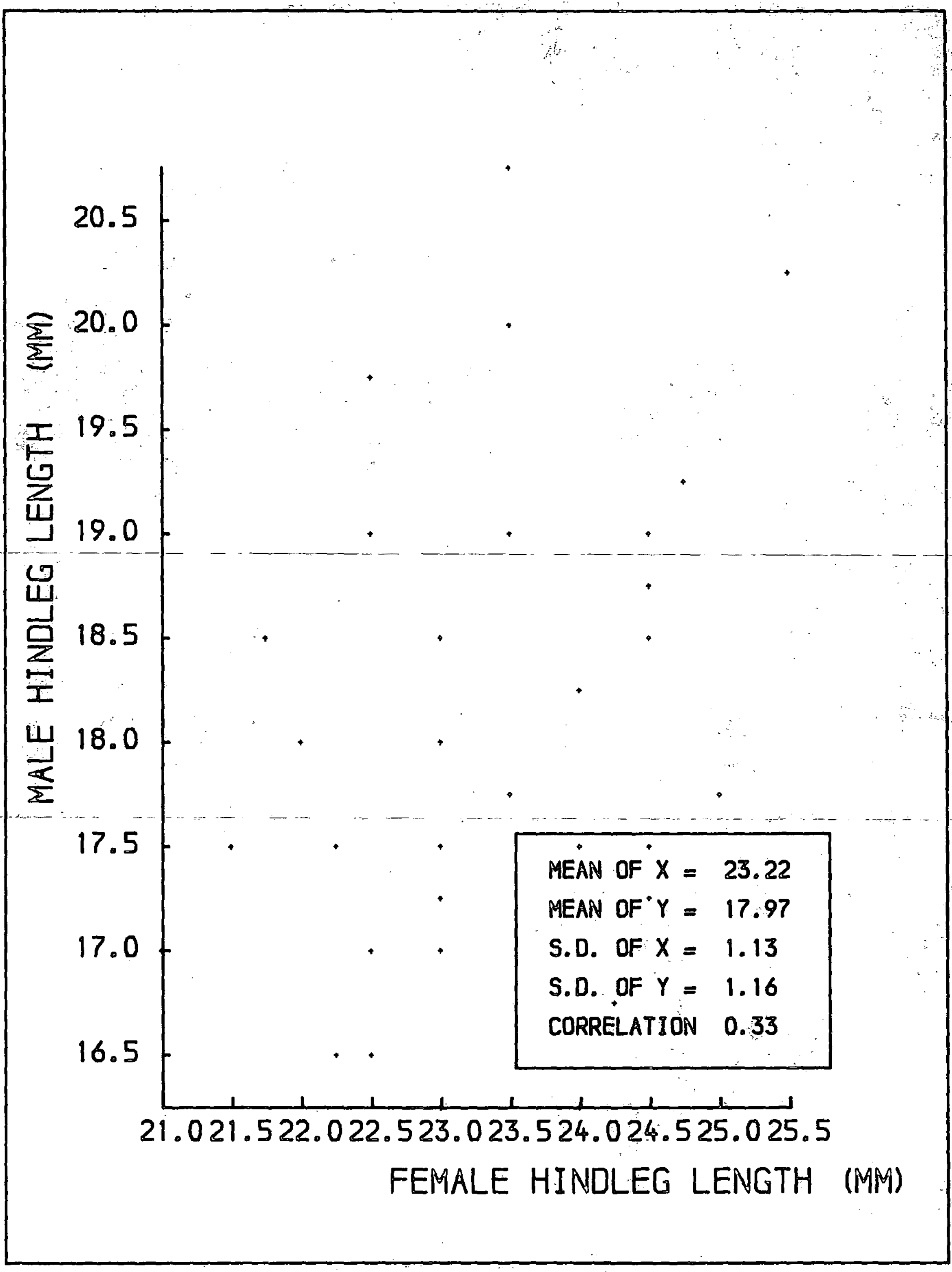
e) body length

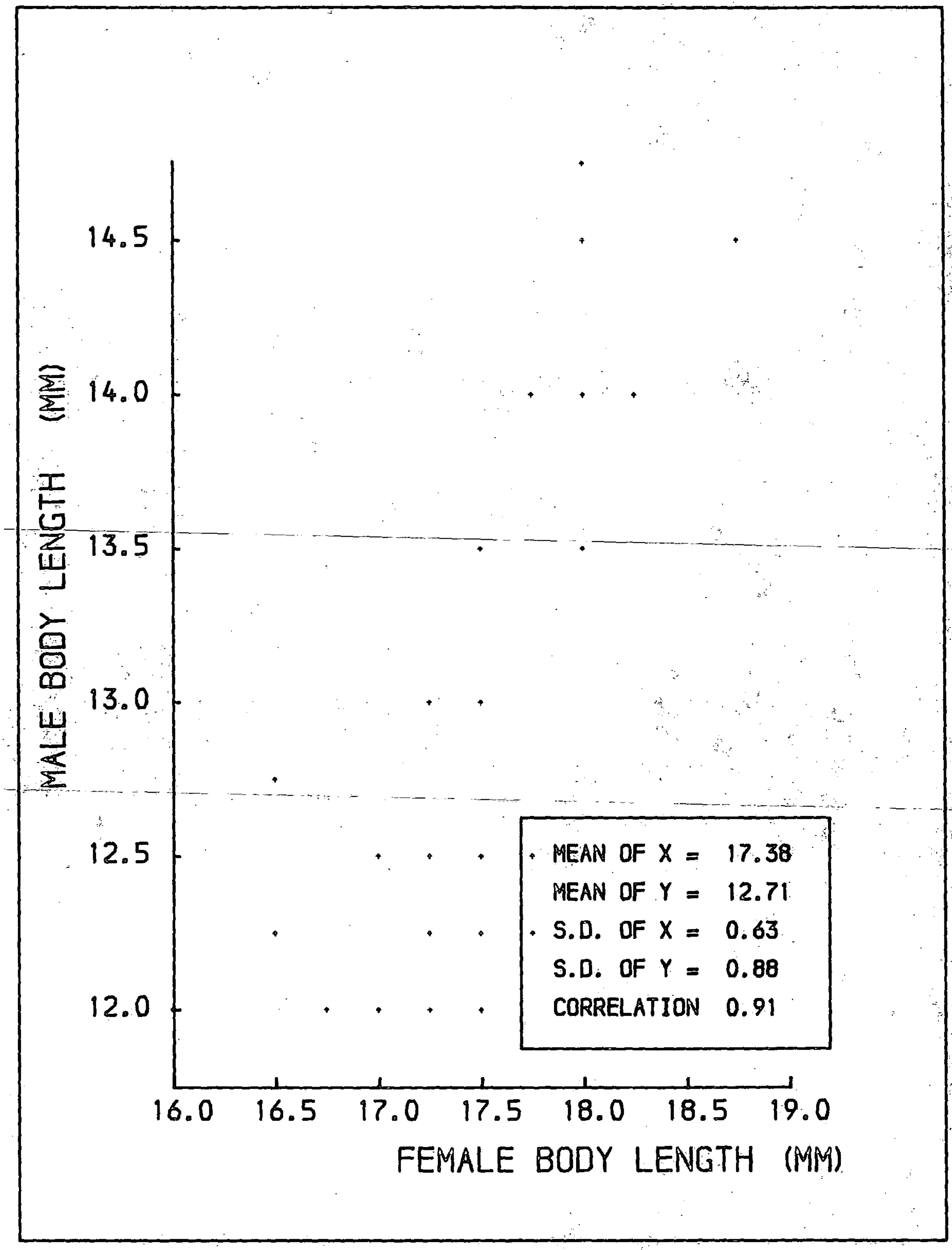
f) body weight

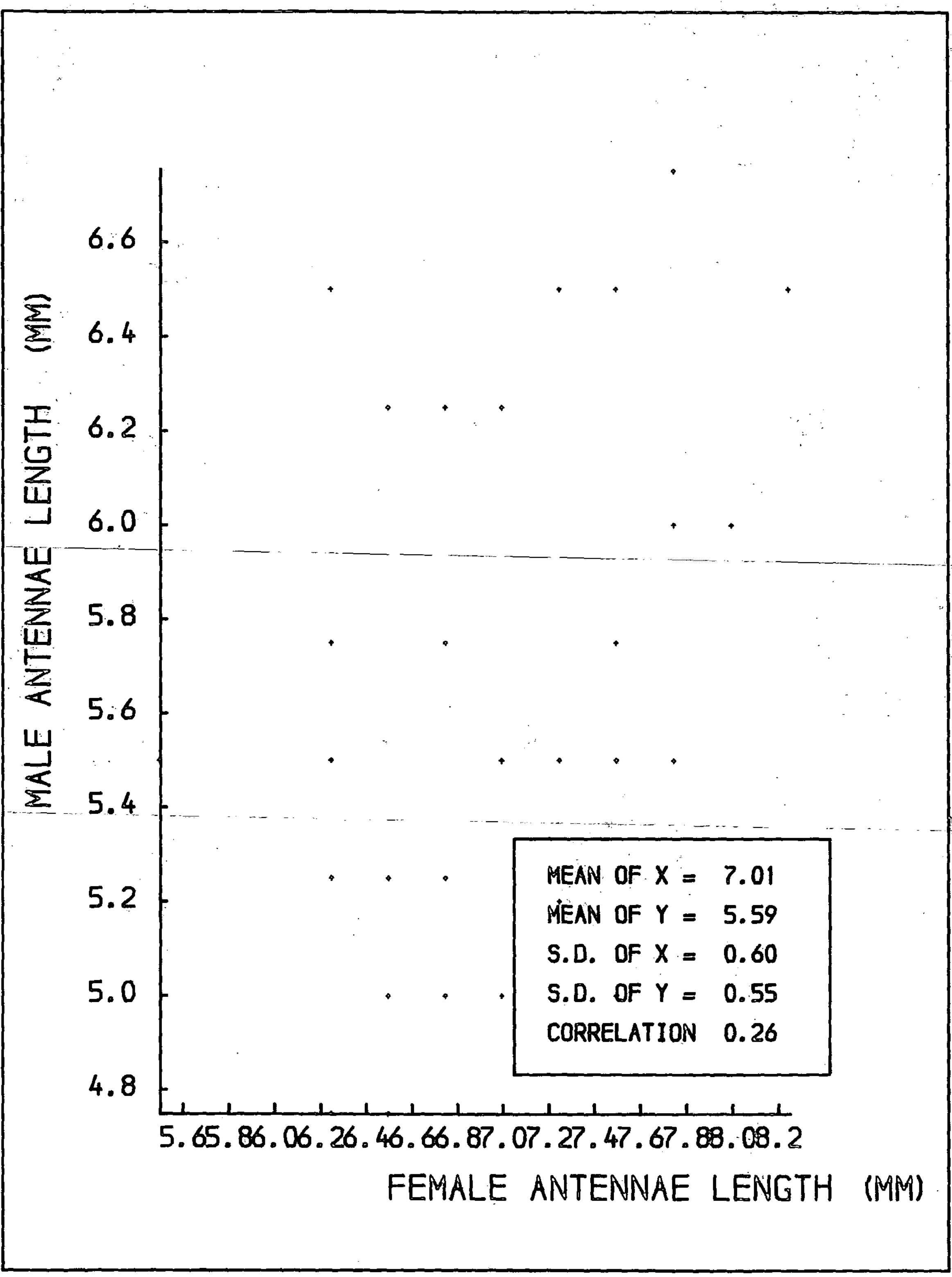
All lengths in mm, weights in mg.

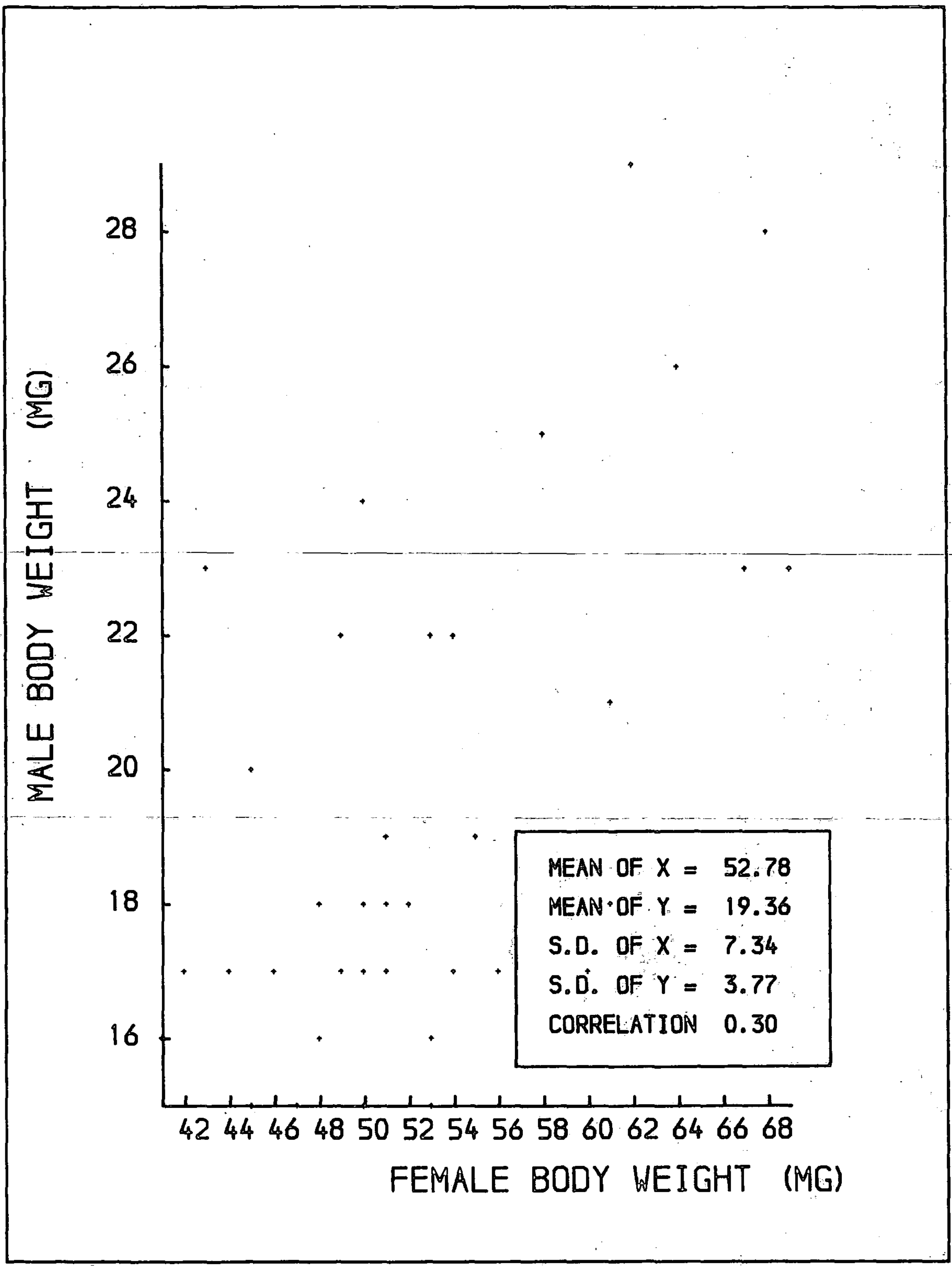

9.5
9.0
8.5
8.0
7.5
7.0
6.5
6.0
5.5
5.0
MALE FORELEG LENGTH (MM)
9.5
10.0
10.5
11.0
11.5
12.0
12.5
13.0
13.5
14.0
FEMALE FORELEG LENGTH (MM)
MEAN OF X = 11.55
MEAN OF Y = 7.83
S.D. OF X = 0.96
S.D. OF Y = 0.92
CORRELATION -0.02


24.0
23.5
23.0
22.5
22.0
21.5
21.0
20.5
20.0
19.5
19.0
18.5
MALE MIDLEG LENGTH (MM)
23.5
24.0
24.5
25.0
25.5
26.0
26.5
27.0
27.5
28.0
28.5
29.0
FEMALE MIDLEG LENGTH (MM)
MEAN OF X = 26.26
MEAN OF Y = 21.03
S.D. OF X = 1.17
S.D. OF Y = 1.50
CORRELATION 0.33


MALE HINDLEG LENGTH (MM)
20.5
20.0
19.5
19.0
18.5
18.0
17.5
17.0
16.5
21.0
21.5
22.0
22.5
23.0
23.5
24.0
24.5
25.0
25.5
FEMALE HINDLEG LENGTH (MM)
MEAN OF X = 23.22
MEAN OF Y = 17.97
S.D. OF X = 1.13
S.D. OF Y = 1.16
CORRELATION 0.33


MALE BODY LENGTH (MM)
14.5
14.0
13.5
13.0
12.5
12.0
16.0
16.5
17.0
17.5
18.0
18.5
19.0
FEMALE BODY LENGTH (MM)
MEAN OF X = 17.38
MEAN OF Y = 12.71
S.D. OF X = 0.63
S.D. OF Y = 0.88
CORRELATION 0.91


MALE ANTENNAE LENGTH (MM)
6.6
6.4
6.2
6.0
5.8
5.6
5.4
5.2
5.0
4.8
5.65.86.06.26.46.66.87.07.27.47.67.88.08.2
FEMALE ANTENNAE LENGTH (MM)
MEAN OF X = 7.01
MEAN OF Y = 5.59
S.D. OF X = 0.60
S.D. OF Y = 0.55
CORRELATION 0.26


MALE BODY WEIGHT (MG)
28
26
24
22
20
18
16
42 44 46 48 50 52 54 56 58 60 62 64 66 68
FEMALE BODY WEIGHT (MG)
MEAN OF X = 52.78
MEAN OF Y = 19.36
S.D. OF X = 7.34
S.D. OF Y = 3.77
CORRELATION 0.30

6.6 Discussion

The predictions made in the earlier sections were not totally fulfilled for the scaling relationships. As expected there was no relationship between the foreleg and the body weight but females did show a relationship between foreleg and body length. The size difference between collected paired and unpaired insects was marked and this may be explained by (a) the unpaired sample population consisted of juveniles as opposed to those engaged in pre-copula, or (b) sampling errors arising from inadequate sample size, or (c) inaccuracies involved in measuring foreleg length since both sexes appear to fold them up beneath their bodies in order to support themselves. In spite of this the relationship of foreleg to body length in the females would imply that the female is using the front legs as a means of support. Although these appendages are used mainly for seizure of prey, Andersen and Polhemus (1976) noted that during copulation the front legs are used by the female as a means of supporting her body weight.

The relationship between both body variables was found to be significant. Morphologically, males appear to be longer and thinner than females. This may well be explained by the increased body size of the female body whilst carrying eggs. Three to four eggs are found in most species but A.najas may have six or more, Brinkhurst (1960) noted that when mature the eggs are so large that they fill the meso- and meta-thorax to such an extent that the abdomen is distended seperating the terga and sterna.

The gradients of the regression lines relating to hindleg length to body length were significantly different (d=2.34, P<0.01) indicating that the hindleg length was relatively longer in males than in females. This implies that the male controls the movement of the female whilst in copula. The male hind legs will not be directly concerned with supporting his body weight during the period of pre-copula mate guarding, and are used to guide the female.

Males, however, appeared to have relatively longer midlimbs with both body variables. According to China (cited in Brinkhurst 1960), the elongation of the limbs is an adaptation to rowing and not to the distribution of insect weight over a wider area of surface. Each limb bears one sixth of the total body weight wherever it is placed, so long as the depressions in the surface film do not co-alesce (see Fig.5.2a). In the light of this it would be expected that there would be no difference in the load bearing capacities of the mid- and hind-limbs.

This appears to hold for males in the unpaired state but not for females, however this could be a result of the small number of females examined. In the paired state it would be expected that the female would have a greater capacity for load-bearing and thus relatively longer legs, which does not appear to be the case. Certainly, when comparing the correlations between both limbs, both sexes show a strong association in the unpaired and unpaired state. Brinkhurst (1960) suggests that an increase in the surface area of the tarsus probably compensates for the increased weight of the larger species, as the relationship between weight and ´limiting value´ of the surface tension is constant. In view of this it may be of interest to investigate the tarsal lengths of both sexes and see if differences exist here.

Significant correlations were found between male and female body length indicating that selection may be acting on body size at the pre-copular guarding stage, suggesting that the second prediction of assortative mating was fulfilled. It seems surprising that no relationship with body weight was shown at all, it might be expected that females would select smaller males in view of their lower weight and the female increased weight load arising from the egg burden. Conversely larger males may be selected by females for their strength and presumably their survival advantage, however when looking at the male data it appears that paired males are slightly smaller than the unpaired (see Tables 6.3a,b).

There are three possible causes of assortative mating in this species. All three are analagous to the situation in the toads. Firstly, there may be mechanical constraints. The nature of the mating strategy employed implies that large males may be too heavy for smaller females. Small males have no such problem when paired with larger females. Secondly, if male:male competition is ocurring then there is a suggestion that big males displace smaller ones from the large females. Finally, there is the question of female choice. Although unknown in the pondskaters, it has been shown that the females of certain toad species choose their mates on the basis of territory size and male calling (Sullivan 1982). When paired to a male not of her own choice females have been observed to adopt tactics to remove the unwanted male. These include swimming into the territory of a stronger male thus inciting male male competition or more active attempts to physically dislodge the male by vigorous twisting movements which in turn attracts other males (Licht, 1976) or they may rub continuously against the vegetation (Sullivan, 1982).

In the situation of the pondskaters it is probably the latter two factors that are contributing towards assortative mating but the mechanical constraints should be seriously considered, especially in view of the results obtained from the scaling relationships. More detailed investigation is required before any definite conclusions can be made.

CHAPTER 7 ......

7.1 Introduction

In the previous chapter the predictions made in the introductory chapter were investigated for a paired example, A.najas. In this chapter the two remaining species that were collected, G.lacustris, of which there are two populations and G.gibbifer, will be considered to see if any further insight may be gained into the loading constraints acting on the sexes of this group.

7.2 Inter-Relationships

As there was a large amount of unpaired material in comparison to the paired material the remaining investigation concentrated on the particular scaling relationships of single insects. As previously the relationships between each of the morphological dimensions for both sexes were determined on log:log transformed data using regression analysis (Figs.7.1a-h). Correlation coefficients were calculated and are tabulated in Tables.7.1-7.5.

7.2.1 Foreleg

In both populations of Gerris, the gradients of the regression lines relating the front limb to both body variables were significantly different, females showing a relatively greater increase in foreleg length with body variables than

Table 7.1

Correlations between limb length and measures of body size for male and female G.lacustris.

	Correlation coefficients			
	Male		Female	
Variable	Body length	Body weight	Body length	Body weight
Fore.lth	0.14	0.07	0.43	0.40
Mid.lth	0.53	0.15	0.42	0.07
Hind.lth	0.37	0.26	0.71*	0.25
Bodylth	-	0.24	-	0.19

* r significant at $P<0.001$

Table 7.2

Correlations between limb length and measures of body size for G.lacustris (French).

	Correlation Coefficients			
	Male		Female	
Variable	Body length	Body weight	Body length	Body weight
Foreleg	0.22	0.26	0.42	0.33
Midleg	0.26	0.42	0.53	0.11
Hindleg	0.33	0.28	0.43	0.20
Bodylth		-0.18		0.38

All non significant

Table 7.3

Between sex comparisons of bodysize parameters for paired G.lacustris (Fr.).

	Foreleg length	Midleg length	Hindleg length	Body length	Body weight
Fore.lth	-0.15				
Mid.lth		0.26			
Hind.lth			0.20		
Bodylth				0.13	
Bodywt					0.36

All non significant

Table 7.4

Correlations of limb length with body weight and body length for male and female G.gibbifer.

	Male		Female	
Variable	Body length	Body weight	Body length	Body weight
Fore	0.55***	0.34*	0.40**	0.17
Mid	0.64***	0.47**	0.49**	0.21
Hind	0.70***	0.59***	0.34*	0.13
Bodylth		0.55***		0.48**

* r significant at P<0.05

** P<0.01

*** P<0.001

Table 7.5

Between sex comparisons of body size parameters for paired G.gibbifer.

	Foreleg length	Midleg length	Hindleg length	Body length	Body weight
Fore.lth	0.92***				
Mid.lth		0.79**			
Hind.lth			0.75**		
Bodylth				0.96***	
Bodywt					0.62

* r significant at	P<0.02
**	P<0.01
***	P<0.001

Figs.7.1a-h Relationships between various body size measurements for three *Gerris* species, both sexes shown seperately (all data Log. transformed).

a) Foreleg length v Body length

b) Foreleg length v Body weight

c) Midleg length v Body length

d) Midleg length v Body weight

e) Hindleg length v Body length

f) Hindleg length v Body weight

g) Hindleg length v Midleg length

h) Body length v Body weight

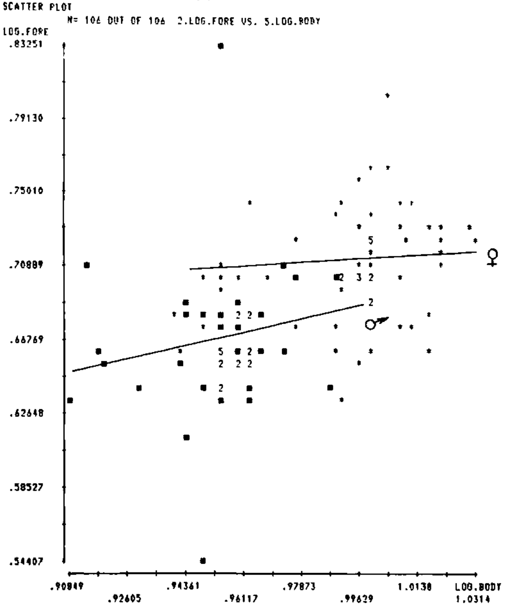
All lengths in mm, weights in mg.

KEY

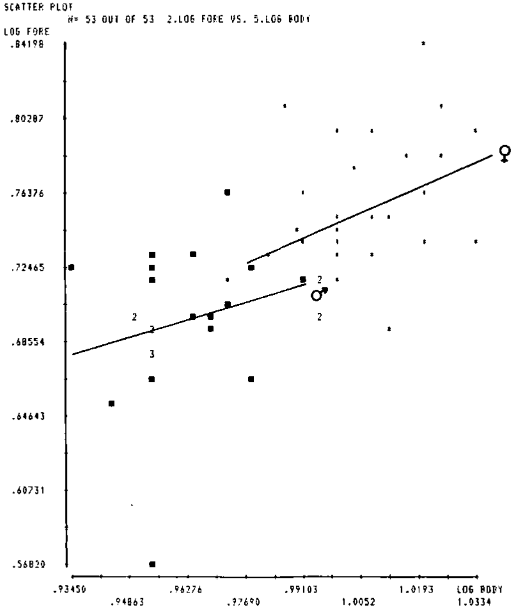
✳ = Females

▣ = Males

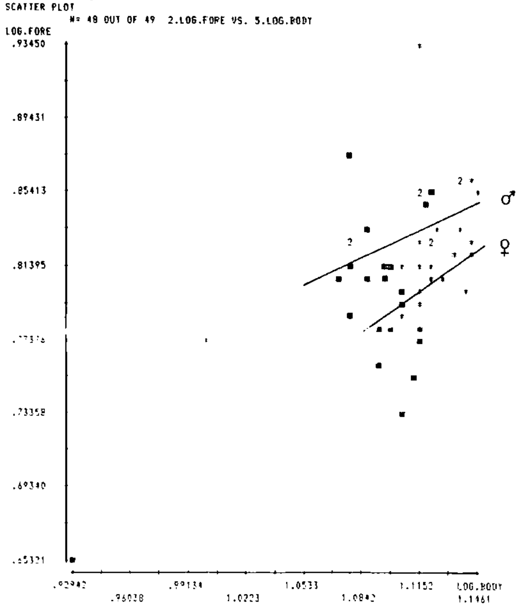
G.lacustris (Eng.)



G.lacustris (Fr.)



G.gibbifer



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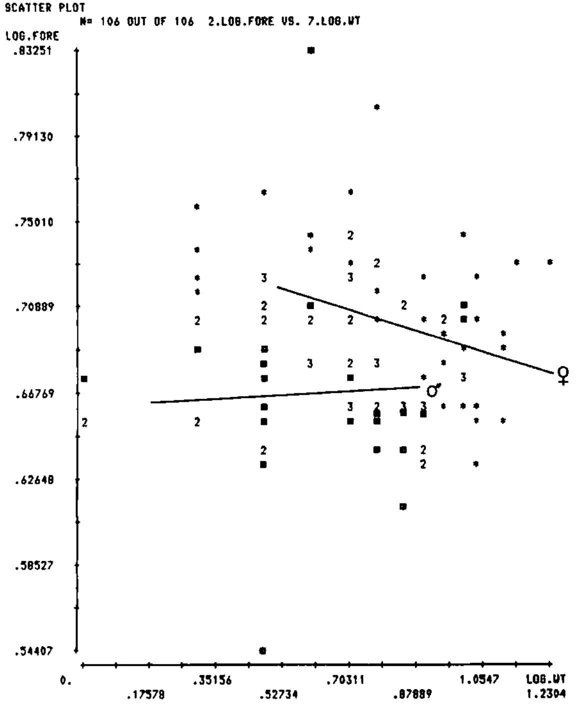

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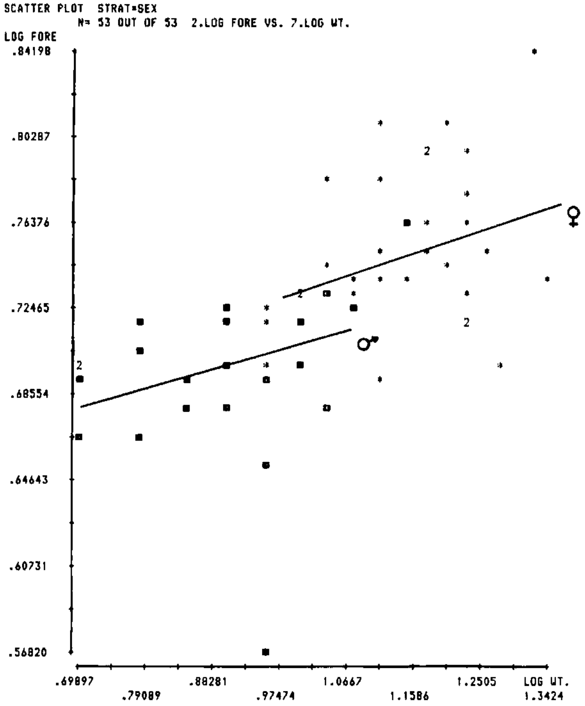
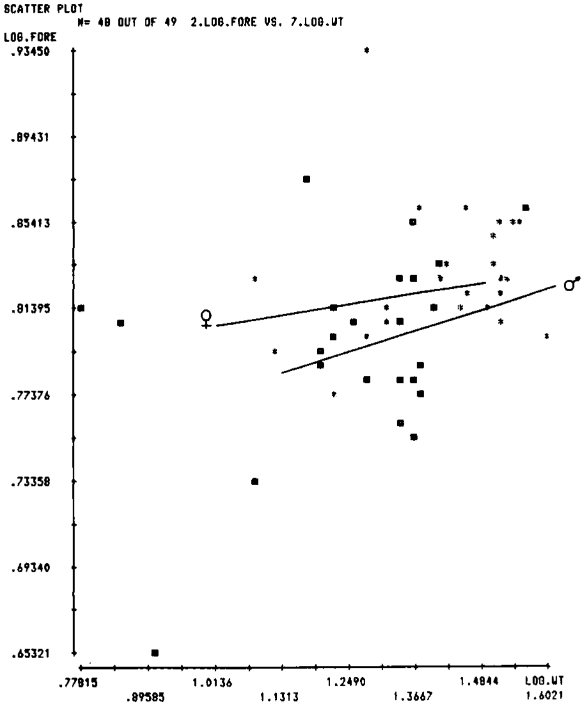
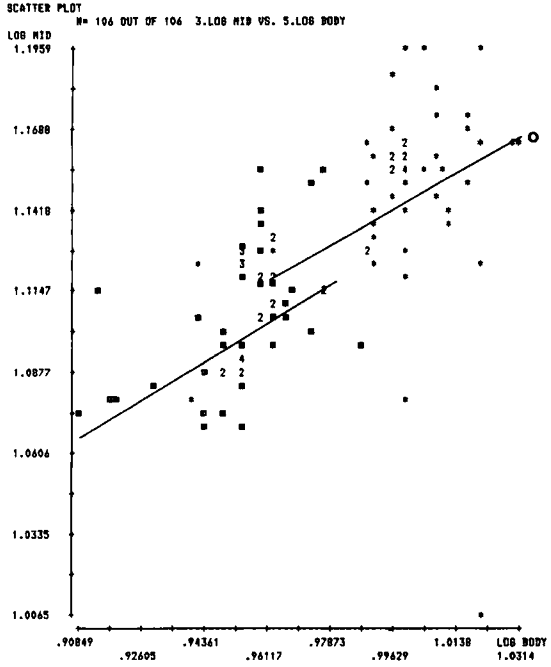


G. gibbifer





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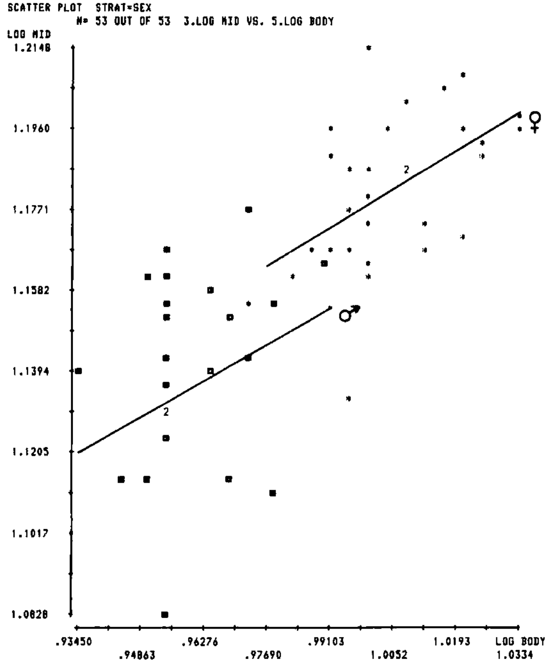
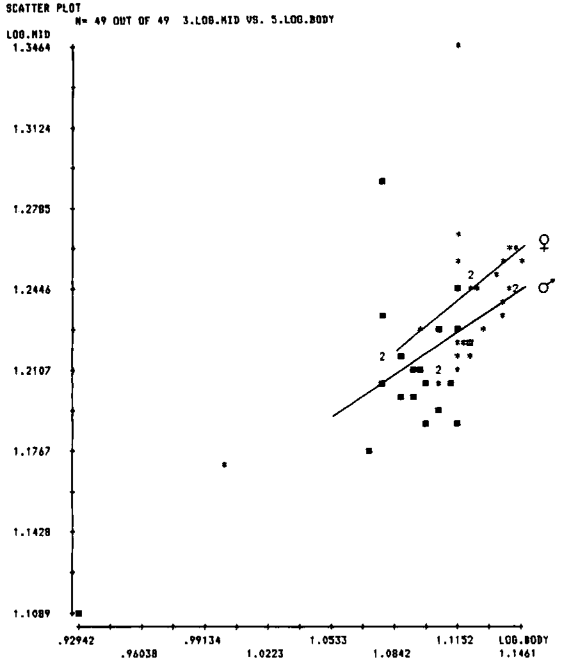
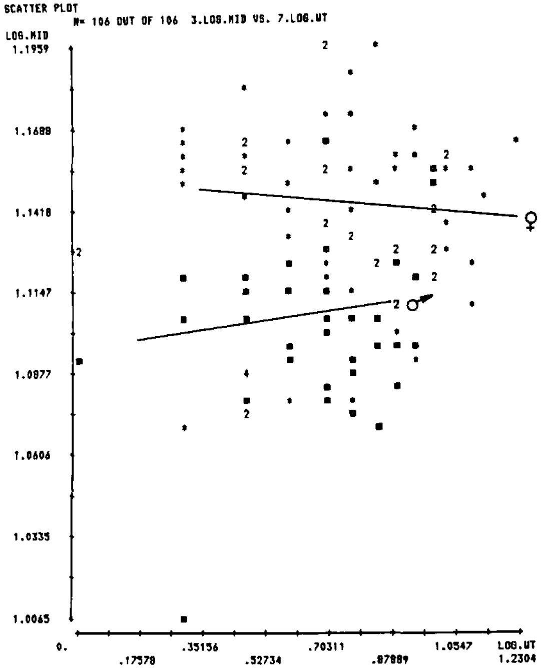


G.lacustris (Fr.)



G.gibbifer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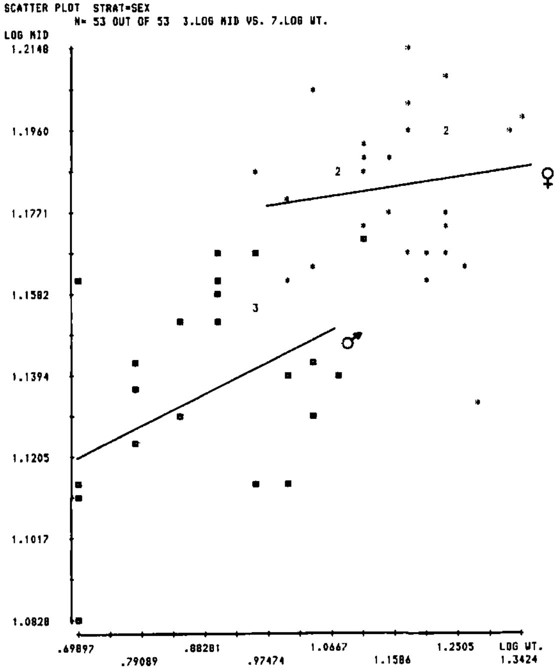
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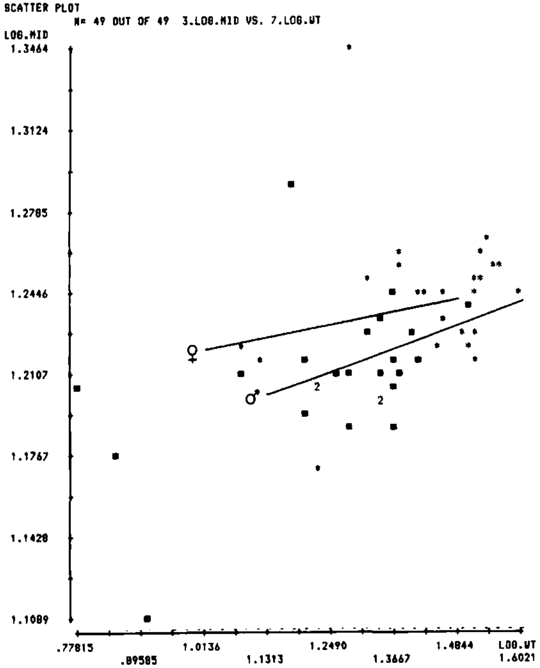
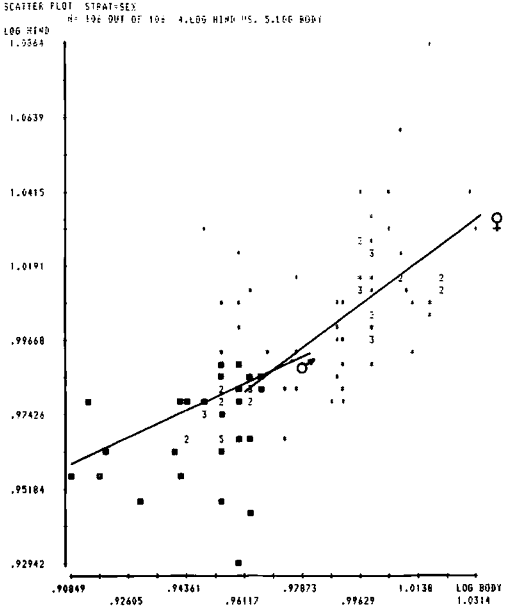
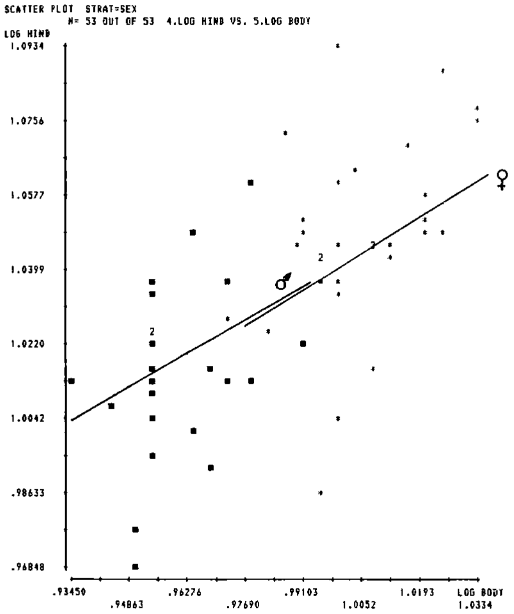

G.gibbifer

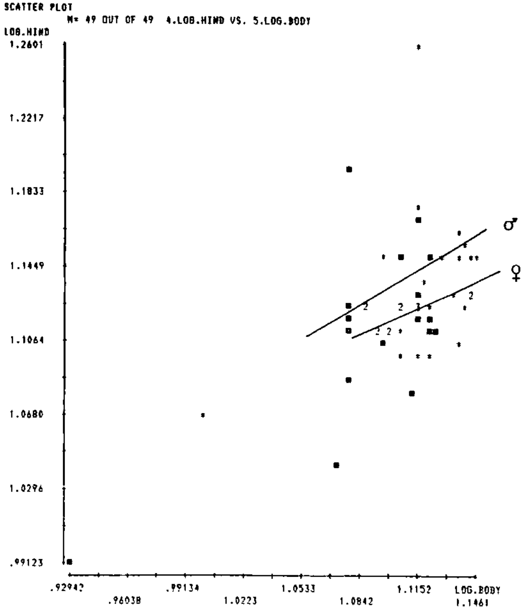
G.lacustris (Eng.)



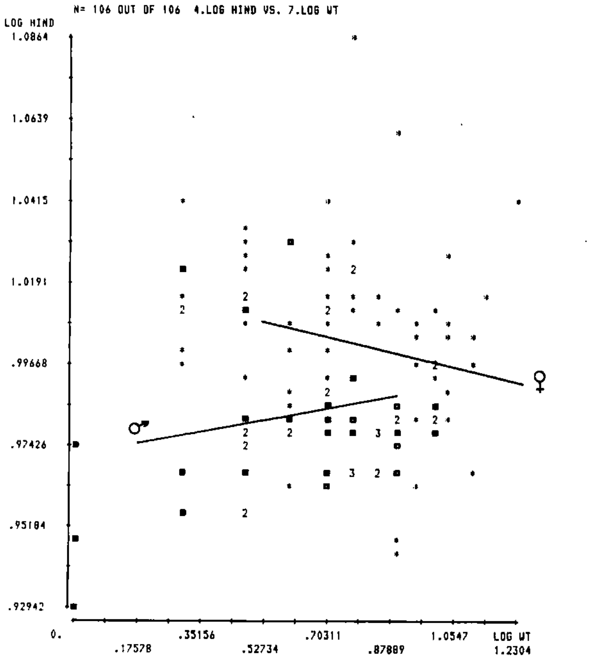
G.lacustris (Fr.)



G.gibbifer



G.lacustris (Eng.)



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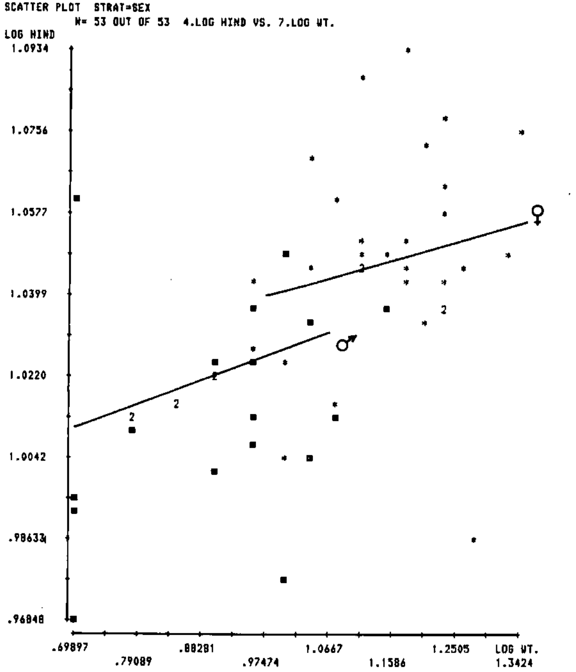
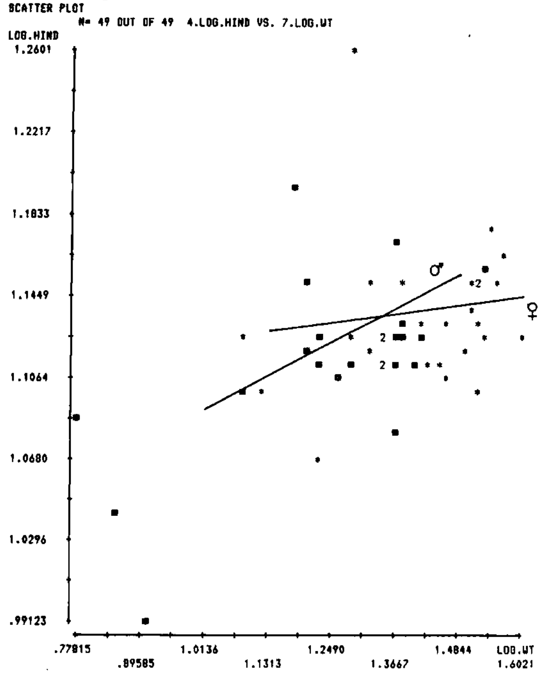
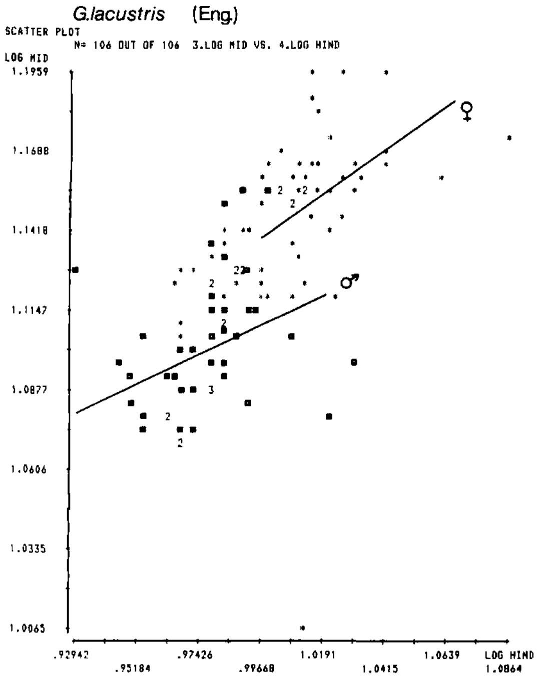
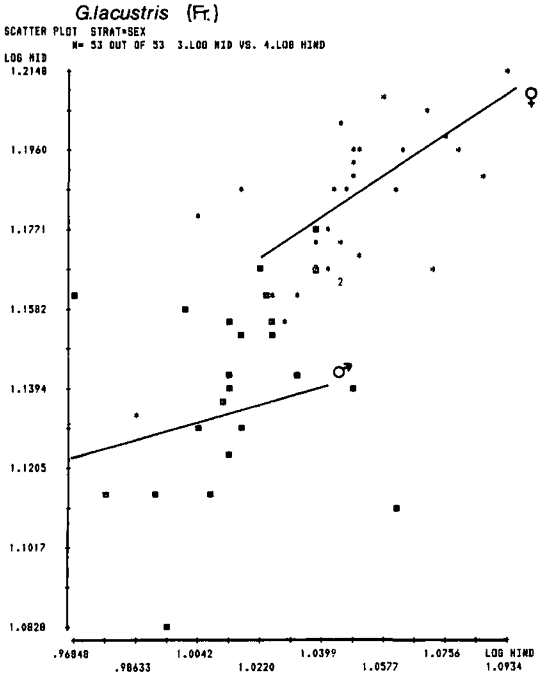
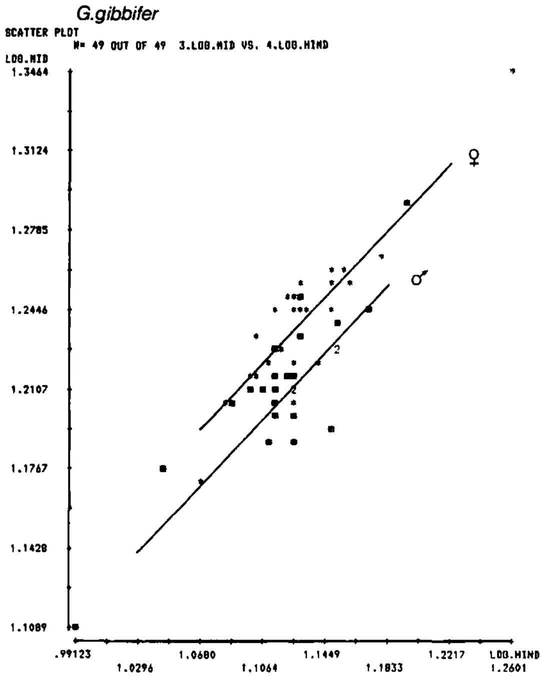


G.gibbifer

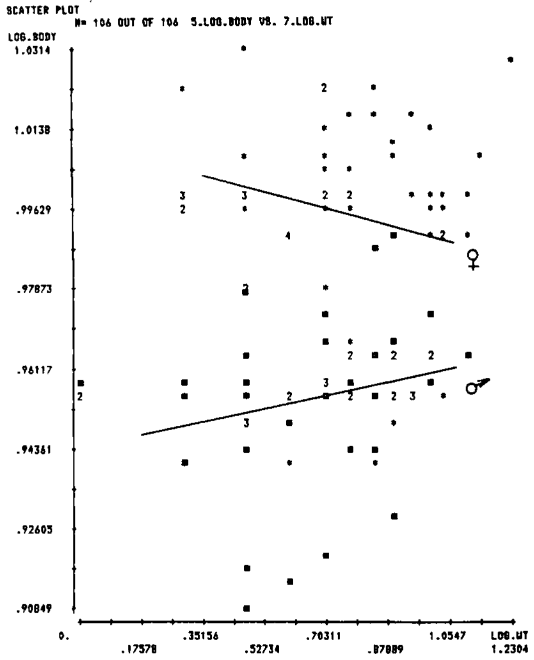



G.lacustris (Eng.)
SCATTER PLOT
N= 106 OUT OF 106 3.LOG MID VS. 4.LOG HIND
LOG MID
1.1959
1.1688
1.1418
1.1147
1.0877
1.0606
1.0335
1.0065
.92942
.95184
.97426
.99668
1.0191
1.0415
1.0639
LOG HIND
1.0864
♀
♂

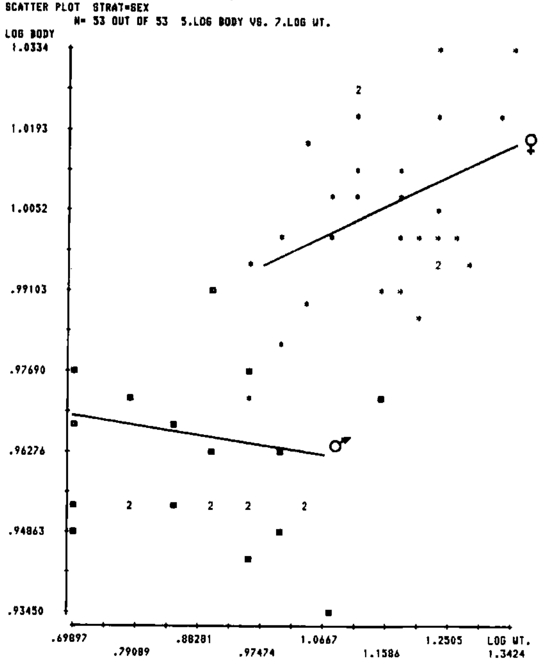

G.lacustris (Fr.)
SCATTER PLOT STRAT=SEX
N= 53 OUT OF 53 3.LOG MID VS. 4.LOG HIND
LOG MID
1.2148
1.1960
1.1771
1.1582
1.1394
1.1205
1.1017
1.0828
.96848
.98633
1.0042
1.0220
1.0399
1.0577
1.0756
LOG HIND
1.0934
♀
♂


G.gibbifer
SCATTER PLOT
N= 49 OUT OF 49 3.LOG.MID VS. 4.LOG.HIND
LOG.MID
1.3464
1.3124
1.2785
1.2446
1.2107
1.1767
1.1428
1.1089
.99123
1.0296
1.0680
1.1064
1.1449
1.1833
1.2217
LOG.HIND
1.2601
♀
♂

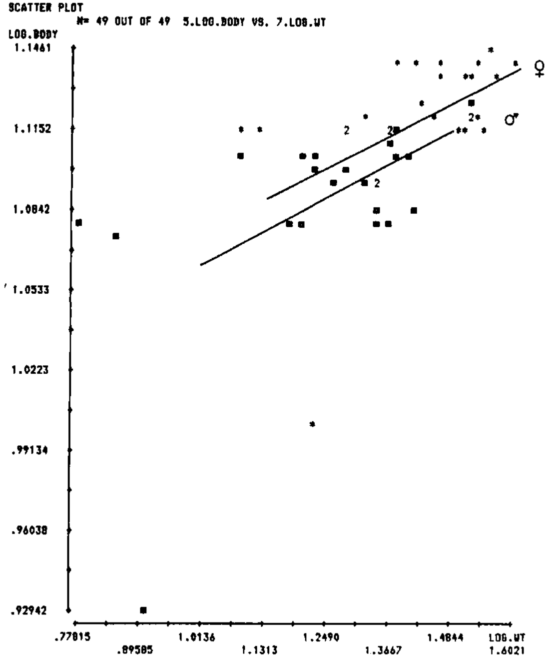
G.lacustris (Eng.)



G.lacustris (Fr.)



G.gibbifer



males (Table 7.1). The data from the populations of *Anajas* and *lacustris* suggest that the foreleg may be used by the female whilst paired as an extra means of support.

7.2.2 Midleg

From both relationships it can be seen that in general males have a correspondingly greater increase in middle leg length with body weight and length than do the females.

7.2.3 Hindleg

The results here are contrasting, in the English population females had a greater relative increase in hindleg length with bodylength but in the French populations of both *gibbifer* and *lacustris* males show an increase in hindleg length with body length.

7.2.4 Midleg v Hindleg

The results were similar for all the populations studied, females showing the strongest correlation between midleg and hindleg (Table 7.6). This implies that there is an increase in female hindleg length with corresponding increase in midleg length.

7.2.5 Body Weight v Body Length

The English population of *lacustris* and French *gibbifer* both showed a stronger correlation between weight and length for males than females, as was the case with both paired and single

Table 7.6

Correlation between midleg length and hindleg length for paired and unpaired male and female pondskaters.

Species		Male	Female
G.lacustris		0.39**	0.52***
G.lacustris (Fr)	a	0.23	0.68***
	b	0.56*	0.81***
A.najas	a	0.79***	0.88***
	b	0.78***	0.45**
G.gibbifer		0.85***	0.88***

* r significant at P<0.05

** P<0.01

*** P<0.001

a=unpaired b=paired

<u>najas</u>. The French population of <u>lacustris</u> however showed the opposite trend which may be a reflection of the smaller sample size (Table 7.2).

Table 7.7

Between species comparisons of morphometric differences between sexes. Sex with longest parameter shown.

	Variable			
Species	Fore leg	Mid leg	Hind leg	Body length
A.najas	F	M	M	M
G.gibbifer	M	M	M	M
G.lacustris Fr.	M	M	M	F
" Eng.	F	M	F	M

7.3 Discussion

The investigation here set out to verify the findings made for the paired A.najas in the previous chapter by using two related species of water bugs. The results indicate that the proportional lengths of comparative sets of limbs varied considerably between the sexes and sometimes for the species, summarized in Table 7.7. The predictions were fulfilled with one exception, thus implying that selection is acting irrespective of the insects condition, ie paired or single.

An opposite trend was found in G.gibbifer for relationships involving the foreleg with body length and weight and this suggests that there maybe either measurement error, most probable in the case of the forelegs, or that different selection pressures are acting on the male with respect to the female. As found earlier for the paired material, males showed a significant relationship between hindleg length and body length indicating a greater relative increase of leg length to body length. This implies that the female is employing a greater portion of her leg to elevate her body from the water and thus only a small percentage of the total leg length is resting upon the water surface. If this is so then males will have proportionately longer legs in order to reach the water, from their elevated position which is necessary in order to control female movements. This could be verified by investigating relative differences in tarsal lengths for both sexes and for all of the species collected. Brinkhurst (1960) in recording that Gerris possess very long tarsi noted that

G.lacustris not only rest upon their tarsi which are in contact with the water but the apical part of the middle tibia and the whole ventral surface of the hind tibia (see Fig.5.2a). Consequently, although it is the tarsus which is important in supporting the insect, in some species the tibia may also be a contributing factor. This needs further investigation before any firm conclusion can be made.

Both species also showed similarities with the paired A.najas in the remaining relationships in that males showed a greater increase in midleg length with bodylength than did females. Thus corroborating the conclusions regarding the loading constraints on both sexes made previously. The insects' capacity to support weight may depend on the proximity of the 'points of contact' of the adjacent limbs on the water surface and this may explain the differences between both sexes and species. If the points of contact are sufficiently close that interference patterns form then those points of contact will be insufficient to support body weight. If this is the case, then there may exist a behavioural difference between the sexes as opposed to a morphological one in that the choice of resting positions may determine the weight loading abilities of the individual.

In summary one can see that although female pondskaters undergo loading constraints there is no clear indication as to which morphological feature has been best adapted. Males may possess the adaptations which one might predict for control of the female during mate guarding i.e. longer hind limbs. A more detailed investigation into the behavioural characteristics of the insects may provide an insight and explanation for certain morphological features revealed during the study.

Chapter 8 ....

Discussion

Sexual dimorphism is generally thought to result from sex-specific differences in either ecological or reproductive selection pressures. It is usually assumed that many selective forces act on each sex jointly whilst only a few act in a divergent manner. Such differential selection might simultaneously affect various morphological, behavioural and life history traits producing a complete suite of adaptations. Thus a complete understanding of sexual dimorphism requires not only the identification of the selective forces involved but also an understanding of the interrelationships between the phenotypic traits they produce. The size data presented on the toad and pondskater populations indicate that females are larger than males. This difference between the sexes did not result from differences in growth rate, rather, they result from differences in the age at which sexual maturation is achieved and the mortality patterns for each sex that produce different age distributions and hence different size distributions. Such life history characteristics are often affected by the same selective pressures that influence adult body size and may complicate evaluation of size dimorphism in any species in which age and size are correlated. The influence of mating effort and parental investment on body size, age at sexual maturation and patterns of adult mortality will be discussed below.

Sexual dimorphism in body size in birds and mammals may often result from differences between sexes in mating effort and parental investment (Alexander & Borgia 1979). Species in which males are larger than females often contain males that expend high mating effort and little or no parental effort, and females that expend low mating effort and high parental effort. In such species, male mating effort is associated with size related reproductive advantages but female parental investment is not necessarily associated with any size advantage in reproduction. Variations in female reproductive success may be more strongly influenced by the number of young successfully reared rather than the number of young produced, and large female size might not greatly enhance rearing ability. In some mammals, however, large female size may increase parental success (Ralls 1976, 1977). In such species, a reverse sexual dimorphism may occur provided that (a) size-related reproductive advantages do not exist for males, (b) male body size is smaller than that of females despite size- related advantages for both sexes, or (c) large male body size results in some disadvantage in male-male competition (Ghiselin 1974, Alexander & Borgia 1979).

In contrast to birds and mammals, most anurans show reversed sexual dimorphism in body size. Shine (1979) pointed out in a recent review that in 90% of 589 anuran species females are larger than males. As with birds and mammals, consideration of how mating effort in males and parental investment in females affects body size may provide an insight into the relative body sizes of the sexes in anurans. In most anurans, females do not provide parental care aside from investment in gametes; hence female reproductive success is determined more by the number of eggs laid than by the number of young reared, and large female size permits a capacity for a greater volume of eggs in each clutch. The influence of male mating effort on male body size is less clear. In many ´explosively´ breeding anurans male mating effort consists of active searching for females, and physical contest with males already in amplexus with females (Wells 1977).

The evolution of dimorphism in age at sexual maturation in birds and mammals depends on ecological and reproductive selection pressures. Wiley (1974, 1980) suggests that polygyny, sexual differences in age at sexual maturation and body size dimorphism may co-evolve as parts of an adaptive complex in response to ecological conditions; no cause-effect relationship need exist between these reproductive parameters. Other authors suggest a definite cause-effect relationship, in that intense sexual competition among males of polygynous species might make mating effort by younger males costly and ineffective thus favouring delayed maturation (eg Selander 1972, Alexander & Borgia 1979).

In polygynous birds and mammals males often mature later than females (Wiley 1974). Unfortunately few studies on anurans have investigated the possibility of sex specific differences in maturation time. Collins (1975) reported that females mature later than males in four of the anuran species he investigated and Gittins (1983) that males breed a year earlier than the females.

Research into sexual dimorphism has been concentrated mostly on homiotherms which for the most part show an association between size dimorphism and the extent of male:male competition. Conversely, in poikiolotherms whilst there is often fierce male:male competition, males are found to be smaller than the females.

In birds and mammals the selection pressures on males and females are seperate even when they pair during the breeding season. In unit maters, however, selection pressures are clearly operating as a result of the length of time spent together during pre-copular mate-guarding, these pressures are consequently regarded as being interactive. In both of the groups investigated in this study the females are larger than the males and undergo loading constraints through (i) their increased body weight from the egg load and (ii) the added weight of the male which is carried around by the female for part of the breeding season. The results of this study reveal how this loading factor may effect female morphometric characters in different ways. In toads for example the female appears to have proportionately longer front legs and this may be as a result of the loading factors which are acting whilst in the paired situation, females using the forelimbs whilst on land to pull themselves along and to support their weight. Once in the pond females use another behavioural adaptation in that they remain in the shallower edges of the pond thereby resting their legs on the substrate so that they are not bearing the full weight of the male without support. Observations in the laboratory of several heavily gravid females with various sized males revealed that when placed in a tank of water females tended to rest on the bottom, only surfacing when necessary for air. Only when the female had an extremely small male on her back would she then remain on the surface.

In pondskaters, females appear to use their forelegs for supporting body weight whilst copulating and appear not to have longer legs relative to those of the males. In addition, the weight of the male is but a fraction of the weight of the female, as much as half of her body weight.

Assortative mating is usually interpreted in terms of male:male competition, larger males getting larger females. Assortative mating will also be determined by the mechanical constraints placed upon each sex, especially in the female. In the case of the pondskaters females would be unlikely to cope with the weight loading of a larger male. Whilst it may be the case that small males can be dislodged from females by larger males, female size should be taken into account. Smaller males may be better adapted to remaining attached to females, consequently making it more difficult for larger males to dislodge them. Two factors mitigate against the success of large males:

i) their weight which may restict female breathing, and

ii) the difficulty of ensuring adequate cloacal contact at egg and sperm release. Once a male contests a rival for a female then the danger to the female is increased as the combined weight may submerge and drown it, as was recorded in this study.

Assortative mating ocurred only in pondskaters and not in toads and two explanations may be possible. Toads are explosive breeders i.e. their breeding season is very short and consequently the ensuing intermale rivalry is concentrated towards fertilization of a female. Consequently males mount the nearest available female and as long as they can maintain their position and defend it from rival males their mating rights are protected. It is essential that the size of the male is compatible with that of the female in order that the eggs are successfully fertilized when released, but the males cloaca does not have to be juxtaposed with that of the females however, since the male spreads his sperm over the extruding eggs using the backlegs. In view of this one would expect males to have relatively longer backlegs than females, not only for ensuring successful fertilization but also for fighting since these limbs that he fends off the rival males whilst remaining clasped to the female with his strong forelegs, and this was so for the population used. Pondskaters on the other hand experience an extended breeding period from May to early September and so both sexes have time to be more selective in their choice of mates.

Secondly the sex ratio in pondskaters appears to approach parity which is not the case for the toad population, the ratio in the population studied was found to be seven males to every female. Consequently, the competition for females is heightened in toads by the short period of mate availability

To summarize, in both toads and pondskaters, males use the tactic of pre-copulatory mate guarding. Assortative mating, which is normally interpreted in terms of male:male competition, was found to be operating in pondskaters and to be absent in toads. The extent to which male:male competition is important in both species is as yet undetermined, except insofar as to be very intensive in toads. The mechanical constraints placed on the animals whilst paired appeared to differ in their effects on the morphological features. Females being larger than males and appearing to possess adaptations to cope with the extra weight of the males. Males, although smaller than the females appear to possess characteristics that aid in copulation and fighting, male toads have relatively longer backlegs; and for control of the females, male pondskaters appear to steer the females whilst in precopular mate-guarding.

Acknowledgements

I would like to thank the following people without whose help this thesis would still be just an idea.

Paul Greenwood for his help throughout this study and to Steve Rushton for his constructive criticisms. Bob Williams, who´s aid with the computing was invaluable. My thanks to David Stubbs, who´s avid collecting provided me with the paired material required for the latter half of the study; Michael Atkinson who has aided me unfailingly throughout the year, and all the staff at 32 Old Elvet. A special thankyou to Dr.T.T.Macan who verified my identifications of the French species by post. For the use of facilities in both the department of Zoology and Adult & Continuing Education I would like to thank Professor Barker and Mr Dixon respectively.

I cannot begin to thank those people who, on dark, cold nights, left the warmth of their pints to help me in the delights of toad collecting; ´those people´ being Johnny Birks, Pete Forsyth, Sue Greig, Simon Pickering, Kathy Ridley, Peter Sloss and Tufty. For allowing access to the pond and the surrounding land to a gaggle of madcap ecologists I must pay my thanks to Mrs Cosker, who sensibly left us to it! For their unerring encouragement throughout the past 18 months, I would like to thank my flat mate, Kathy, for enduring the reams of computer paper and continuous stream of animal life, Pete Sloss for his help and especially Pete Forsyth, who suffered the moods of a field biologist with good humour. I would like to thank all those people who I have met whilst in Durham for making the ´cold´ North seem a little warmer! and, finally, Gordon Port (Newcastle University), who allowed me time to finish this thesis whilst in his employ. The research was supported by a studentship from the University of Durham's Research Fund for Special Projects.

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APPENDIX I

Vegetation found around the study site

RANUNCULACEAE

Ranunculus sp.

CARYOPHYLLACEAE

Silene alba (Mill)

Cerastium fontanum (Baumg)

HYPERICACAE

Hyperum sp.

PAPILLIONACEAE

Melilotus officinalis (L)

Trifolium pratense (L)

T. Repens (L)

T. Dubium (Sibth)

Vicia sativa (L)

ROSACEAE

Filipendula ulmaria (L)

Potentilla erecta (L)

Rubus spp.

Cratageus monogyna (Jacq)

HALORGACEAE

Hippus vulgaris (L)

CALLITRICHACEAE

Callitriche palustris (L)

ONAGRACEAE

Epilobium angustifolium (L)

E. Hirsutum (L)

E. *Montanum* (L)

UMBELLIFERAE

RUBIACEAE

Galium *aparine* (L)

COMPOSITAE

Achillea *millefolium* (L)

Chrysanthemum *parthenium* (L)

Artemisia *vulgaris* (L)

Cirsium sp.

Picris *echioides* (L)

Hypochoeris *radicata* (L)

ERICACEAE

Calluna *vulgaris* (L)

SOLANACEAE

Solanum *dulcamara* (L)

SCROPHULARIACEAE

Verbascum *lynchnitis* (L)

Linaria *vulgaris* (Mill)

Digitalis *purpurea* (L)

Rhinanthus *minor* (L)

LABIATAE

Mentha *aquatica* (L)

M. *Spicata* (L)

Lavandula *angustifolia* (L)

URTICACEAE

Urtica *dioeca* (L)

SALICACEAE

Salix cinerea (L)

ALISMATACEAE

Alisma plantago-aquatica (L)

BUTOMACEAE

Butomus umbellatus (L)

LEMNACEAE

Lemna minor (L)

POTAMOGETONACEAE

Potamogeton natans (L)

GRAMINACEAE

Agrostis spp (L)

Dactylis glomerata (L)

Holcus lanatus (L)

APPENDIX II

Figs. 4.1a-d. Variation in four body size parameters in the *Bufo* population, sexes treated seperately.

a) armlength

b) leg length

c) body length

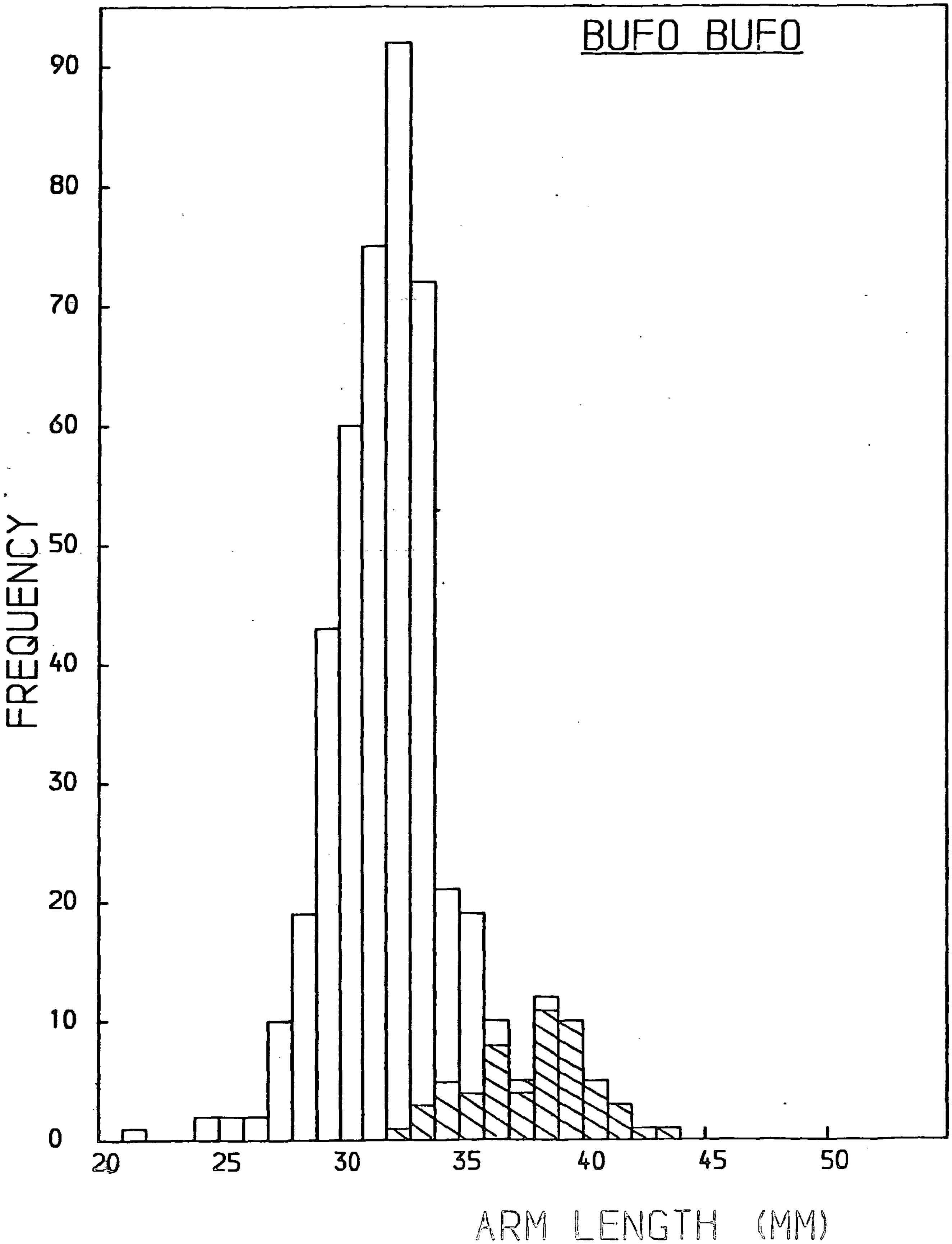
d) body weight

All lengths in mm, weights in mg.

Key

▨ = Females

□ = Males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FREQUENCY
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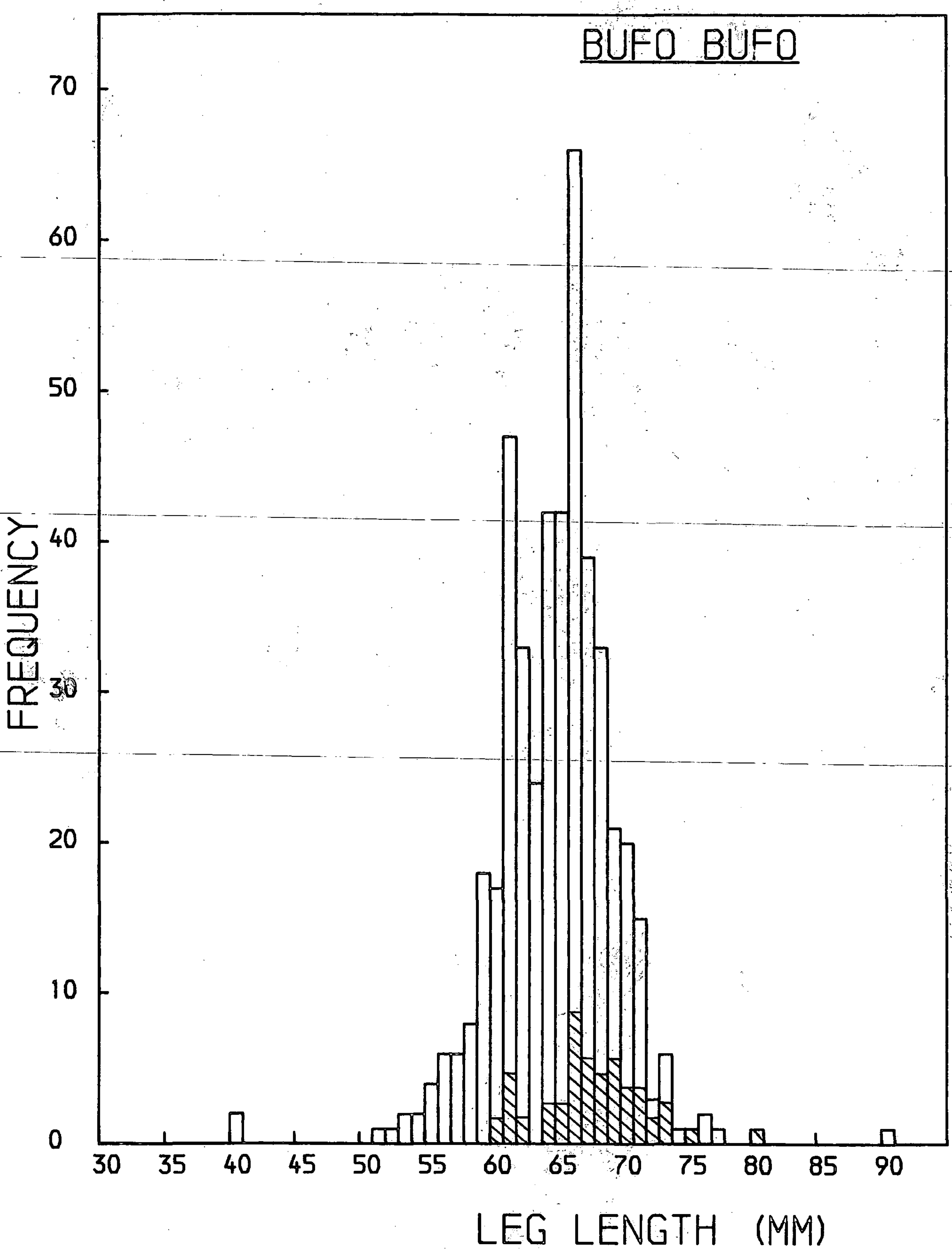
45
50
ARM LENGTH (MM)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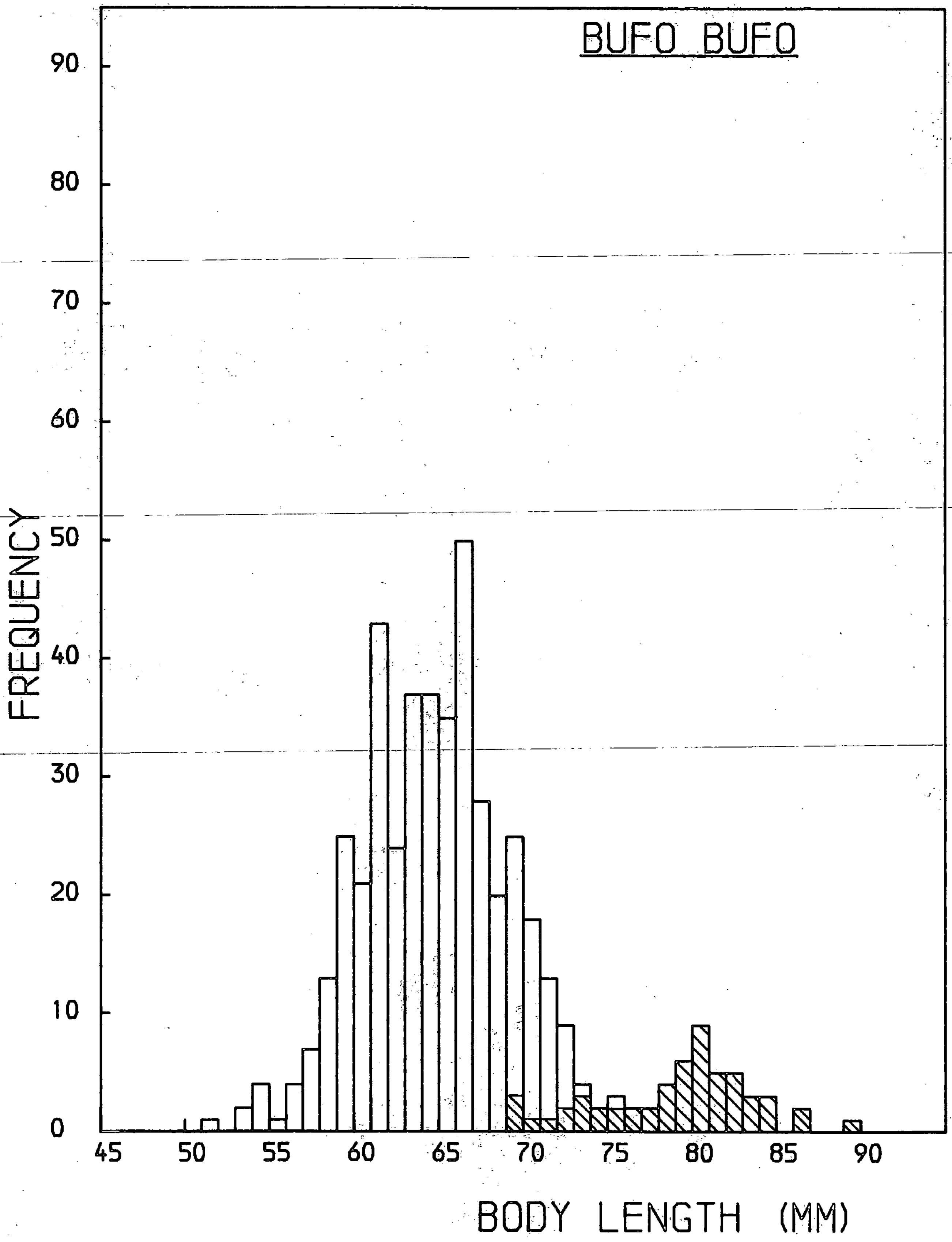
80
85
90
LEG LENGTH (MM)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70
75
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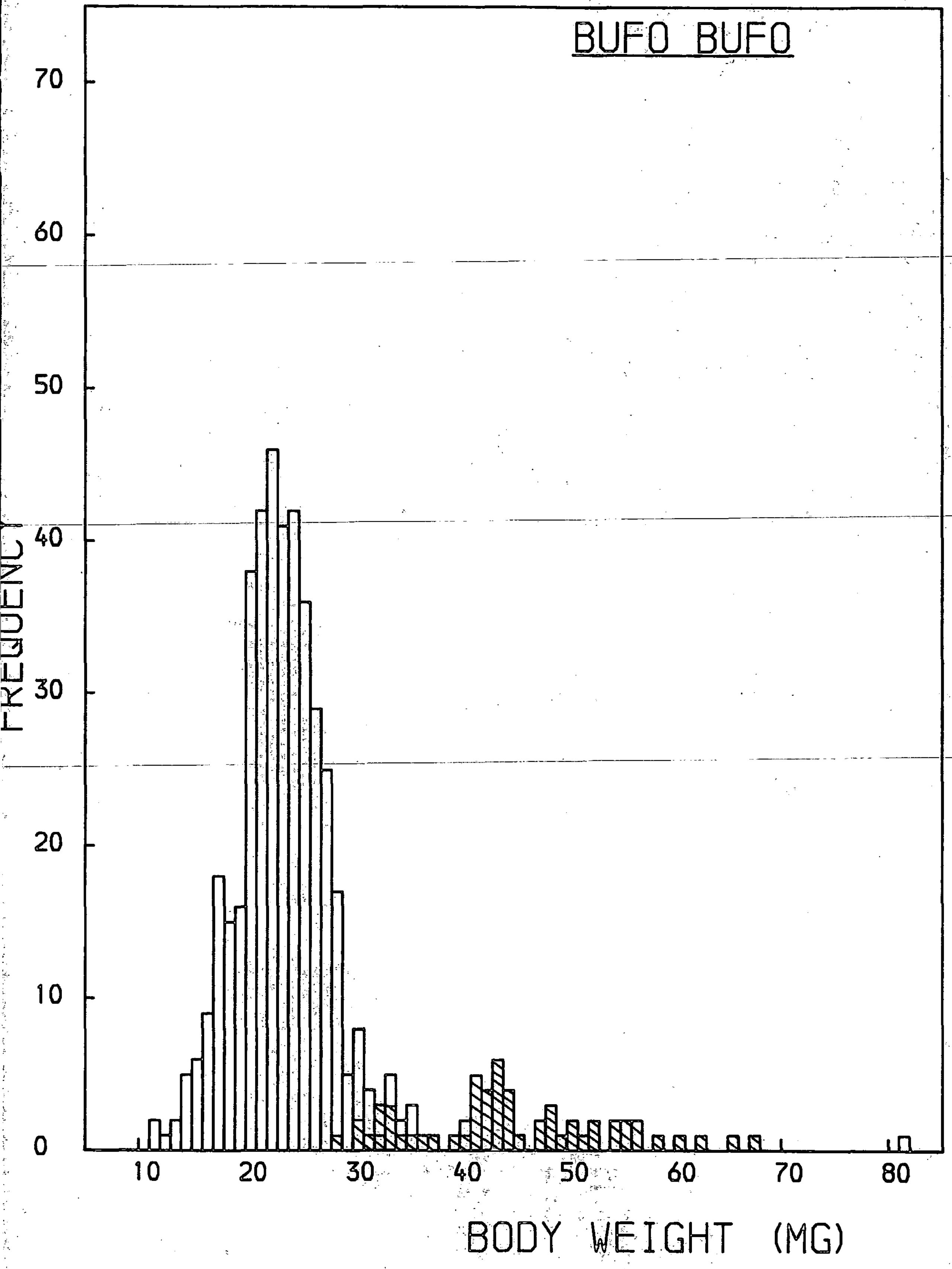
85
90
BODY LENGTH (MM)


BUFO BUFO
FREQUENCY
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30
20
10
0
10
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30
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50
60
70
80
BODY WEIGHT (MG)

Fig.6.2a-f Variation in six body size parameters for four species of <u>Gerris</u> with estimated means and standard deviations.

a) Foreleg length

b) Midleg length

c) Hindleg length

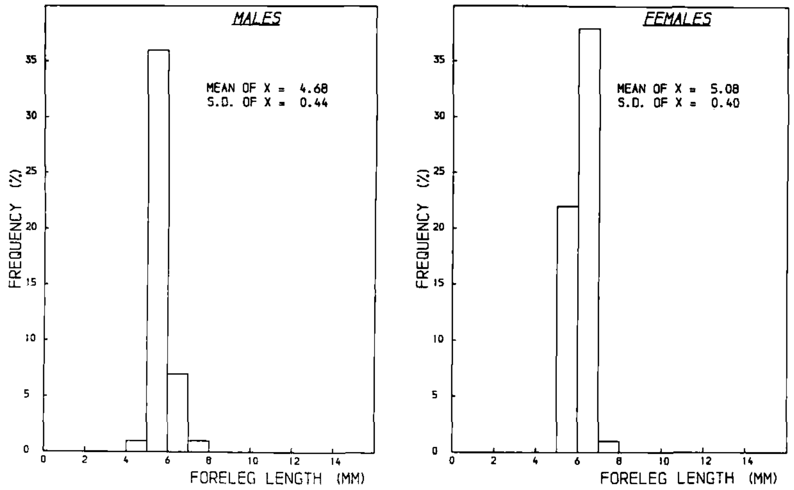
d) Body length

e) Antennae length

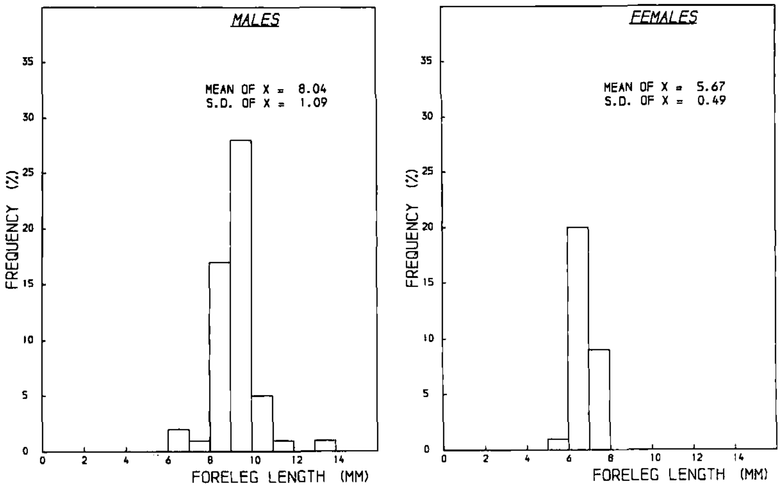
f) Body weight

All lengths in mm, weights in mg.

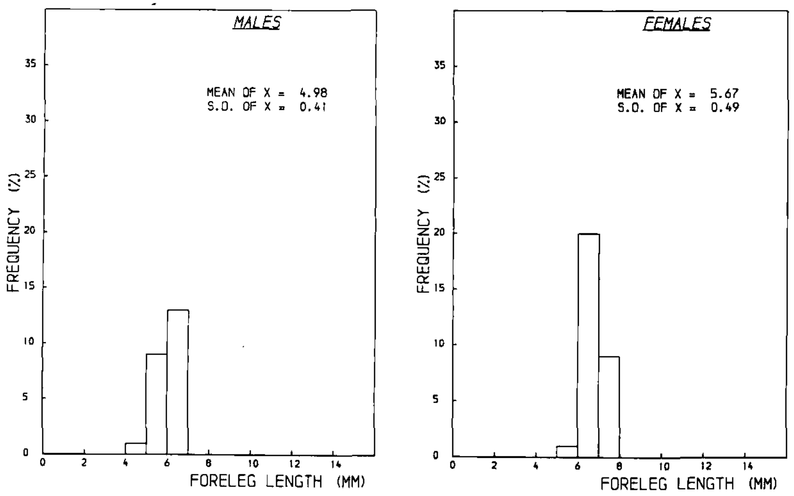
G.lacustris (Eng)



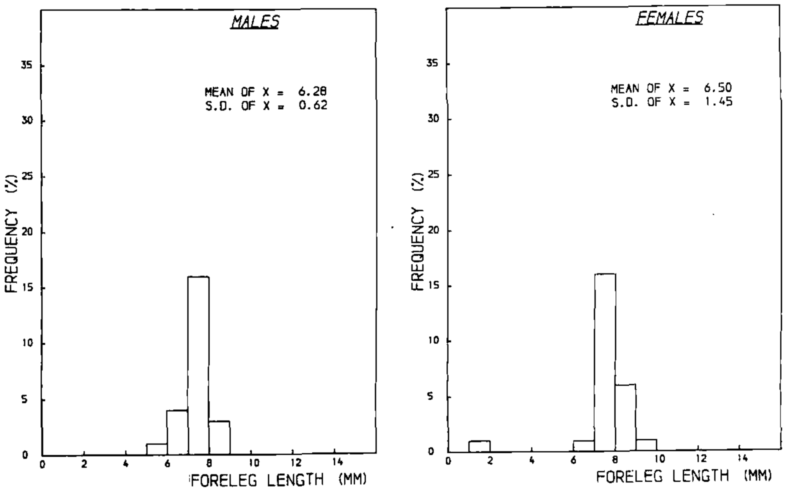
A.najas



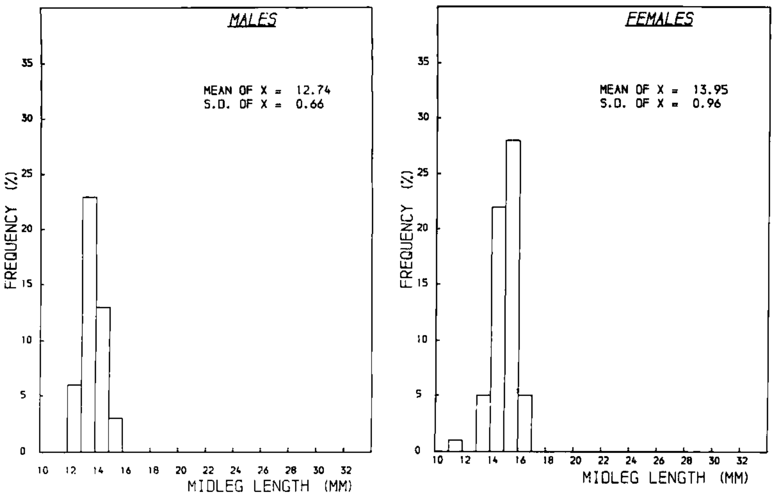
G.lacustris (Fr)



G.gibbifer



G. lacustris (Eng)



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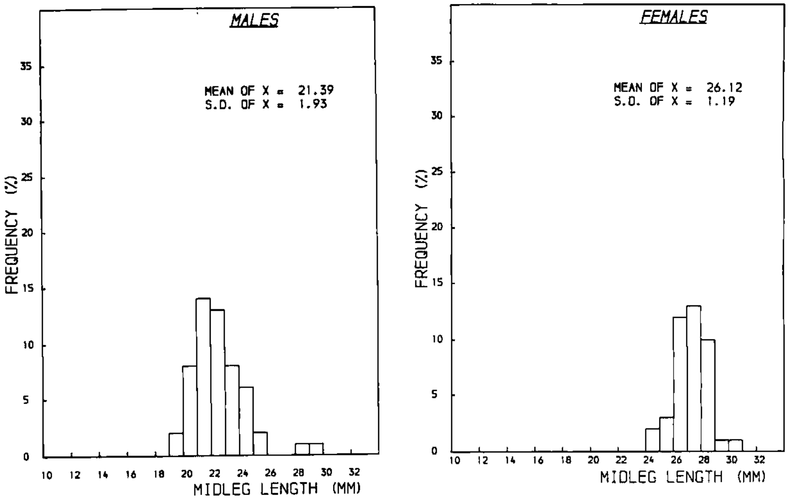

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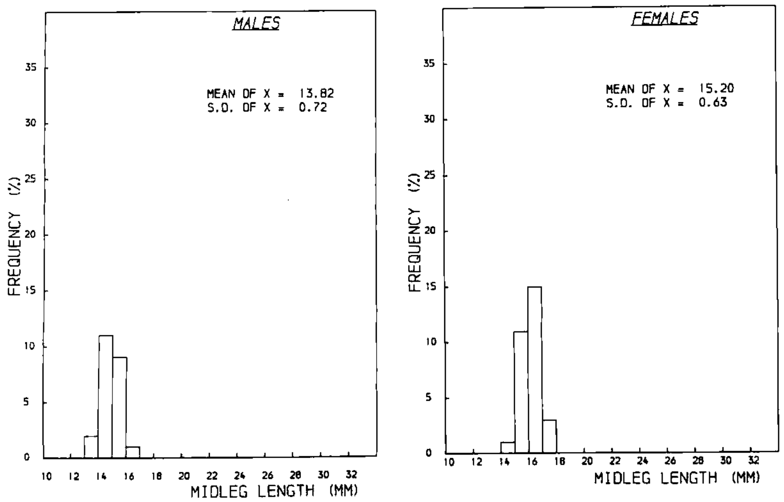
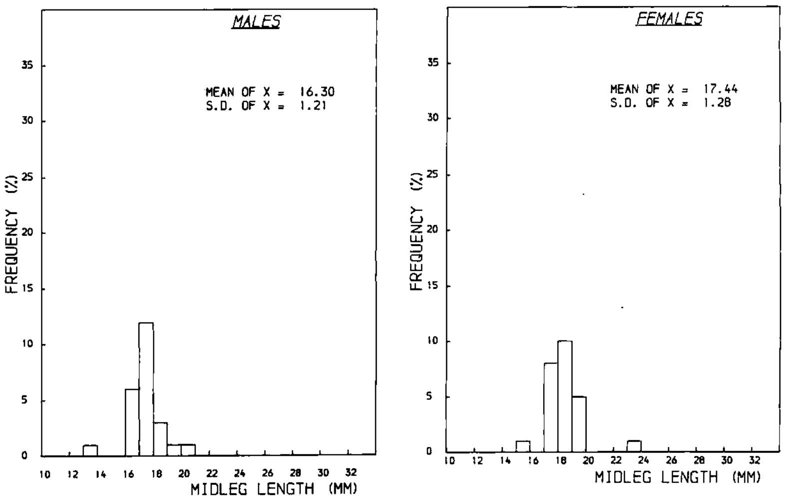


G. gibbifer



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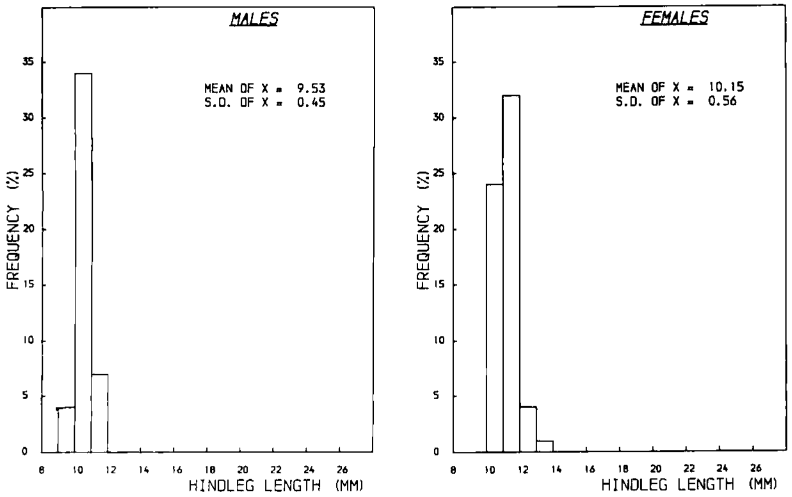

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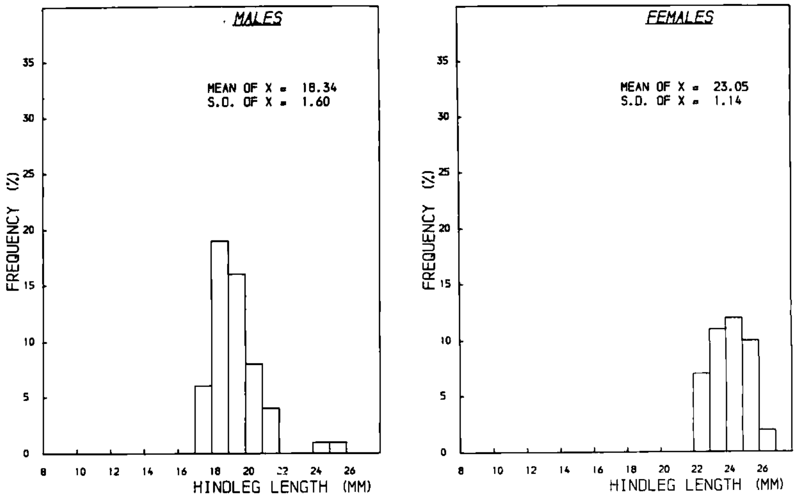

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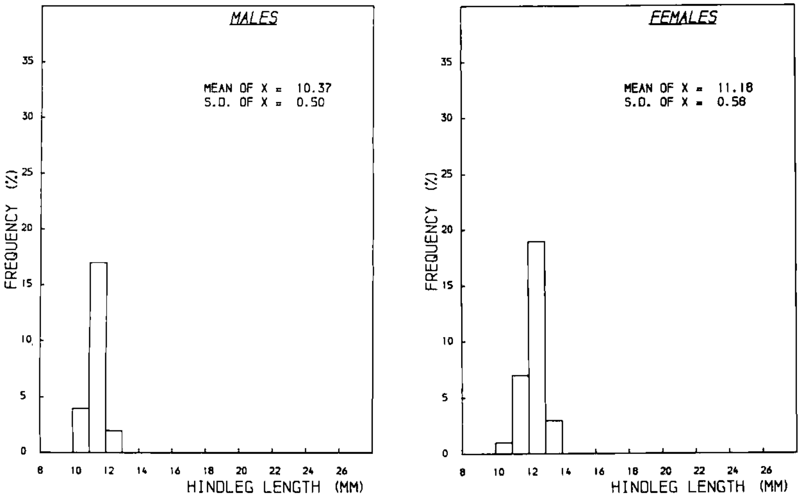
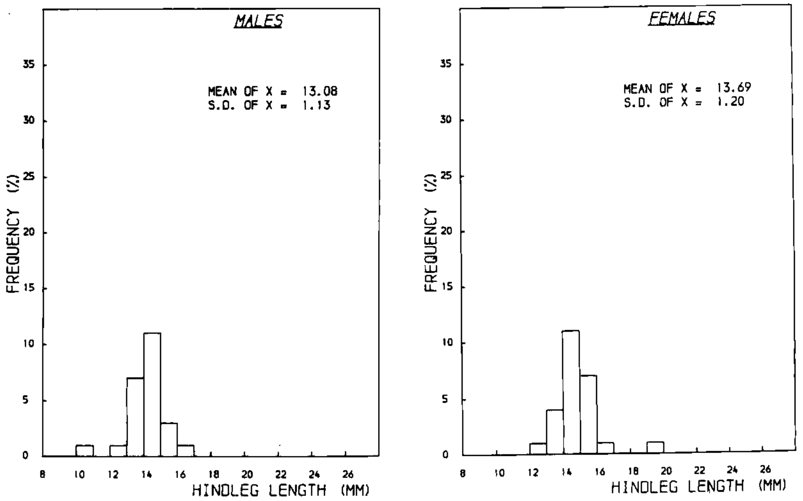


G.gibbifer



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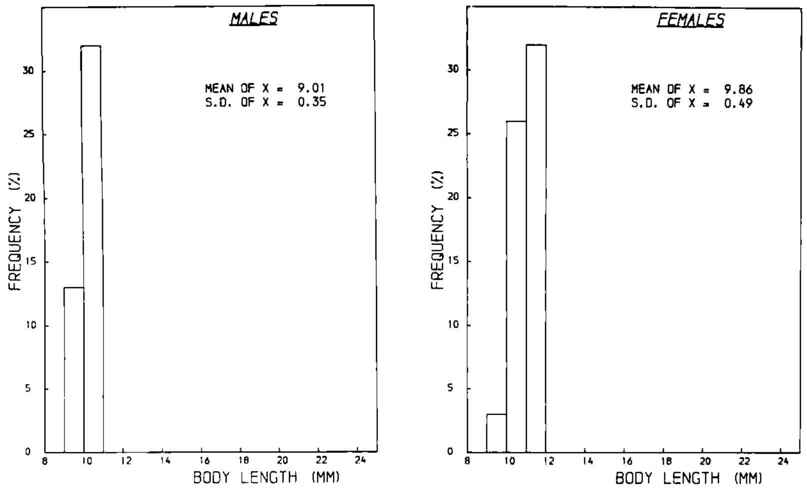

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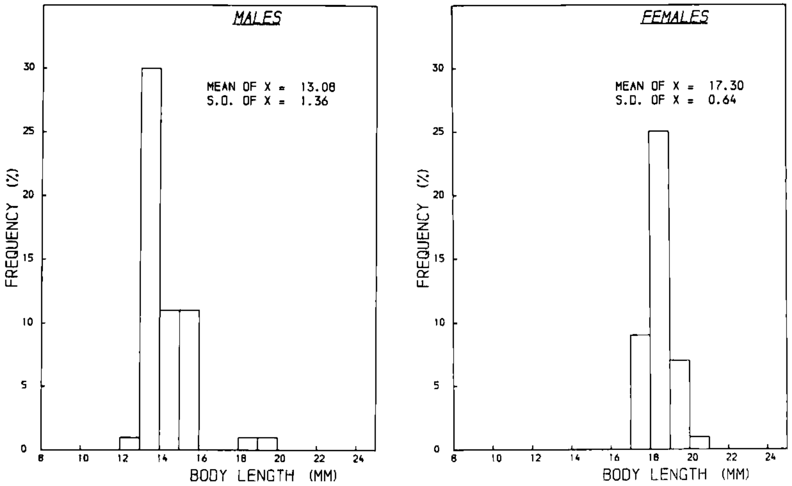

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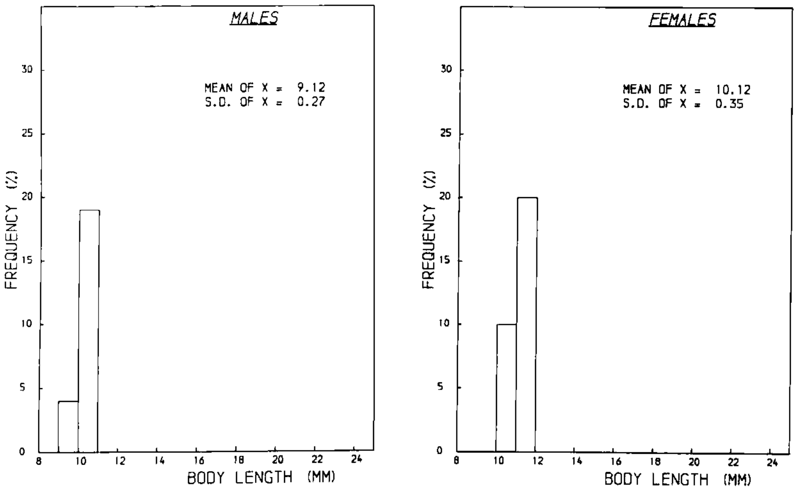

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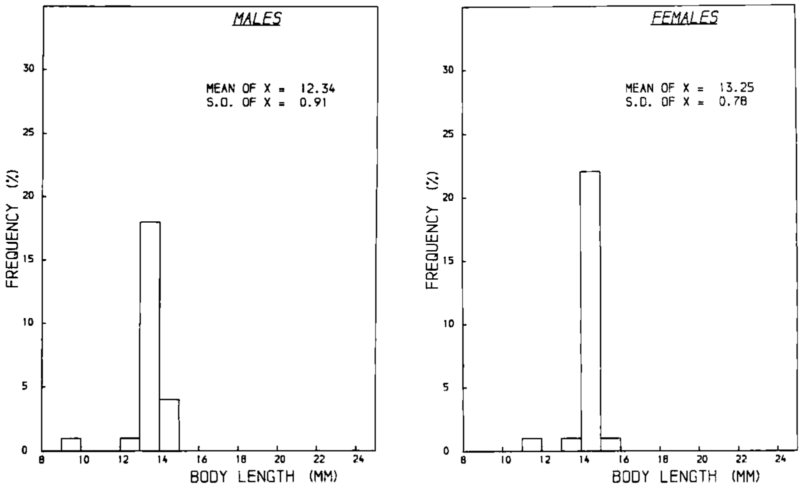
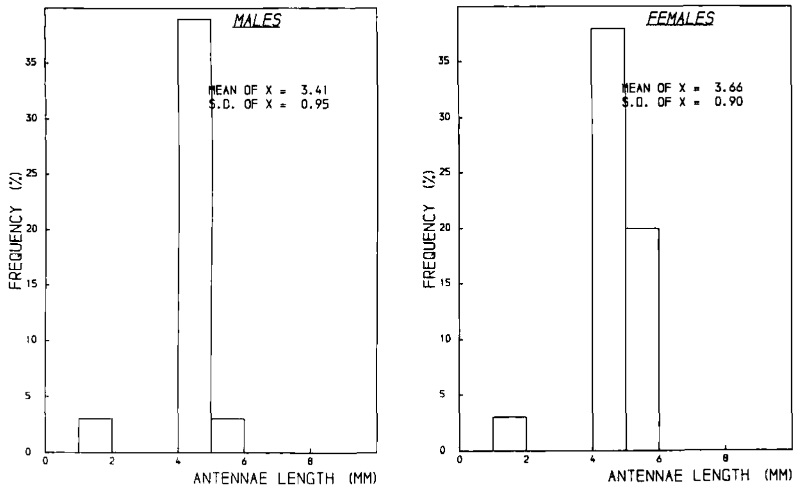
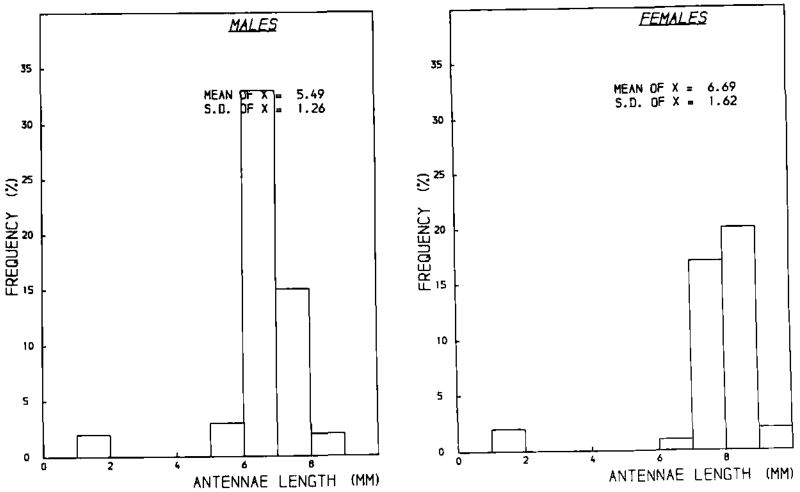




G.lacustris (Eng)



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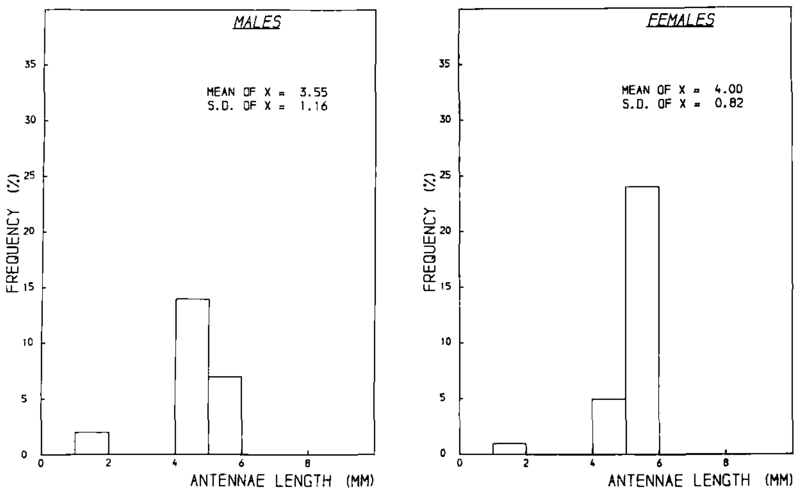

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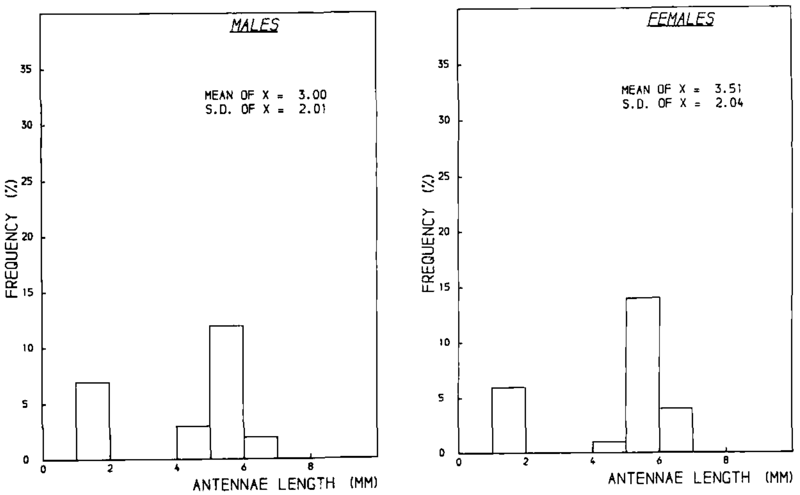
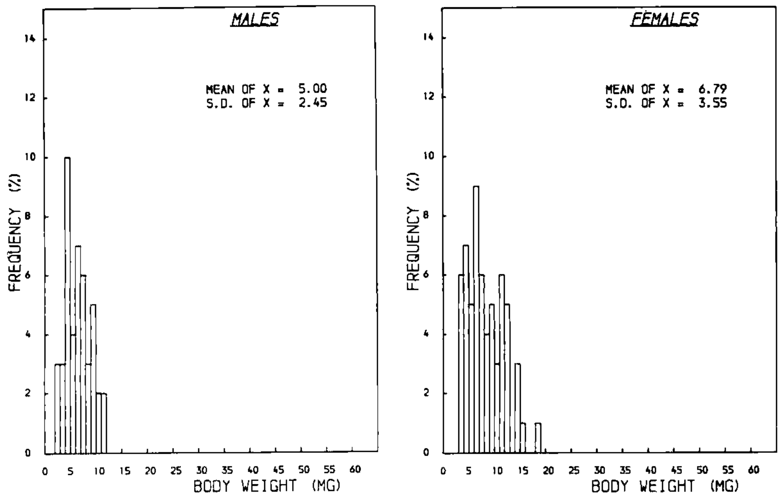


G.gibbifer

G.lacustris (Eng)



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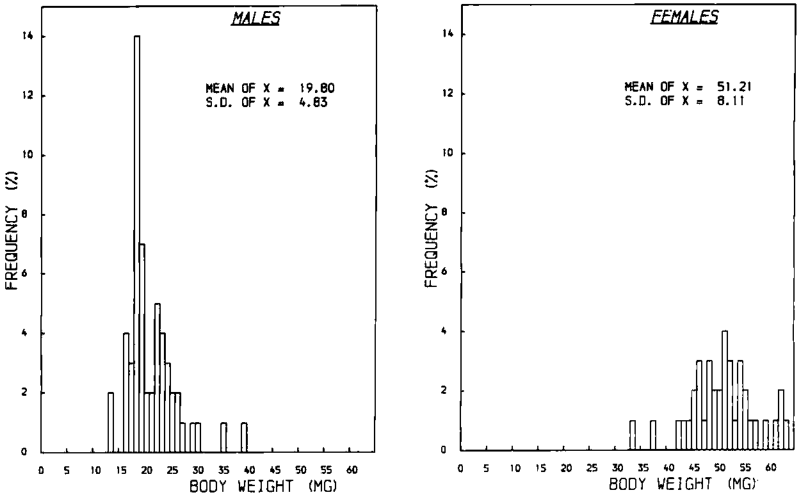

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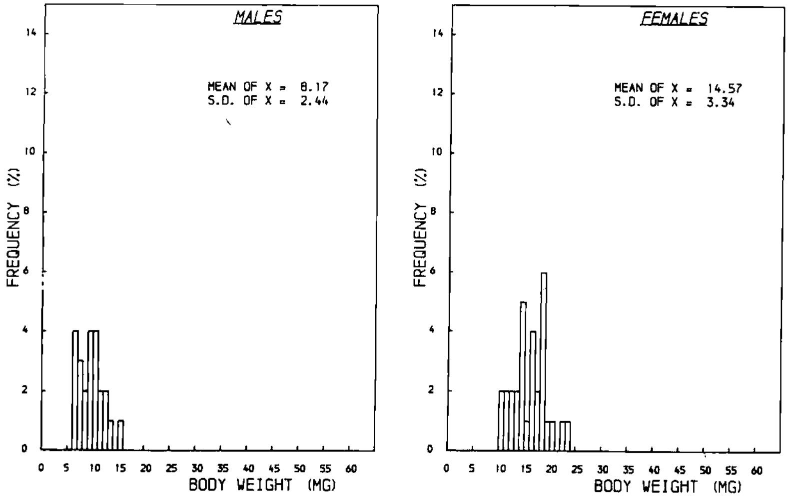

G.gibbifer