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Some Potential Evolutionary Costs Associated with Paternal Care in the Water Bug Belostoma flumineum Say

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Some potential evolutionary costs associated with paternal

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BY

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ABSTRACT

Female water bugs (Belostoma flumineum) deposit eggs in a mucilaginous cement on the back of conspecific males, who then brood these eggs until hatching. Sex role reversal, in which females compete for males and males are discriminating, is predicted in this species because males provide parental care exclusively, and represent a limited resource. Presumably the advantage of this paternal behavior is increased survival of young. However, the potential exists for this egg-brooding behavior to incur evolutionary costs, and quantifying some of these costs was the thrust of this study.

One cost, a loss of polygynous opportunity, was investigated in both laboratory and semi-natural field conditions by measuring the length of time the male spends brooding to the time females spend between successive clutches. Results suggest that females, after ovipositing one clutch of eggs, will oviposit a second clutch before her first clutch has hatched, if a mate is available. This suggests a cost of decreased polygynous opportunity for the male.

Presumably, male water bugs would be less able to escape predators or capture prey while egg-ladden because of decreased swimming capabilities. Therefore an experiment was designed to measure swimming speed. Encumbered male B. flumineum swam significantly slower than unencumbered males or females. In addition, an experiment was

undertaken to measure food intake. It was found that males eat less during the brooding period than after hatching. Therefore swimming speed reduction and decreased feeding may also be potential costs to male care.

ACKNOWLEDGEMENTS

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Natural selection is the differential reproductive success of certain individuals in a population due to their heritable, beneficial characteristics. By natural selection, individuals who possess the heritable phenotypes best suited for survival produce more offspring than those that do not. Sexual selection, described by Darwin (1871), is set apart from natural selection in that it involves differential reproduction due to a difference in the abilities of members of the one sex to compete for access to members of the opposite sex. Sexual selection consists of both intrasexual selection and intersexual selection. In Darwin's terms, intrasexual selection is "the [male's] power to conquer other males in battle," while intersexual selection refers to "the [male's] power to charm the females" (Darwin, 1871). In most species sexual selection works more strongly on males. Males typically compete for females, and often "display" certain attractive characteristics to gain female receptivity.

According to current sexual selection theory, the relative parental investment made by the two sexes should be important in accounting for any competition or discrimination observed (Trivers, 1972). Parental investment consists of "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring"

(Trivers, 1972). Paternal investment may be manifested in
various ways, and usually this investment is post-zygotic
(i.e. incubation, brood defense, feeding etc). In some
species, males invest prezygotically in the form of nuptial
gifts such as spermatophores in mormon crickets (Gwynne,
1981), or insect prey as in scorpionflies (Thornhill and
Gwynne, 1986). Trivers (1972) predicts that the sex which
invests the least in offspring will compete for the sex who
invests the most, and that the latter will be the
discriminating sex. In most species the female invests
more than the male, and therefore are more discriminating
with whom they mate (i.e., selection favors mate quality).
Males, on the other hand, are typically more promiscuous,
prefering mate quantity to mate quality.
     In species where the male appears to invest more than the
female, sex roles are altered. Females display intrasexual
competition to a higher degree than do males, and
consequently, "are larger, more aggressive, or more
brightly colored than the males" (Barash, 1982). Some
species exibiting a form of role-reversal include: giant
water bugs (Smith, 1979a), sea horses and pipefish
(Fiedler, 1954; Strawn, 1958; Takai and Mizokami, 1959);
several families of frogs (Wells, 1977, 1978); and several
bird species (Hohn, 1969; Hilden and Vuolanta, 1972;
Ridpath, 1972; Jenni, 1974; Graul et al., 1977; Oring and
Maxon, 1978).
     Some examples of species in which the male provides the

parental care exclusively include all species of the frog families Leiopelmatidae, Rhinodermatidae and Sooglossidae (McDiarmid, 1978), and several species of birds in the Jacanidae (Jenni and Collier, 1972).

In five families of insects in the order Hemiptera, there are species in which care is provided exclusively by the male (Smith, 1980b). The waterbug family Belostomatidae is comprised of the sub-families Lethocerinae, Horvathiniinae, and Belostomatinae (Menke, 1979) and consists of approximately 150 species. In all species of the subfamily Belostomatinae, males carry eggs deposited on their backs by conspecific females (Lauck and Menke, 1961). Williams (1966, 1975) suggested that water bugs could be used in studies of altered mating behavior because of the investment the males make beyond gametes, and it has been studied in part by smith (1979a). Belostoma flumineum is a member of the subfamily Belostomatinae. It is a predaceous insect, approximately 2 cm in length, and is found in ponds and lakes throughout the continental United States. Belostomatids overwinter by burrowing a few centimeters into the bottom ooze of ponds (Menke, 1979).

Between alternating bouts of courtship and copulation, the female deposits eggs, about three at a time, in a mucilaginous cement on the back of the male. It takes approximately 6-12 days for these to hatch (Torre Bueno, 1906). During this period males brood their egg pad, and

this has been shown to be vital to egg-nymph survival
(Smith, 1976a). Brooding behavior consists of resting at
the surface (for aerating purposes), egg patting, brood
stroking, sawing and kicking.

The services an egg-ladden, or encumbered male provides
appears to represent a considerable parental investment.
As mentioned, in species which display sex role reversal
males tend to make a significant parental investment:
Mormon cricket males donate a spermatophore (up to 27% of
body weight) which contributes to reproduction, and
presumably this represents a relatively large investment on
the part of the male (Gwynne, 1981). This may be the
reason for the observed sex-role reversal resulting in
females competing for males. The parental investment that
male Belostoma flumineum make in their offspring is largely
shareable (Wittenberger, 1981), since regardless of the
number of eggs comprising the egg pad, males will still
perform the same brooding behaviors. However, these
behaviors do reduce future reproductive potential (i.e.,
his potential to invest in more clutches) because time
spent brooding eggs may impinge upon that which could be
spent mating with other females (Smith, 1980b).

Presumably, the most significant cost which has resisted
the evolution of male care in most species is the fact that
the males risk being cuckolded (i.e., caring for offspring
which possess genes of another male). However, the male
water bug has evolved a mechanism to circumvent this

problem. The female is required to copulate between each

short period of oviposition, at which time the male

deposits his own fresh sperm into the female's spermatheca.

This precludes fertilization by sperm from other males and

assures confidence of paternity (Smith, 1979b). Ultimately

this would favor the evolution of paternal care in this

species (Smith, 1980a).

   Not only must the male be certain of paternity, but

brooding must enhance survivability of the eggs. Paternal

care may have represented an opportunity to reduce the

severity of various mortality factors, which likely

included egg parasitism, predation and cannibalism (Smith,

1980b).

   There have been no previous experimental investigations

dealing with evolutionary costs associated with paternal

care. Smith (1980b) suggested five ways that male care may

be costly to male water bugs. Two of these were: direct

energy expenditure during brooding; and the inability to

fly, and hence to disperse. The objective of this research

is to quantify the three other evolutionary costs, as

suggested by Smith (1980b), that is, a reduction in

polygyny, an increase in vulnerability to predation, and a

loss of foraging efficiency.

MATERIALS AND METHODS

GENERAL

Giant water bugs (Belostoma flumineum) were collected in May-August of 1986 from various ephemeral and permanent ponds in Coles County in east-central Illinois. Adults were collected using aquatic insect nets, and transported to the laboratory in plastic coolers containing floating vegetation (e.g. cattails and willow branches). In the laboratory, individuals were placed in covered plastic shoe boxes (8 cm x 15 cm x 30 cm) containing tap water, gravel and plastic vegetation. Females were distinguished from males by the presence of two tufts of setae located mesally near the apical margin of the genital plate (Menke, 1960). Each individual was marked with an identification number on its pronotum, using white india ink covered with a thin layer of cyanoacrylate glue. In all phases of experimentation the bugs were fed dragonfly naiads and/or crickets *ad* *libitum*.

TIME COSTS

Laboratory and field experiments were implemented to compare the time males spend brooding a clutch and subsequently receiving a second clutch of eggs, to the time females spend between ovipositing successive clutches. Initial experiments were conducted in a Percival lighted environmental chamber set at 25°C and a 14L:10D photoperiod.

FEMALE LABORATORY ASPECT (MAY-JUNE)

Five female water bugs were each paired with a randomly selected unencumbered male, and were checked daily. After the females oviposited, each was provided with a new (randomly selected) unencumbered male. These pairs were also checked every 24 hours until the female oviposited again. Number of eggs per clutch and days between successive clutches were recorded.

MALE LABORATORY ASPECT (JUNE)

Due to egg pads falling off before hatching and one death, only 3 encumbered male interclutch intervals (time from discarding a hatched egg pad to becoming encumbered again) were available. Unencumbered male water bugs were randomly paired with females. When a male became encumbered it was isolated and allowed to brood the eggs and hatch the young. The day the egg pad was discarded, the male was paired with a different female that was rotund and presumably physiologically prepared for breeding. The pair was then checked every day until the male became encumbered. The length of time to brood and hatch young, and length of time to rebreed were recorded.

FIRST FIELD ASPECT

After males became encumbered in the laboratory, they were transferred to 1 M x 1 M field enclosures, located in a small pond in Coles County, IL, in which _B. flumineum_ are

found. Brooding time and the time between discarding a
hatched-egg pad and becoming re-encumbered were measured.
The females who had oviposited on these males were also
transferred to the field and paired with a new male.
Clutch sizes and the length of time between consecutive
ovipositions were also measured.

SECOND FIELD ASPECT (JULY-AUGUST)

This experiment was a modification of the previous "time
cost" experiment. Two males and a female were placed
inside a field enclosure, the males were allowed to become
encumbered, and at this point the female was re-paired with
a randomly selected unencumbered male in a separate
enclosure. The original two males remained in the first
enclosure and were checked daily until the eggs hatched and
the egg pad was discarded, at which time they were
presented with a new gravid female. This design allowed
the second female to be given a choice between a male that
had just finished brooding and one that had not recently
bred.

SWIMMING SPEED (JUNE)

Encumbered males with known-aged egg pads were available
in the laboratory by continually pairing males and females.
One encumbered male that had been caught in the field and
transferred to the lab was also used. It was assumed that
it had become encumbered less than one day previously

because its eggs hatched after the same number of days as
the lab-bred males.

Following the method Smith (1976a) used in measuring
swimming speeds of <u>Abedus herberti</u>, concentric circles were
drawn 10 cm apart on the bottom of a children's wading
pool. The pool was then filled to a depth of 2.5 cm with
tap water. Before each experimental run, each water bug
was placed in a screen enclosure, about 4 cm in diameter,
at the center of the pool. This procedure allowed each bug
to acclimate to the water temperature for one minute before
the screen was removed. In general, bugs would immediately
swim from the center of the pool to the outer edge. A
stopwatch was used to measure the time it took for the bug
to swim from the 10 cm marking to the 40 cm marking, and
speeds were calculated from those values.
Trials in which the bugs failed to swim straight were not
used in the calculations of averages. All bugs were run 10
times each day. Only the first five runs were used in the
calculations of average swim speeds to help control for the
effect of fatigue or habituation, since it appeared that a
large reduction in speed usually occurred after about the
fifth run. Seven encumbered males were run from the day
after oviposition to hatching, and again the day the pad
came off and for four subsequent days. In addition, 10
unencumbered males, and 10 females were monitored for
swimming speed over the same time period. Due to time
constraints and availability of bugs for this particular

experiment, some bugs from the latter two groups were run
for fewer consecutive days: 5 males were run for 9 days,
and 5 other males were run 6 days; 4 females were run for 5
days, while 6 others were run for 6 days.

The average swimming speed for each group is actually the
average of the averages of each individual. The number of
runs on which the average swimming speed for an individual
was based ranged from 5 to 31, but most were between 15 and
20.

FORAGING EFFICIENCY (AUGUST)

The prey species used in attempting to measure foraging
efficiency of B. flumineum was a species of water boatman,
Hesperocorixa obliqua (Corixidae; Hemiptera). Feeding
rates were monitored by recording the number of water
boatmen eaten by 5 encumbered males each day through an
entire brooding period (6 days) and for 5 days after egg
pad discardment. For comparative purposes feeding rates of
5 unencumbered males were measured for 9 days and 5 females
(one of which died in the middle of the experiment) were
measured for 8 days. Each individual was placed in a
separate container equipped with the same volume of gravel,
water and amount of green plastic aquaria vegetation. Five
water boatmen, collected fresh from an ephemeral pond known
to contain water bugs, were placed in each container; no
prey items were used for more than the 24 hour period. A
control of 5 boatmen with no water bug present was run for

seven days to determine if anything other than water bug predation could cause mortality.

MALE LABORATORY COHORT

FEMALE LABORATORY COHORT

FIRST FIELD COHORT

RESULTS

TIME COSTS

MALE LABORATORY ASPECT

Encumbered males were maintained in the environmental chamber for several experiments, so there is a substantial amount of data on brooding times. The average brooding time (end of oviposition to egg pad discardment) at $25^{\circ}C$ was 10.3 days (s.d.=0.9, n=13); at $28^{\circ}C$ brooding time dropped to 6.6 days (s.d.=0.5, n=5). Thus, developmental time and temperature are inversely related. The average time from discarding an egg pad to becoming encumbered again was 2.3 days (s.d.=1.5, n=3). Therefore total time between clutches averaged 12.6 days (at $25^{\circ}C$).

FEMALE LABORATORY ASPECT

The average number of eggs for the first clutch oviposited was 69.8 (s.d.=36.9, n=5) and the mean for the second clutch was 85.8 (s.d.=10.2, n=5). The mean number of days between successive clutches was 13 days (s.d.=7.2, n=5).

FIRST FIELD ASPECT

Encumbered males' brooding times averaged 7.7 days (s.d.=.9, n=11) with temperatures ranging from $26^{\circ}C$ to $31^{\circ}C$. Interclutch intervals averaged 2.2 days (s.d.=2.6, n=6), which makes the total time between clutches approximately 9.9 days. The average number of eggs laid

was 88 (s.d.=29.3, n=3) for the first clutch and 96.3 (s.d.=38.7, n=3) for the second. An average of only 6.0 days (s.d.=6.2, n=6) passed between successive clutches.

SECOND FIELD ASPECT

Table 1 compares male brooding times with female clutch synthesis time. Male brooding times averaged 8 days (s.d.=1.1, n=6). Upon the opportunity to rebreed, all males took only one day to rebreed. An average of 2.6 days (s.d.=1.6, n=7) passed between successive clutches. Table 2 shows the egg pad sizes for the first and second clutches of each female. Egg pads that the females produced on their first opportunity to mate averaged 97.2 eggs (s.d.=30.4, n=6), whereas on their second opportunity to mate, an average of only 30.9 eggs (s.d.=7.7, n=7) were produced. Out of six times that females had a choice between mating with a male who had just been brooding or with a male who had not, 4 times it was the former and one time the latter. One female oviposited eggs on both males.

SWIMMING SPEED

No significant difference in swimming speed was found between unencumbered males (18.5 cm/sec, s.d.=3.6, n=10) and females (18.6 cm/sec, s.d.=2.9, n=10). However, encumbered males swam significantly slower (13.4 cm/sec, s.d.=2.1, n=5) than either of these two groups (one-way

ANOVA, $F=5.65$, $\underline{P} < 0.05$, see fig. 1). The egg pad size for
these males averaged 91.6 eggs (s.d.=31.4, n=5), which
approximately covers an entire male's dorsum.

Figure 2 shows the average swimming speeds of 5
encumbered males 4 and 3 days before the pad was sloughed
off (11.2 cm/sec, s.d.=1.6 n=5, and 11.5 cm/sec, s.d.=1.8,
n=5, respectively), and the day the pad came off, and again
the subsequent day (i.e., swimming speeds were not measured
during the hatching period). Speeds for the 2 days after
hatching were 18.6 cm/sec, s.d.=4.9, n=5, and 17.4 cm/sec,
s.d.=2.5, n=5, respectively. This represents a significant
increase in swimming speed following egg pad sloughing
(repeated measures ANOVA, $F=8.3$, $\underline{P} < 0.01$).

Figure 3 is a scatter diagram showing the negative
relationship between swimming speed and weight of
encumbered bug. These values were obtained from the same
5 individuals as were used in fig. 2. The heavier,
encumbered males are represented by the cluster down in the
lower range of swimming speeds, while the lighter,
unencumbered males are grouped in a cluster situated in a
higher range of speeds.

FEEDING EFFICIENCY

None of the water boatmen in the container without a
water bug predator died, thus any boatmen found dead on a
given day were assumed to be the result of predation.
Typically a predated water boatman's head would fall off

(probably indicating the internal tissues had been digested) when removed from the container.

Separate values of feeding rate were calculated for the brooding period and post-brooding period of encumbered males. The average number of boatmen eaten per day was also calculated for the female and unencumbered male groups.

Figure 4 shows the difference in feeding rate during and after the brooding period of the encumbered group. A paired t-test showed that the males ate significantly less during the brooding period (0.06 boatmen/day, s.d. = 0.08, n = 5) than afterward (0.18 boatmen/day, s.d. = 0.10, n = 5) [t-cal = 2.3, $P < 0.05$]. Figure 5 shows the feeding rates for unencumbered males ($\overline{x} = 0.244$ boatmen/day), females ($\overline{x}=0.66$, s.d.$=0.06$, n=4) and brooding (encumbered) males ($\overline{x}=0.06$ boatmen/day, s.d.$=0.08$, n=5). Encumbered males ate significantly less (one-way ANOVA, F=44.4, $P < 0.05$) than unencumbered males. Females ate significantly more boatmen ($P < 0.001$) than either of the male groups.

DISCUSSION

Male Belostoma flumineum appear to have a number of significant evolutionary costs associated with caring for their offspring, and these factors may have offered considerable resistance to the evolution of paternal care in this species. Males are obligated to spend considerable time brooding eggs, and this lessens their opportunity for future polygynous matings. They are also slower swimmers, and this may account for the fact that they are more likely to be preyed upon (as described subsequently), and less likely to capture prey.

In the laboratory "time costs" experiments, it appeared that males and females spend approximately the same amount of time per clutch. The first indication that there may be a difference in the time investment per clutch for males and females came during the first field study. Females required only 6.0 days between successive clutches, while males averaged 7.7 days for brooding a single clutch, plus an average of 2.2 days to rebreed.

In the second field aspect, however, females oviposited their second clutch less than 3 days after the first, and the second clutches were smaller than in previous experiments. Male brooding time for a single clutch averaged 8 days.

Data from this field investigation strongly suggest that when females are given the opportunity to breed continuously (i.e. male back space is not limiting), they

will oviposit smaller clutches which do not necessarily fill the entire backspace of a given male. The backspace of a male can hold over 100 eggs when fully encumbered. The fact that females can oviposit these "partial clutches," which averaged about 31 eggs, suggests that males undergo a loss in polygynous opportunity. It appears that as long as the female has mature eggs, she will breed and oviposit them as soon as a suitable male becomes available. Females are apparently constantly undergoing oogenesis and will deposit partial clutches long before their mates have finished brooding and hatching. On the other hand, males which have received a completely full egg pad must forego any additional matings until their eggs have hatched.

Smith (1979a) provides a model whereby such asynchrony in breeding, resulting from the females ovipositing sub-maximal sized clutches, results in males becoming a limiting factor. Assuming that males do not mate after their eggs become a certain size, the major thrust of Smith's argument is that male back space could become unavailable due to many males carrying small clutches. This would result in an excess of reproductively ready females and a limited number of available males. The potential evolutionary consequence of this is best understood in light of the idea of the operational sex ratio. The operational sex ratio, or OSR, of a population is defined as the "average ratio of fertilizable females to

sexually active males at any given time" (Emlen and Oring, 1977). For example, if there were many sexually active males, and if female receptivity came only in short, isolated bursts of only one or a few females at a time, then the OSR would be strongly skewed toward males. If the OSR were skewed toward males, then males should demonstrate intrasexual competition for females. On the other hand, if the OSR were skewed toward females, as would be the case if available males were limited with respect to available females, then females should compete for males.

Another factor which could result in sex role reversal is if the male provides a limited resource (Petrie, 1983b). For example, moorhen females compete for the smaller, fatter males who are likely to be able to brood longer. It is thought that these males (who perform 72% of the incubation) represent a scarce resource (Petrie, 1983a). Male back space in Belostoma flumineum has been shown to represent a limited resource during parts of the season in field studies by Kruse (unpublished data). No matter the size of his investment, the male's services (which can not be performed by the female) are essential to the survival of offspring. If females were limited by the availability of that service, then they would be expected to compete among themselves, while males would be expected to be discriminating (i.e. prefer certain female phenotypes). The ramification of this is that females, when limited in reproductive capacity by the availability of male back

space, may actually compete for access to males. In the water bug _Abedus_ _herberti_, Smith (1979a) has seen "females actively approach males during courtship and males reject certain females as mates."

Smith (1980a, 1980b) suggested risk of predation as another potential cost of brooding in water bugs. Subsequent testing of that hypothesis revealed that encumbered male water bugs are 2-3 times more likely to be preyed upon by aquatic fishing spiders (_Dolomedes_ _triton_) than are unencumbered males or females (Kruse, unpublished data). Either brooding behaviors act as a cue for location by the predator, or encumbered males are less capable of escape from the predator because of decreased swimming speed, or a combination of both. Smith (1976a) measured swimming speed of a closely related water bug (_Abedus_ _herberti_) and found encumbered males swim about one half as fast as those without eggs. In the present investigation, speed of _B._ _flumineum_ was also found to be significantly slower in encumbered males. Therefore, it may be that decreased swimming speed is a contributing factor in their increased predation vulnerability.

Another contributing factor to increased vulnerability of brooding males to spider predation observed by Kruse may be the various movements associated with brooding, described by Smith (1976b). Such movements may betray the bug's location because fishing spiders sense surface vibrations (Bleckman and Barth, 1984). Also, encumbered _B._ _flumineum_

probably spend more time at the surface of the water than
do unencumbered males, to permit aeration of the eggs, and
perhaps incubation at the higher-temperature surface water.
Therefore it is possible that, by spending more time at the
surface of the water, encumbered male B. flumineum increase
their chance of being located by a predator. In the water
bug Diplonychus indicus, encumbered males, "...make little
attempt to ...escape from predators" (Venkatesan, 1983).
If the same were true of B. flumineum, then this also could
contribute to their increased vulnerability to predation.
 In connection with predation, but not brooding, it is
notable that, "the act of insemination may decrease
monitoring of the environment by burdening the nervous
system" (Jackson 1976). If this is true of water bugs,
then this too may be a cost of the lengthy courtship and
copulation/oviposition period associated with their mating
behavior. In addition, differential predation on males
could potentially cause a shift in the operational sex
ratio, resulting in even fewer males with which the females
can breed.
 Another cost of male parental care in water bugs seems to
be a decrease in food intake. As shown in the present
study, encumbered males eat less than unencumbered males or
females. There are two obvious possibilities why brooding
males would eat less: male ability to capture prey while
encumbered may be substantially reduced because brooding
behaviors cue potential prey, and/or encumbered males can't

swim fast enough to catch their prey.

Feeding inhibition may also be a reason for decreased feeding in encumbered males. If chances of capturing prey are low while brooding, selection may have resulted in diverting energy into brooding activities rather than prey capture. Encumbered <u>A</u>. <u>herberti</u> deprived of food for three weeks did not attack first instar water bug nymphs or crickets while eggs were hatching (Smith, 1976b). In the water bug <u>Diplonychus</u> <u>indicus</u>, encumbered males, "restrict their movements, do not show voracious feeding habits and make little attempt to catch prey..." (Venkatesan, 1983). Whether the decrease in food intake is actually due to a decrease in ability to capture prey or due to feeding inhibition, is uncertain. However, some of my brooding males did feed, and none of them fed during hatching, suggesting that feeding inhibition may only occur then. A decrease in food intake could potentially be a serious energetic cost, particularly where there are fewer chances to capture prey, as in low prey density situations.

According to Kopelke (1981), male <u>B</u>. <u>thomasi</u> undergo eating binges (presumably to replenish metabolic reserves) following the hatching of a clutch. It follows that if males are obligated to devote time to feeding between clutches, males who have just discarded an egg pad may make themselves unavailable for breeding, and hence more severely limiting to females. Data on male interclutch intervals suggest this may not be the case, however,

because males who had not been brooding did not show any reproductive advantage over males who had just been brooding. In fact, most of the males who bred were those who had just been brooding.

The fact that females had such a high rate of feeding compared to males is probably due to the need of females to obtain enough food for the continual production of eggs.

The mechanism which seems to have protected paternal care from elimination is paternity assurance (Werren et al., 1980), or in other words a low risk of cuckoldry (caring for young not containing one's own genes). As is true in any species where paternal care is employed, the only way the male can increase its fitness by parental investment is if it is certain that its offspring will bear its genes. Where you find that "there is a promiscuity cost to providing care" (Werren et al., 1980) you should also find some mechanism of paternity assurance. Parker (1970) proposed several behavioral and physiological mechanisms to prevent cuckoldry in insects: mating plugs; prolonged copulation; passive phases such as amplexus; and non-contact guarding phases. Water bugs belong to the prolonged copulation strategy. Sperm competition studies in Abedus herberti have demonstrated almost complete paternity assurance (Smith, 1979b).

Exclusive male care is a rarity in the animal kingdom, but what makes it even more unusual is when it is found in a species with internal fertilization. Usually maternal

care is associated with internal fertilization. This is probably due to the male's option to desert the female immediately after fertilizing her eggs (Dawkins and Carlysle, 1976). Upon desertion, the only means by which the female can maximize her fitness is to provide care. Therefore, species in which males provide exclusive post-copulatory paternal care tend to be those in which fertilization is external (Dawkins and Carlysle, 1976; Ridley, 1978). However, in water bugs, male paternal care exists despite internal fertilization. Part of the reason is that fertilization is so closely tied to oviposition, and eggs are immediately deposited on the male`s back.

SUMMARY

There are many factors determining whether the female or male performs parental care in a given species. Theoretically, once fertilization has occurred, either sex would gain reproductive success by having the other provide care for their offspring (Knowlton, 1982). The fact that females make a larger investment in gametes than males is presumably the reason why females usually are the ones who provide parental care (Wilson, 1975). However, under the right conditions, the potential exists for males to provide parental care.

In animals in general, if parental care does exist, it is most frequently maternal. Most insects do not show any kind of parental care. However there are a few Hemipterans

in which exclusive male care occurs. In <u>Belostoma</u>
<u>flumineum</u>, as in the whole subfamily Belostomatinae,
exclusive male care occurs. Several factors seem to have
been involved in the evolution of paternal care in water
bugs: relative parental investment; confidence of
paternity; and operational sex ratio are some of these. By
better understanding what kinds of costs and benefits are
associated with the particulars of a mating system, one can
better understand how it has evolved.

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Table 1. Comparison of male brooding time and female clutch synthesis time in **Belostoma** **flumineum** in the field.

Trial	female clutch synthesis time (days)	male brooding time (days)
1	2	9
2	6	7
3	1	7
4	2	9
5	3	9
6	2	–
7	2	–
8	–	7
$\bar{x}$	2.6	8.0
s.d.	1.6	1.1
n	7.0	6.0

t-cal = 7.42, $\underline{P}$ < 0.05

Table 2. Sizes of consecutive clutches.

Trial	# of eggs oviposited in clutch 1	# of eggs oviposited in clutch 2
1	*123	34
2	100	28
3	70	22
4	?	42
5	55	39
6	100	28
7	*135	23
$\overline{x}$	97.2	30.9
s.d.	30.4	7.7
n	6	7

* about 20 of these eggs were deposited on the

back of a second male.

Speed (cm/sec)
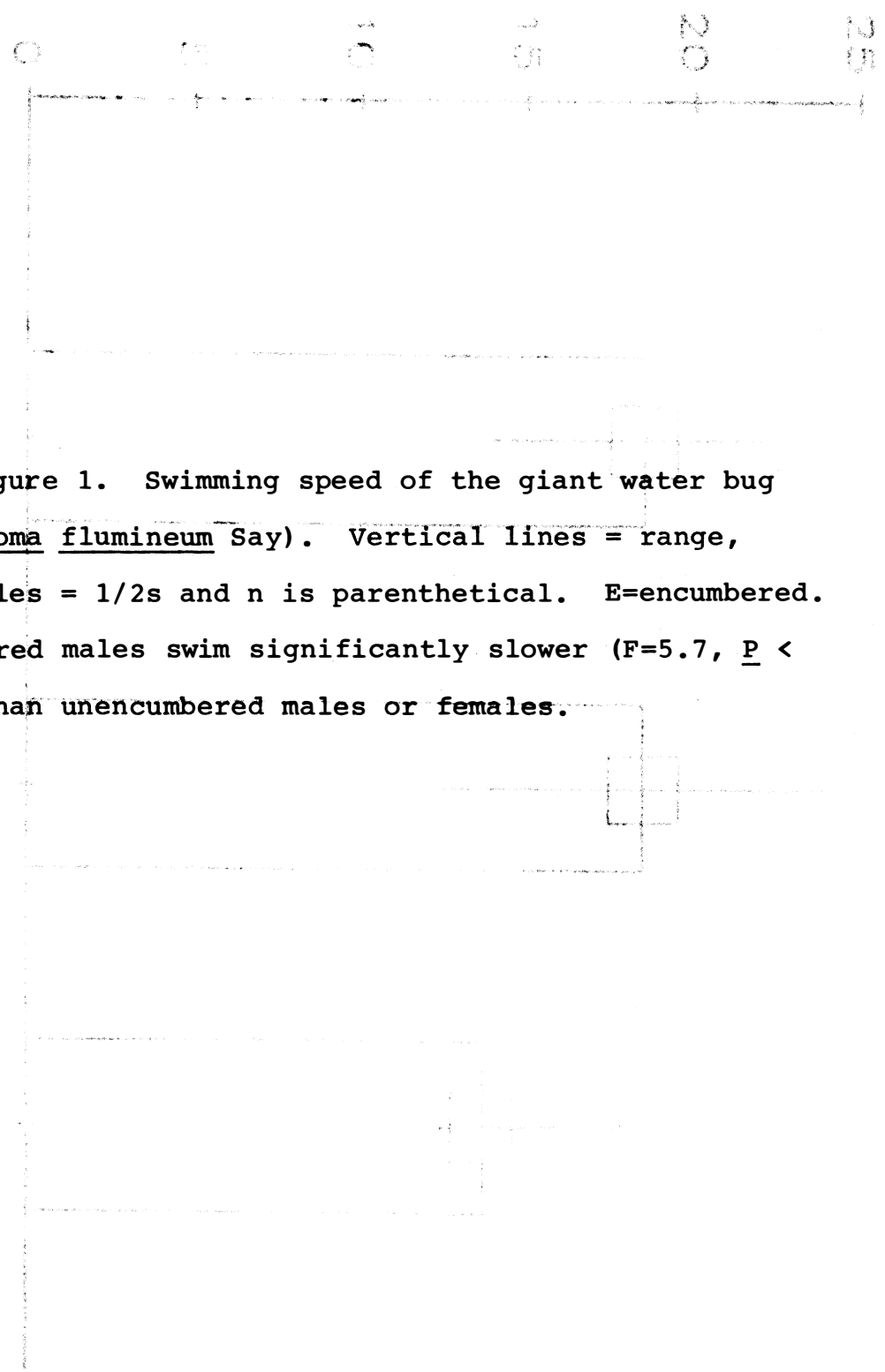
Figure 1. Swimming speed of the giant water bug (Belostoma flumineum Say). Vertical lines = range, rectangles = 1/2s and n is parenthetical. E=encumbered. Encumbered males swim significantly slower (F=5.7, $P < 0.05$) than unencumbered males or females.

Speed
(cm/sec)

0   5   10   15   20   25

♀♀   (10)

♂♂   (10)

E ♂♂   (5)
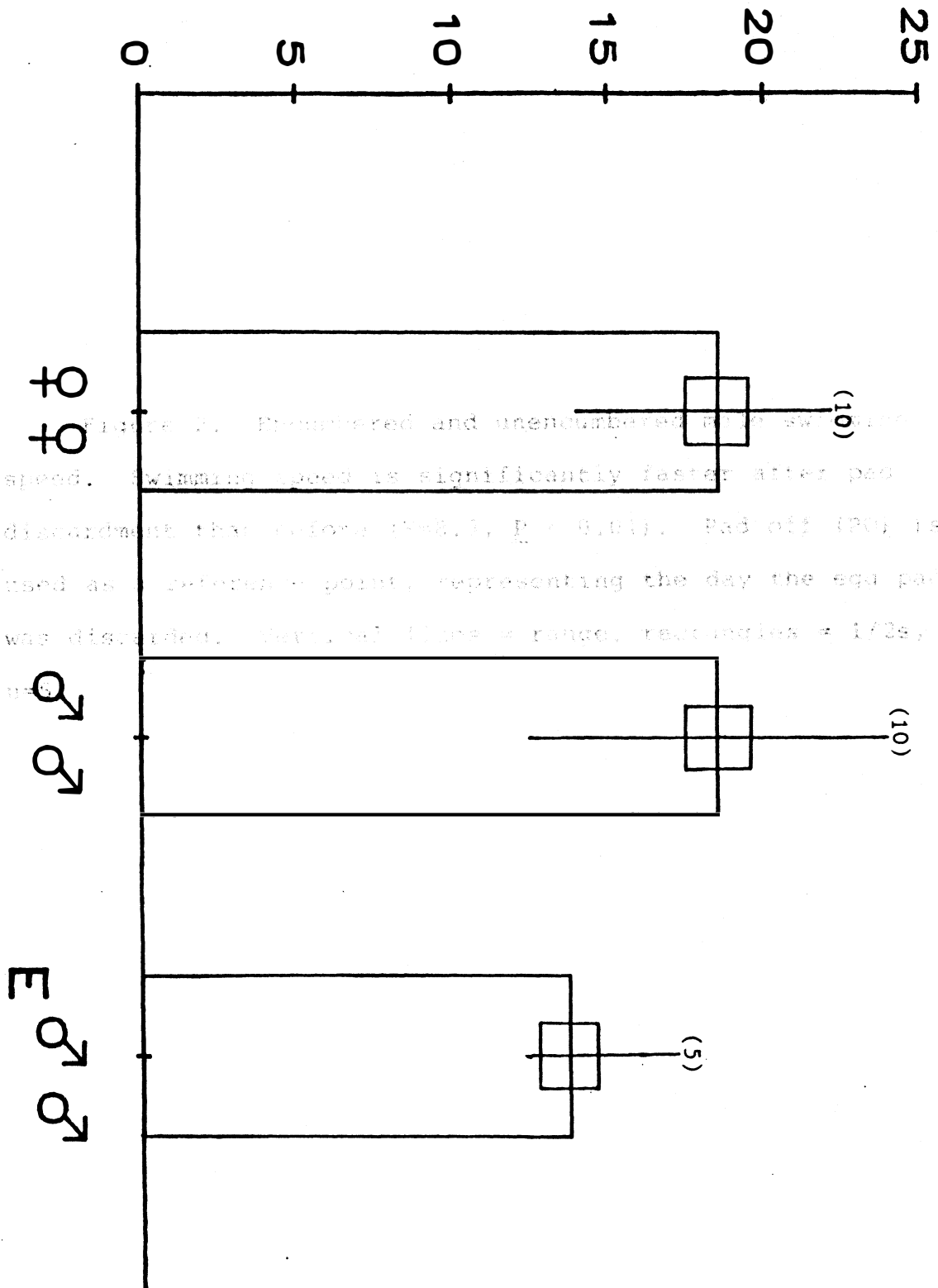
Figure 2. Encumbered and unencumbered male swimming speed. Swimming speed is significantly faster after pad discardment than before (F=8.3, $\underline{P}$ < 0.01). Pad off (PO) is used as a reference point, representing the day the egg pad was discarded. Vertical lines = range, rectangles = 1/2s, n=5.
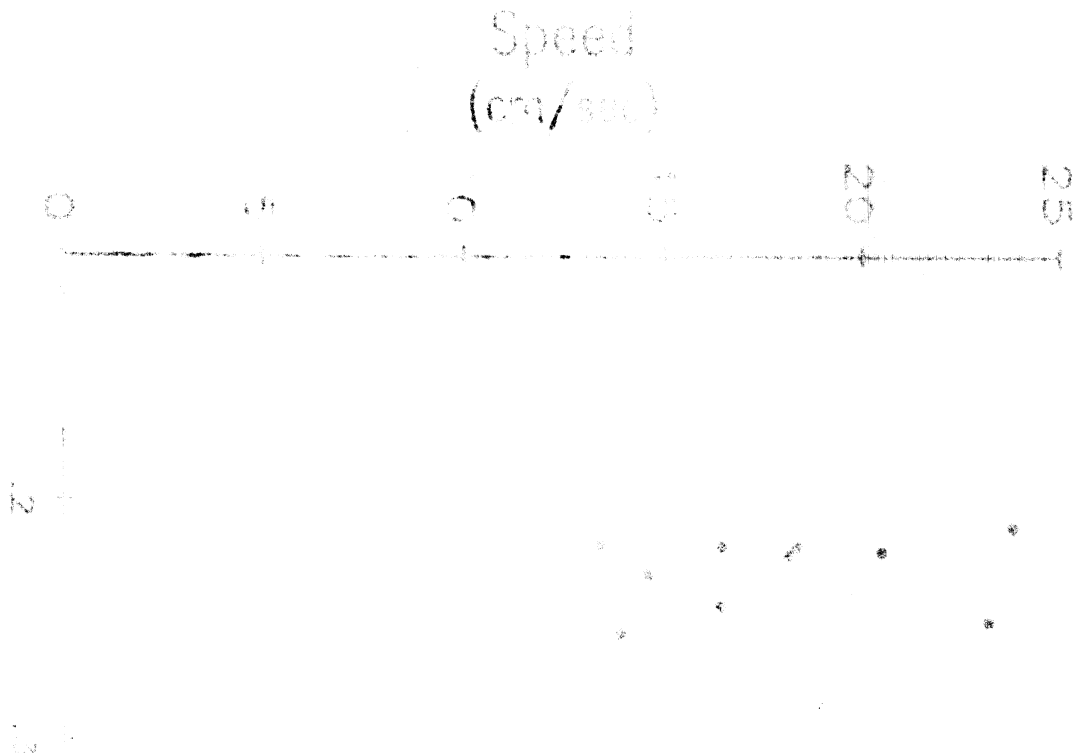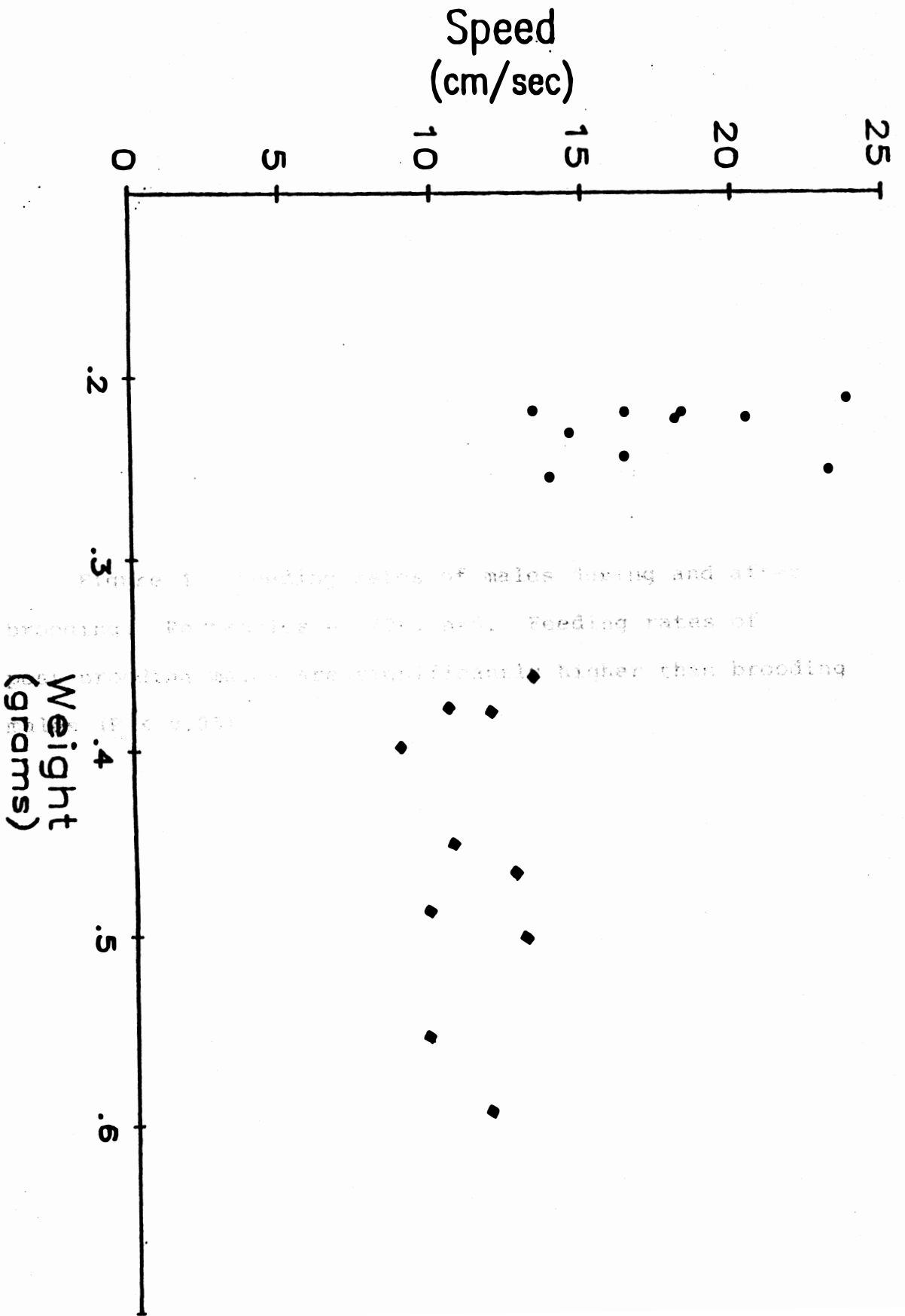
Figure 10. Speed and weight of encumbered and
unencumbered water bugs. Dots = unencumbered males,
diamonds = encumbered males.
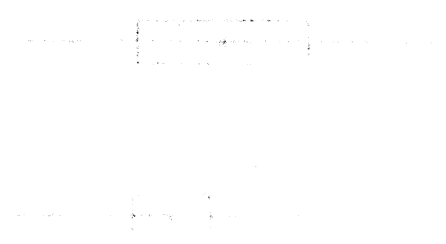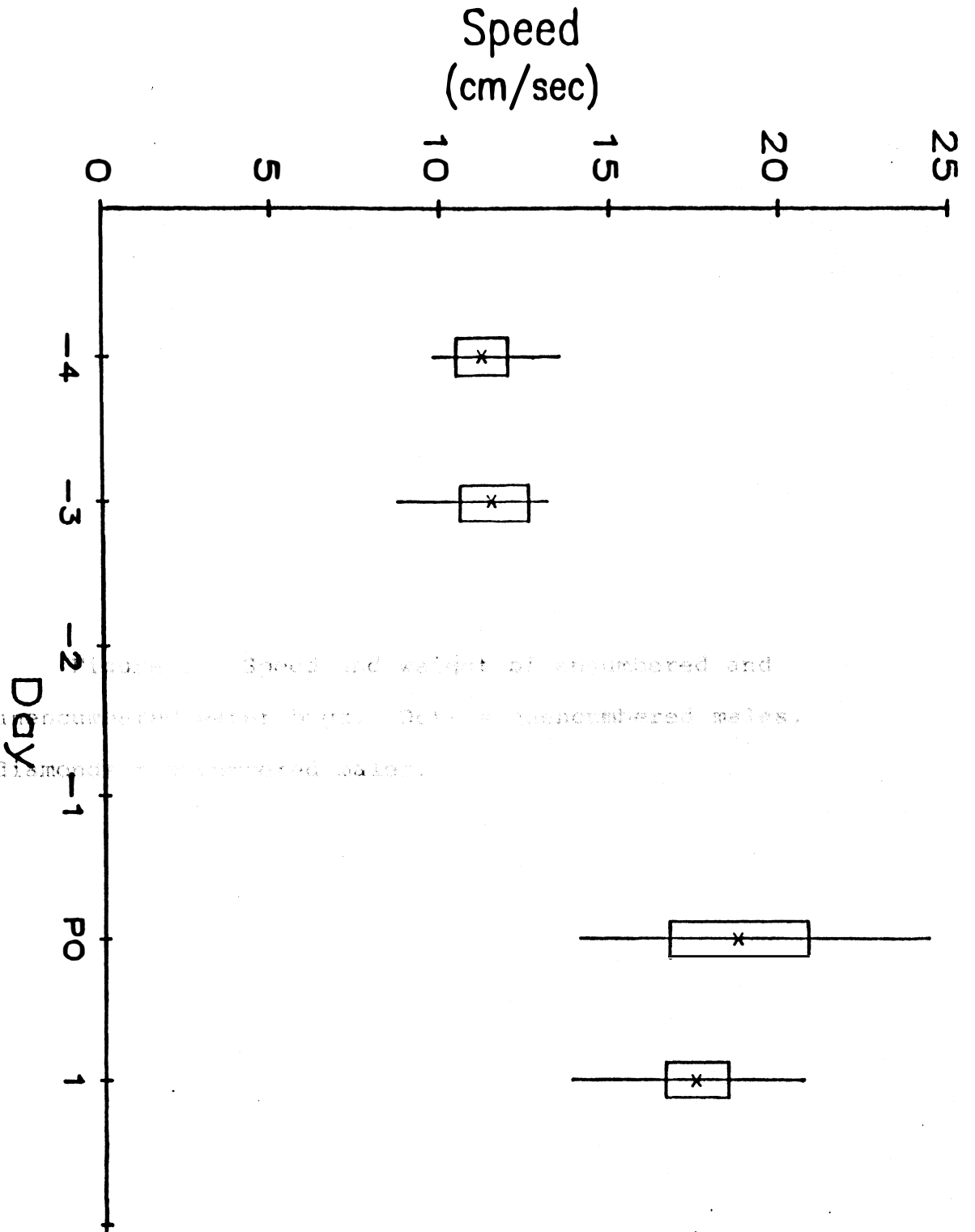
Figure 3. Speed and weight of encumbered and unencumbered water bugs. Dots = unencumbered males, diamonds = encumbered males.

Speed
(cm/sec)

25
20
15
10
5
0

Weight
(grams)

.2   .3   .4   .5   .6

Figure 4. Feeding rates of males during and after brooding. Rectangles = 1/2s, n=5. Feeding rates of post-brooding males are significantly higher than brooding males ($P < 0.05$).
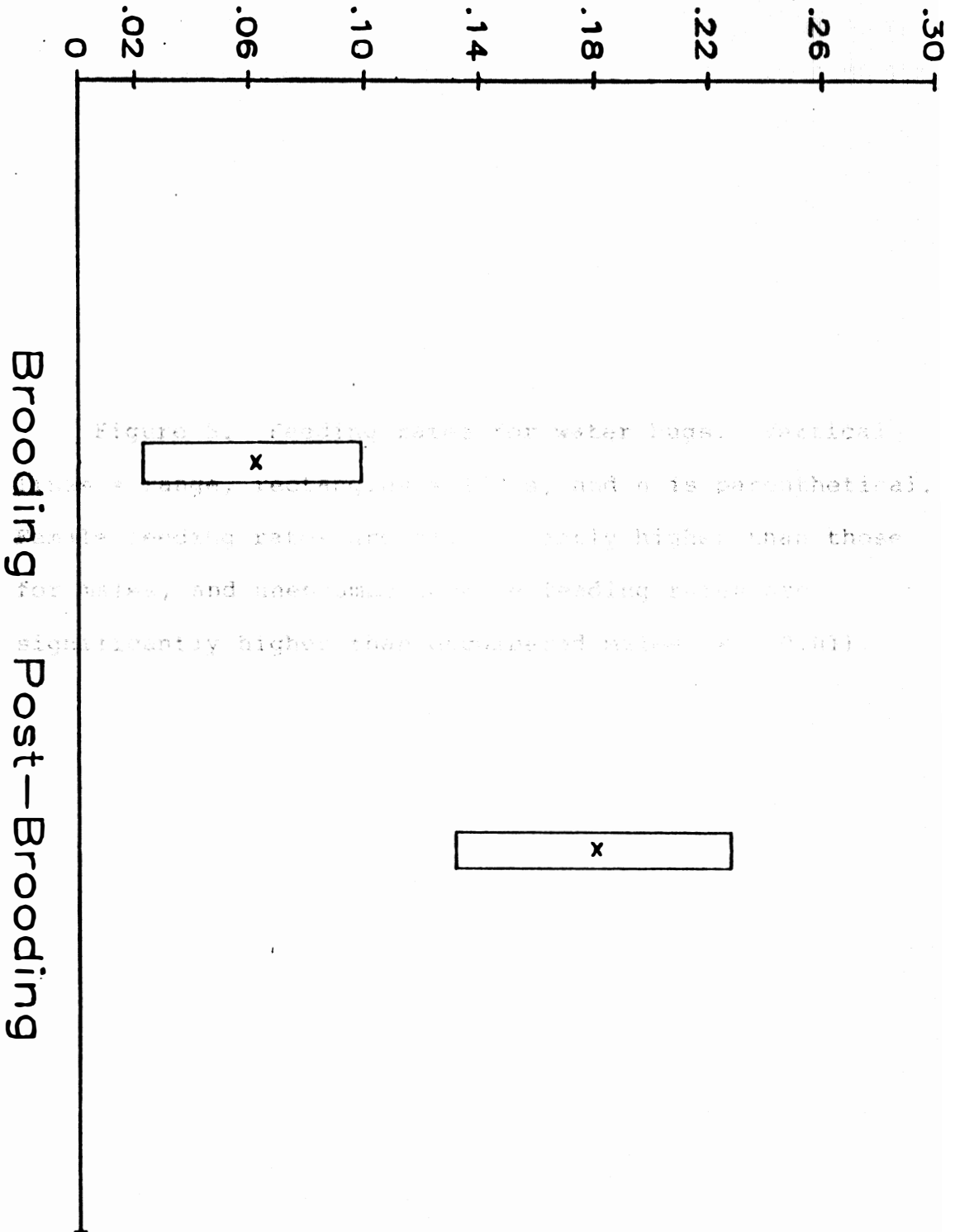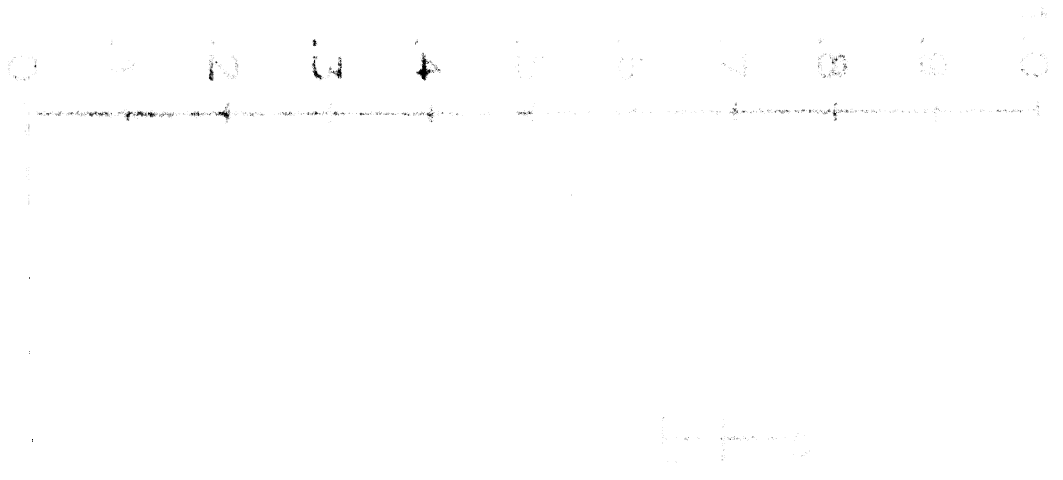
Rate
(# water boatmen eaten/day)

Figure 5. Feeding rates for water bugs. Vertical lines = range, rectangles = 1/2 s, and n is parenthetical. Female feeding rates are significantly higher than those for males, and unencumbered male feeding rates are significantly higher than encumbered males ($P < 0.01$).