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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

care in the water bug Belostoma flumineum Say (TITLE)

Larry Johnson

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THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

Master of Science

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY CHARLESTON, ILLINOIS

1987 YEAR

I HEREBY RECOMMEND THIS THESIS BE ACCEPTED AS FULFILLING THIS PART OF THE GRADUATE DEGREE CITED ABOVE

<u>8 May 1987</u> ™ 5 / 8 / 87

ABSTRACT

wis for d'that males

Female water bugs (<u>Belöstoma flumineum</u>) 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 <u>B. flumineum</u> swam significantly slower than unencumbered males or females. In addition, an experiment was

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ACKNOWLEDGEM®NTS

undertaken to measure food intake. It was found that males éat léssiduring the broodingpperiód than after Hatching. In Thérefore Swimming speed reduction and décreased feedings a timay also be potential costs toymale care. In evolutionary ecologic with the act of the National Costs for the rowletion or on BER-Rathan is de concrete source rowledge, eact dis, and code code care to evolutions.

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ACKNOWLEDGEMENTS 5

I would like to express my appreciation to my advisor, Dr. Kipp C. Kruse, for making it possible for me to work on a thesis that was well suited to my interest in evolutionary ecology. With the help of the National Science Foundation (grant BSR=8415487), he provided me with the knowledge, materials, and funds necessary to carry it out. McI would like thank my colleagues Todd Campbell, Frank Jakubicek, and Janet Ruppert in their help with field collection and data measurements, and Patti Roberts for offering her organizational skills and helping with calculations. I would also like to thank Dr. Kruse, Dr. Michael Goodrich, and Dr. Edward Moll for serving on my graduate committee and for their comments, suggestions, and corrections relating to this thesis. Thanks also to my colleague John Rowe for his helpful suggestions.

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(Trivers, 1972). PateINTRODUCTIONent may be manifested in

sanious ways, and unually thus investment is post-sydemic Natural selection is the differential reproductive (i.e. iccubation, brood defense, feeding etc.). In some success of certain individuals in a population due to their species, males invest anergotically on the form of maptial heritable, beneficial characteristics. By natural alits such as thereastophones in marks structures (Swyphe, . selection, individuals who possess the heritable phenotypes 1981), or insect previos in scorpiosilies thermhill and best suited for survival produce more offspring than those 2) predices that the sex which 杨华的行动之后, 医静脉后的 that do not. Sexual selection, described by Darwin (1871), invests the least an offspring will compute for the say who is set apart from natural selection in that it involves もれやときした。も我の「ののちも」」なたが、 小的来来,她抱着一直没有着在了 differential reproduction due to a difference in the de sorimination - 1月14日ませら abilities of members of the one sex to compete for access mare that here main, which there are more atest ini na ' to members of the opposite sex. Sexual selection consists with whom they make (thell balactics forers mate parties). of both intrasexual selection and intersexual selection. Males, on the other hand, are evolvally more promission In Darwin's terms, intrasexual selection is "the [male's] preferier cale quantity for th 0008 power to conquer other males in battle," while intersexual ecies where the us more than the selection refers to "the [male's] power to charm the fraale, se intrasexusi females" (Darwin, 1871). In most species sexual selection competition to a distance despes works more strongly on males. Males typically compete for consequently, "are females, and often "display" certain attractive berghnly colored characteristics to gain female receptivity. scocies extbitio

According to current sexual selection theory, the catch days (Shith) as selection theory, the relative parental investment made by the two sexes should tradictal as a second frequency of the two sexes should tradictal as a second frequency of the two sexes should discrimination observed (Trivers, 1972). Parental bits accords frequency of the two seconds, 1952; investment consists of "any investment by the parent in an bits accords for the tradictal as a second frequency of the two seconds individual offspring that increases the offspring's chance be second frequency of conductive success) at the cost for any investment by the parent's ability to invest in other offspring"

(Trivers, 1972). Paternal investment may be smanifested in varioussways pandousually this investmentais post-zygotic (içe. aincubation, brood defense spreeding etcras intheme species, males invest prezygotically in the form of nuptial gifts such as spermatophores in mormon crickets (Gwynes and the second 1981), or insect prey as in scorpionflies (Thornhill and Gwynne, 1986). STrivers (1972) predicts that the sextwhich invests the least in offspring will compete for the sex who invests the most, and that the latter will be the set discriminating sex. In most species the female invests more than the male, tand therefore are more discriminating with whom they mate (i.e., selection favors mate quality). Males, on the other hand, are typically more promiscuous, prefering matesquantity to matesquality. On the cause of the :::In species where the male appears to invest more than the female sexproles are altered po Females display intrasexual competition to a higher degree than do males; and consequently a "are larger, more aggressive, or more stated at brightly colored than the males (Barash, 1982) prosone at species exibiting afform of role reversal includer with ant by watersbugsa (Smithga1939a), asea horsest and pipefish for ends (Fiedler, 1954; Strawn, 1958; Takai and Mizokami, 1959); several families of a frogs (Wells pul937, 1978); and several bird species (Hohn; 1969; Hilden and Vuolanta; 1972; Ridpath; 1972; Granni, 1974; Graub et also 1977; Oringsand Maxony (1978), sold days for these up harch (forre Aueno, 19Some examples of species in which the male provides the

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

In five families of indects in the order Hemipters, 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, the Norvathiniinae, and Belostomatinae (Menke, 1979) and the 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 by studied in (part by smith (1979a).

Belostoma flumineum is a member of the subfamily still Belostomatinae Itais apredaceous insect; approximately 2 ombin length, and is found in ponds and lakes throughout the continental United States. Belostomatids overwinter by burrowing a few centimeters into the bottombooze of ponds (Menke, 1979), oth colors described (States 1979).

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

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this has been shown to be vital to eggenymph survival and (Smith, 1976a). Brooding behavior consists of resting at the surfaces (for acrating purposes), eggs patting pobrood and Stroking, sawing and kicking. The second success are and

SThe services an egg-ladden, or encumbered male provides ly 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 278) of 1 body weight) which contributes to reproduction, and presumably this represents a relatively large investment on the part of the male (Gwynne, 1981). ad This may be the set of 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 ma 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). Lice, and a Depresumably, 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

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problem. The female is required to copulate between each

short period of oviposition, at which time the male GENERAL

deposits his own fresh sperm into the female's spermatheca. Giant water burs (Bolottoma fippinger) were collected in This precludes fertilization by sperm from other males and May-August of 1985 from various aphendral and permanent assures confidence of paternity (Smith, 1979b). Ultimately ponds to doles former in east-central fillers. Adults this would favor the evolution of paternal care in this ware collected using against indext pets, and transported species (Smith, 1980a).

to the laboratory in terestning flooting Not only must the male be certain of paternity, but vegetation (e.g. cattails and wi 10.12 10 the CLARE EVEN brooding must enhance survivability of the eggs. Paternal laboratory, individuals were placed on covered plastic care may have represented an opportunity to reduce the boxes (8 cm x 15 cm x 30 cm) conta. severity of various mortality factors, which likely and plastic vacatories consider ware conclusions included egg parasitism, predation and cannibalism (Smith, males by the presence of two, tofts of schee located messily 1980b).

There have been no previous experimental investigations Sach characteristic problem of the second structure number on dealing with evolutionary costs associated with paternal its second structure dealers and the second vite this care. Smith (1980b) suggested five ways that male care may layer of contracteristic disconding. Two of these were: direct energy expenditure during brooding; and the inability to criteries ad histories. The objective of this research

is to quantify the three other evolutionary costs, as

suggested by Smith (1980b), that is, a reduction in Laboratory and field experiments were implemented on polygyny, an increase in vulnerability to predation, and a compare the time toles speed broodtal mathematical loss of foraging efficiency. subsected for receiving a second concerned compare, to the field

females deem i bottman constructions a concernation with table b

Initial eventiments were consisted in 9 Percivel lighted

environmental chasses set at 25°C and 1 har100

photocerica.

PEMALE LABORATORY ASSECT (MAY-JUNE)

GENERAL female water boys were each parted with a randomly seGiantdwater bugs (Belostomanflumineum) were collected in May-Augustsof 1986 from various sephemeral and permanent ponds thy Coles County in ceast central Illinois a Adultse were collected using aquatic insectinets; and transported to the laboratory in plastic coolers containing floating vegetation (evelocattails and willow branches). In the laboratory, individuals were placed in covered plastic shoe boxes: {800m xx15 Acm:x230 (Cm)) containing tap water, gravel anduplastic vegetation. Females were distinguished from males by the presence of two tufts of setae located mesally near the apical margin of the genital plate (Menkep)1960). **Each** individual was marked with an identification number con itsopronotum; dsing white india ink covered withea thin layer of cyanoacrylate glue and In all phases of the logoexperimentation the bugs were fed dragonfly natads and for chickets addlibitum. Ante o different fomste than was notued and presumably presidentially repared for breading. The pair was then checked to TIME (COSTS till the male receive enLaboratory and field experiments were implemented to any compare the time males spend brooding a diutch 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 enveronmental: chamber set at 25°Cland al 44Dr + 0D located in photopériodd in Coles County, IL, to which B. flumineum are

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FEMALE LABORATORY: ASPECT: (MAY-JUNE) between discarding a haFive female water bugs were reach paired with ear randomly selected unencumbered male; band were checked daily. alAfter then females oviposited, leach was provided with a abew (randomly selected) unencumbered male. Where pairs were also checked every 24 hours until the female oviposited again. Number of eggs per clutch and days between successive clutches were recorded.

This experiment was a sold to at the alternative provides the MALE LABORATORY ASPECT (JUNE) at the first of which places in Dude to egg: pads falling off before hatching and one was death, conly 3 menumbered, male interclutch intervals (time of from discarding a hatcheduegg pade to becoming ensumbered again) were available. Unencumbered emale water bugs were randomly paired with femaled; When a male became stoked and ensumbered dit 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.

Encambered boles with those equal opproved were available FERST-FIELD:ASPECTBY controls by paratime suber and females. OnAfterumales/became tencumbered in the laboratory jetheynd were stransferred to lbMvx slaMsfield enclosures jslocated hin at small bonds in Coles: County j IL; nin which Breflumineum are

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found: Brooding time and thertike between discarding sads hatched egg pad and becoming re-encumbered were measured. The females who had oviposited on these males were raiso transferred to the field and paired with a new maleles were Clutch sizes and the length of time between consecutive ovipositions were also measured. He a here a 2.5 cm with top water.

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 the bus 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 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.

lacke selection of end end line towned a free constitue i if for the second states of SWIMMING&SPEED. (JUNE) which the two second

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 bar

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because its eggs hatched after the same number of wdays cas the labebredomalesise days, 5 maler water a for 9 days, apFollowing the method Smith (1976a) used in measuring for 5 swimming speeds of Abedus herberti; concentric circles were drawn 10 cm apart on the bottom of a children's wading the pool of the pool was then filled to a depth of 2.5 cm with f tapswaters 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 swimefrom the center of the pool to the outer edge. As an stopwatch was used to measure the time it took for the bug to swim from the 10 cm marking to the 40 cm marking pand speeds were calculated from those values. Note the water borrials 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 harge reduction in speed usually occurred after about the fifth run coseven encumbered males were run from the day at a after oviposition to hatching, and again the day the pade to came coff and for four subsequent days. In addition # (10 cons unencumbered males, and 10 females were monitored for the swimming speed over the same time period. Due to time A constraints and availability of bugs for this particular or

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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

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

MABE LABORATOR / ABUTCT

Encretered to be an every value viet in the environmental channel for every expression, as there is a substantial amount of data as brood we treat. From the reading time form is a brood we treat. From the arcoding time form is a brood we treat discustion of 20°C was 10.3 door (sideo), robul at 50°C provides time dropped to fill door (sideo), robul at 50°C provides time dropped to fill door (sideo), robul at 50°C provides time time to be compared and constant returned on compared time the discounding on the second concepted again was 0.6 down (sideo) and to permitte the issue between obsplies averaged 10.5 days (at 50°C).

FRMALE LABOREMONT AND FOT

The everage multiplief of owner but the title starms eviperated we set a faid rank to see and the sean for the second classic ways of a fail of the second classic ways of fail the second meter of days between successive clatthes set of days (success), a=5).

STRST STREETS SHEETS

Encurrenced matrix formulting times a spaged 1.7 days (s,d,a,b) poill with tumplicurves concentrate $2s^{0}C$ to $31^{0}C$. Interval otherwals propaged 7.2 days loid.=2.6, n=61, which raises the forst time because clusters of eqgs laid

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RESULTS

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TIME COSTS

MALE LABORATORY ASPECT

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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

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wasvas (sidi=29:3; n=3) for the second (s An average of , only 6.0 (sode=3817; n=3) for the second (s An average of , only 6.0 days (sodr=6:2; n=6) passed between successive clutches.

Figure 3 shows the average systeming specie of 5

SECOND FIELD ASPECT und beiner beinert und erst storghen ofTable 1 compares male brooding times with female clutch. synthesis time: Male brooding times averaged 8 days & age to (sed.=1.1, on=6) .avUpon the opportunity to rebreed, allowed mates took only one day to rebreed. An average of 2.6 days (sid.=1.6; n=7) passed between successive clutches. Table 2. shows the egg padesizes for the first and second clutches of ceach female. Egg pads that the females produced on their first opportunity to mate averaged 97.2 eggs (srd;=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 a bar. These vs as were of court from the same 5 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. higher repart of structure

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, and encumbered males swam significantly slower (13.4 cm/sec, s.d.=2.1, n=5) than either of these two agroups (one-way)

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ANOVA > F=5.65; P < 0.05; set efig. 1) . The egg pad size for these males averaged 91.6 equae (set = 31,4, n=5), which approximately covers an entire anale's dorsum. and for the brEigure 20shows the average swimming speeds of us bered endumbered males 4 and 3 days before the pad was syoughed off (11.2 cm/sec, s.d.=1:6 m=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 (ife. ; swimming speeds were not measured during the hatching period) i Speeds for the 2 days after hatching were 1806 dm/sec, ised =409, an=5; and 17:4 dm/sec; sud: #2.5; n#5; respectively. This represents a significant increase in swimming speed bfollowing legg pad. sloughing frepeated measures ANOVA, F=8.3, FPg<r0.01). We the feeding raFigure 3 is a scatter diagram showing the megative, relationship between swimming speed and weight (of cumbered) encumbered bug. These values were obtained from the same 5aindividuals as were used in fig. 22. AThe heavier 4, 6 - 6 encombered 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

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COSSION .

(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 mater per day was also calculated for the female and unencumbered male enable groups.

after the brooding period of the encumbered group. A paired t-test showed that the makes are 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) for be females ($\overline{x}=0.66$, s.d.=0.06, n=4) and brooding (encumbered) males ($\overline{x}=0.66$ boatmen/day, s.d.=0.08, n=5). Encumbered males ate significantly less (one-way ANOVA, F=44.4, $P \le$ 0.05) than unencumbered males. Females ate significantly more boatmen (P < 0.001) than either of the male groups.

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DISCUSSION

will prevent realier Cletches which do not recessarily

Male <u>Belostoma flumineum</u> appear to have a flumber 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.

continuouslys (i.e. malesback space is not limiting) patheyrs

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will oviposit smaller clutches which do not necessarily age 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 the clutches," which averaged about 31 eggs, suggests that the 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 dogenesis 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 submaximal 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 fémales 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

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sexually active males at any given time" (Emlen and Oring, 1977). b For example, if thereivere many sexually mactive les males, and if female receptively came only in wshort, each isolated bursts of only one or a few females at a time, then the OSR would be strongly skewed toward males. as If the OSR were skewed toward males othen 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 competed for the smaller, fatter males who are likely to be able to brood honger. It is thought that these males (who perform 72% of the second 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 Soffspring. If females were limited by the availability of that service, then they would be expected to compete when 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 fback our

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space, may actually compete for access to males with the waterebug Abedus herberti, Smith (1979a) has seen stemales actively approach males during courtship and males reject Certain females asomates. What, by such that what the susmith (1980a, 1980b) suggested risk of predation as crease another potential cost of brooding in water bugs. Be water Subsequent testing of that hypothesis revealed that 1999 14 encumbered male water bugs are 2-3 times more likely to be preved upon by aquatic fishing spiders (Dolomedes triton) than mare unencumbered males or females (Kruse, unpublished data) : Bither brooding behaviors act as a cue for location by the predator; or encumbered makes 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 (Abedusand 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.

beAnother 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 tocation because fishing spiders sense surface vibrations (Bleckman and Barth; 1984) \$; Also, encumbered B. Slumineum

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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 incr∉ase 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 Bruflumineum, then this also could contribute to their increased vulnerability to predation. main 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 makes could potentially cause a shift in the operational sex ratio, resulting in even fewer males with which the females can breed as to some start (381), set a for obtaining and the

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

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swim fast enough to datch their prey. and do not show any 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 A. herberti 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 Diplonychus indicus, encumbered males, "restrict their movements, do not show voracious feeding habits and make little attempt to catch prey... " (Venkatesan, 1983). an Whether the decrease in food intake is yactually due to a decrease in ability to capture prey or due to feeding at inhibition, is uncertain. However, some of my brooding makes 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 B. thomasis 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 access severely limiting to females. Data on male interclutch intervals suggest this may not be the case, however grad

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because makes 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 make or 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 noncontact 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

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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 postcopulatory 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

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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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field.	# of prov			
Trial	female clutch synthesis time (days)		male brooding time (days)	
1	2.00	3.5	9	
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t-cal =	7.42, P < 0.05	5		

Table 1. Comparison of male brooding time and female clutch synthesis time in Belestoma flumineum in the Table 2. Sizes of consecutive clutches.

Trial	<pre># of eggs oviposited in clutch 1</pre>	<pre># of eggs oviposited in clutch 2</pre>
1	*123	34
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7	*135 (*****	
x	97.2	30.9
s.d.	30.4	7.7
n	6	7
4 - 1,		

* about 20 of these eggs were deposited on the

back of a second male.





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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.

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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 (<u>P</u> < 0.05).

Post - Breeding



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Rate (# water postman ealen/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 (<u>P</u> < 0.01).

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