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Factors Affecting Parental Investment Strategies in Male Waterbugs

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FACTORS AFFECTING PARENTAL INVESTMENT STRATEGIES IN MALE WATERBUGS

(TITLE)

BY

SCOTT KIGHT

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

MASTER OF SCIENCE

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY
CHARLESTON, ILLINOIS

1991
YEAR

I HEREBY RECOMMEND THIS THESIS BE ACCEPTED AS FULFILLING
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ABSTRACT

Male giant waterbugs (Belostoma flumineum Say) brood eggs oviposited on their dorsi by conspecific females. Preliminary observations indicate that viable egg pads are sometimes discarded before hatching. Theory predicts that such behavior should occur only if costs incurred by brooding exceed benefits of hatching the egg pad. The amount of paternal investment per pad should be similar for both large and small pad sizes, but as egg pads become smaller, investment per egg increases. Thus, smaller pads should be more likely to be discarded unhatched than larger ones. Similarly, egg pads containing inviable eggs should also be more frequently discarded than viable egg pads of the same size. Egg pads should be less frequently discarded as the time invested increases. Effects of these factors (egg pad size, time invested, and egg viability) upon the continuation of paternal care in the giant waterbug were investigated. Results of laboratory experiments suggest that smaller egg pads are less likely to hatch than larger ones, and males appear to be less likely to discard egg pads as temporal investment increases. However, inviability of eggs did not appear to affect the probability of an egg pad being discarded.

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INTRODUCTION

Parental investment, as defined by Trivers (1972) is "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." This may include cytoplasmic investment by females in eggs, as well as behavioral care such as incubation, guarding, and feeding of young by one or both parents. The degree of parental care given, however, is often not fixed and may be variable (Clutton-Brock 1991). The mechanism animals utilize in the allocation of parental care is presently under discussion (Trivers 1972; Dawkins & Carlisle 1976; Maynard Smith 1977; Sargent & Gross 1985).

Trivers (1972) suggested that organisms should avoid wasting past cumulative parental investment. If this is true, the value of a brood should be a function of the amount of care already invested. Other authors disagree, reasoning that the decision to continue investing should depend upon expected future benefits (Boucher 1977; Dawkins & Carlisle 1976; Maynard Smith 1977). Animals which appear to base decisions on prior investment are said to commit the "Concorde Fallacy" (Dawkins 1976) in reference to the fallacious economics involved in continued investment in the Concorde airliner project to avoid wastage of past investment. Some examples of species that commit the "concorde fallacy" include savannah sparrows (Weatherhead

1979) and digger wasps (Dawkins & Brockmann 1980).

It is likely that both past parental investment and future reproductive prospects play a role in decision making processes involving parental care (Williams 1966; Carlisle 1982; Sargent & Gross 1985). Williams (1966) implied that natural selection should operate such that parents will maximize remaining lifetime reproductive success, subject to a tradeoff between present versus future reproduction. Consequently, selection should favor animals who base their investment into current offspring on the value of the brood at stake relative to the value of the parent's own expected future reproduction (Sargent & Gross 1985). By using past investment as an indicator, some animals may be capable of estimating future benefits (Carlisle 1982, 1985; Sargent & Gross 1985), and thus do not in fact commit the Concorde fallacy. The feasibility of such a strategy should be a function of the predictability of future events (Weatherhead 1979).

The giant waterbug, Belostoma flumineum Say, is a predaceous aquatic insect inhabiting ponds across the United States (Usinger 1956; Smith 1976). As in all species of the subfamily Belostomatinae, the male broods eggs deposited as a cohesive unit (egg pad) upon his dorsal surface by females (Torre Bueno 1906; Smith 1976) and provides exclusive post-copulatory paternal care. Male brooding behavior involves remaining at the water surface, which has the effect of exposing the eggs to atmospheric oxygen while simultaneously preventing desiccation (Smith 1976; Kopelke 1980). Brooding males also stroke the eggs with the rear legs, presumably to prevent the establishment of fungi (Cullen 1969) and possibly to assess the status of egg development. Male brooding continues until the eggs hatch, which takes 6 to 12 days depending upon the temperature of the water (Torre Bueno 1906; Kruse 1990).

Previous studies (Kraus et al. 1989; Smith 1979b; pers. obser.) reveal that egg pads may become detached from a male's back prior to hatching, resulting in the death of the eggs. Laboratory observations indicate that egg pads can be actively removed by males. Such behavior appears to be maladaptive, because a loss of offspring should be detrimental to the male's fitness. It is possible, however, that such behavior could increase net lifetime fitness if, by discarding, a male is more likely to obtain and successfully brood a larger number of eggs in the future. This strategy of parental care allocation appears to exist in some avian species (Mock & Parker 1986). Because male waterbugs are captured bearing various numbers of eggs (Kruse 1990), such a strategy may have evolved in this species.

Carlisle (1985) suggests that when animals are not likely to encounter changes in brood or individual offspring quality independent of parental investment during the parental care period, parental strategy should be based on past investment. This scenario applies to the egg pad during brooding in B. flumineum, suggesting that male waterbugs are likely to use past paternal investment to establish the value of the present brood relative to future reproductive potential.

Because male waterbugs appear to either brood or discard egg pads, they are a useful system for investigating the parental investment decision rules. This study was designed to investigate the effects of three factors upon the probability of egg pads being discarded by male giant waterbugs: the size of the egg pad, the time invested in brooding the eggs, and viability of the eggs in the pad. If waterbugs use previous investment as an indicator of future reproductive success, older egg pads should not be discarded. Also, if waterbugs weigh the value of the present brood against future reproduction, larger (see Carlisle 1982; Mock & Parker 1986; Armstrong & Robertson 1988) and more viable egg pads, which are more valuable, should have a lower probability of being discarded unhatched.

Methods

Adult and last instar nymph giant waterbugs were field captured (Coles County, IL) from May to September, 1990. Nymphs were allowed to molt into adults in captivity. Waterbugs were collected by sampling temporary and permanent ponds with aquatic insect dip nets; individuals were immediately transported to the laboratory in plastic coolers containing pond water. Sex was determined by examining the genital plate under a dissecting microscope. Females exhibit two apical tufts of setae; males lack this characteristic (Lauck & Menke 1961). Individuals were marked with white india ink (sealed with "superglue" cyanoacrylate ester) and placed in 40-l aquaria filled with dechlorinated tap water at 25-30°C. Each aquarium contained plastic vegetation upon which bugs could perch. Approximately 30 waterbugs were placed in each aquarium at a sex ratio of 1:1. All animals were maintained on a diet of crickets and dragonfly naiads (in the spring/early summer) administered *ad libitum*. All experiments were run in an environmental chamber at 27°C in which a 14L:10D photoperiod was maintained. Upon initiation of each trial, individuals were isolated in cylindrical 1-l plastic containers containing 0.5-l of water (approximately 10 cm deep) and plastic vegetation.

Experiment I investigated the relationship of egg pad size to the probability of the egg pad being discarded. Within 12 hours of cessation of breeding, males fully encumbered with eggs were randomly assigned to one of four egg pad size groups: 25%, 50%, 75%, and 100% (control) of a full egg pad. A "full" egg pad was designated as one in which the entire backspace (up to and including the pronotum) was filled with eggs. Various egg pad sizes were attained by carefully removing eggs from the anterior part of the dorsum with a scalpel until the assigned percentage remained. Eggs were removed from the anterior portion of the dorsum because females almost always oviposit eggs beginning at the posterior portion of the dorsum and proceed anteriorly (Smith 1974; pers. obser.). Therefore, treatments simulate males that have received a partial clutch. The 100% group served as a control in which the males were touched with the scalpel and handled as in other treatments but no eggs were removed.

Experiment II was designed to control for the possibility that manipulation of the animal during treatment administration in Experiment I effects the probability of an egg pad being discarded. Breeding males were removed from the presence of gravid females at various times during breeding to attain desired egg pad sizes (25%, 50%, 75%, or 100% (control) of a full egg pad).

Experiment III was identical to Experiment I, except a two, four or six day delay was inserted between the time the individual became fully encumbered and the time the treatment (egg removal) was administered. Therefore, egg pads were in various stages of development when treatments were administered. As in Experiment I, egg pad sizes were manipulated to 25%, 50%, 75%, and 100% of a full egg pad.

Experiment IV involved rendering portions of a full egg pad inviable. Fully encumbered males were randomly assigned to one of five treatment groups: 0%, 25%, 50%, 75%, and 99% inviable egg pads. Treatments consisted of administering fingernail polish to a randomly designated portion of the pad (anterior, posterior or mixed). The fingernail polish treatment kills the developing eggs (probably by preventing oxygen exchange) while having no detrimental effects upon the male. The 0% group served as a control in which egg pads were swabbed with a brush dipped in water instead of polish (i.e., no eggs rendered inviable).

All experiments were monitored daily (by looking through glass lids placed on the isolation containers) and terminated following either the hatching of eggs or the discarding of an unhatched egg pad. Data from repeated treatments of the same individual were tested for statistical independence with Cochran's Q test with an alpha = 0.05. Data were also analyzed with the Fisher Exact test and two-and three-dimensional contingency table chi-square procedures with an alpha = 0.05 (Zar 1984).

RESULTS

Data from experiments I and II (n=8; n=7 respectively) were tested with Cochran's Q test to determine whether repeated treatment of the same individual affected the probability of an egg pad being discarded unhatched. Whether an egg pad was hatched or discarded was determined to be independent of prior treatment ($Q_{cal}=3.00$; df=2; $P>0.05$). Consequently, I analyzed frequency data using chi-square contingency procedures and/or the Fisher Exact test.

EXPERIMENT I - EFFECTS OF EGG PAD SIZE (egg removal) ON PROBABILITY OF DISCARDING

Fifteen of the 32 (46.9%) males that received the 25% egg pad size treatment discarded the egg pad unhatched; 19.4% (6 of 31), 18.8% (6 of 32) and 13.8% (4 of 29) of the egg pads were discarded in the 50%, 75% and 100% egg pad size groups, respectively (Fig. 1). Chi-square procedures demonstrated that fate of an egg pad depended on the treatment received ($X^2_{cal}=11.30$; df=3; $P=0.0102$). Males with egg pads that were reduced to 25% of the backspace area discarded unhatched pads significantly more often than males with larger egg pads (Fisher Exact test: 25%-50% groups $P=0.02$; 25%-75% groups $P=0.02$; 25%-100% groups $P=0.01$) while egg pads of other sizes were discarded in equal proportion (Fisher Exact test: 50%-75% groups $P=0.60$; 50%-100% groups $P=0.41$; 75%-100% groups $P=0.43$).

EXPERIMENT II - EFFECTS OF EGG PAD SIZE (oviposition termination) ON PROBABILITY OF DISCARDING

Eight of the 27 (29.6%) males in the 25% egg pad size treatment group discarded the egg pad unhatched; 13% (7 of 54), 5.9% (4 of 68) and 27.3% (3 of 11) of the egg pads were discarded in the 50%, 75% and 100% egg pad size treatment groups, respectively (Fig. 2). These results were determined to be dependent upon treatment ($X^2_{cal}=11.0$; df=3; $P=0.01$).

The Fisher Exact test demonstrated that the results of this trial are not statistically different from those of Experiment I in which egg pad size was altered by egg removal (25% groups $P=0.14$; 50% groups $P=0.31$; 75% groups $P=0.054$; 100% groups $P=0.29$). Thus it appears that the scalpel manipulation had no direct effect upon the probability of discarding.

Because the data from this experiment are not statistically different from that of Experiment I, results from both experiments were pooled. Analysis of the pooled data suggest that males with egg pads that were reduced to 25% of the backspace discarded unhatched pads significantly more often than males with larger egg pads (Fisher Exact test: 25%-50% groups $P=0.001$; 25%-75% groups $P<0.0001$; 25%-100% groups $P=0.02$) while egg pads of other sizes were discarded in equal proportion (Fisher Exact test: 50%-75% groups $P=0.19$; 50%-100% groups $P=0.47$; 75%-100% groups $P=0.17$).

EXPERIMENT III - EFFECTS OF EGG PAD SIZE AND TIME INVESTED ON PROBABILITY OF DISCARDING

Only a single male (n=4, 25%) in the 25% egg pad size treatment group discarded an unhatched egg pad following treatment on day 2; 40% (2 of 5) of males in the 25% egg pad size treatment group discarded after being treated on day 4, and 16.7% (1 of 6) of males in the 25% egg pad size treatment group discarded after treatment on day 6. Males in the 50% egg pad size treatment group did not discard after being treated on day 2 or day 6 (n=5;n=7), but 16.7% (1 of 6) discarded after being treated on day 4. In all trials, no males in the 75% and 100% groups were observed discarding unhatched egg pads. Data from Experiment I in which treatments (egg pad reduction) were administered within 24 hours of oviposition were included in the analysis as a "day zero" category (Fig. 3). A three-dimensional contingency table demonstrated that there were significant interactions between some of the variables ($X^2_{cal}=37.18$; df=24; $P<0.05$). Tests for partial independence revealed that the fate of an egg pad was not independent of time invested and size of egg pad ($X^2_{cal}=31.99$; df=15; $P<0.05$). Further analysis revealed that the fate of an egg pad depended upon both the time invested in the pad ($X^2_{cal}=11.24$; df=3; P=0.04) and the egg pad size ($X^2_{cal}=21.30$; df=3; P=0.0001). Males treated on day zero were more likely (Fisher Exact test P=0.0006) to discard unhatched egg pads than males treated on or after two days

(Fig. 4).

EXPERIMENT IV - EFFECTS OF EGG VIABILITY ON PROBABILITY OF DISCARDING

None of the males in the sham egg pad group discarded (n=14); one of the eight males (12.5%) in the 25% inviable area size group were discarded; no males in the 50% inviable area size group discarded (n=6); two of twelve (16.7%) and one of six (16.7%) egg pads were discarded in the 75% and 99% inviable area size groups, respectively (Fig. 5). Chi-square procedures demonstrated that the fate of an egg pad was independent of treatment (X^2cal=3.5; df=4; P=0.48).

TIME BETWEEN TREATMENT ADMINISTRATION AND DISCARDING OF THE UNHATCHED EGG PAD

In all experiments, the amount of time which elapsed between egg pad treatment and the time at which the egg pad was discarded was generally between two and three days (Table 1).

DISCUSSION

Coleman et al. (1985) stated that the evolutionary value of a brood is a function of their number (brood size), their probability of surviving to reproduce, and their relatedness to the parent. In _B. flumineum_, the male's ability to influence the probability of offspring survival is limited to the period of egg development, because paternal care is terminated upon hatching. Given that an encumbered male performs the necessary brooding behaviors, offspring survival is high (Smith 1976). Also, the breeding behavior of this species, characterized by repeated bouts of oviposition and copulation, results in a high confidence of paternity for the brooding male (Smith 1979b). Therefore, offspring survival and relatedness are probably not important factors affecting brood value to the male waterbug. The size of the brood, however, may vary widely among encumbered males (Kruse 1990) and is likely the most important factor influencing male fitness.

Male _B. flumineum_ have been observed to occasionally become detached from their egg pads before the eggs hatch (Smith 1976; Smith 1979b; Kraus et al. 1989; pers. obser.). Kraus et al. (1989) noted that small egg pads of a waterbug are more likely to become detached than larger pads, either because they are "unprofitable" or they peel off because of drag. Smith (1976) reported that egg-laden males placed in aquaria lacking a floating substrate could not keep their respiratory structures above the water's surface. Males under such conditions were reported to kick at the egg pad until it fell off.

The costs incurred during brooding are probably very similar for all male waterbugs, regardless of the size of the egg pad. Such costs include energy expenditure during brooding, inability to fly (and thus disperse), increased vulnerability to predation, reduced foraging efficiency and loss of polygynous matings (Smith 1980). The benefits received by a brooding male, however, are a function of the egg pad size. Assuming females do not differ dramatically in genetic quality, males hatching larger egg pads receive a greater net fitness benefit than males with smaller pads, because the former produce more offspring at the same cost. Pressley (1981) indicates that risks taken by a parent should be greater for a larger number of eggs. Males with smaller egg pads might therefore be expected to exhibit a greater likelihood of discarding egg pads before they hatch. This occurred in experiments I and II, in which males with the smallest egg pads (25% of a full egg pad area) discarded at a significantly higher proportion than males with larger pads.

Theoretically, males should be selected to discard unhatched egg pads only if their fitness is increased by doing so. Thus males could be discarding in the event that a second, larger pad might be obtained after discarding the first. The probability of receiving a larger pad, however, must be sufficiently high to warrant the loss of even a small number of potential offspring. The fact that males in experiments I and II with egg pads that occupied 50% or greater of their backspace area discarded with similar and relatively low probability indicates that such males are perhaps unlikely to receive a larger pad. Males in the 25% egg pad size group, however, which discarded at a much higher proportion, may be likely to receive significantly more eggs if they can secure a second mating. Given a sufficient probability of remating, they have little to lose except the time invested brooding the original pad.

In the spring and early summer, male backspace availability has been shown to limit _B. flumineum_ female reproduction (Kruse 1990). At this time, essentially all males in the population are completely egg-laden. Under these conditions, males that are only partially egg-laden might be more likely to discard than males breeding later in the year when backspace availability is not a limiting factor for female reproduction (Kruse 1990).

Continued brooding behavior in the giant waterbug may be contingent upon the amount of time already invested. Dawkins (1976) reasoned that basing present decisions upon past investment was fallacious, and that the decision to continue investing should be based upon future benefit (the "Concorde fallacy"). However, according to Coleman et al. (1985), a relationship between past investment and present decision making need not constitute committing the Concorde fallacy. Depending on the time of year and the water temperature

(Kruse 1990), males which brood egg pads to hatching spend 8 to 16 days between matings (including time spent in copulation, time spent in brooding, time to discard the hatched egg pad and breed again). Considering a breeding season of approximately three months, a male waterbug has a limited number of potential opportunities to breed. Males that invest a large amount of time in an egg pad before discarding it may actually receive a smaller net fitness benefit even if they receive a larger second pad, simply because the wasted time results in a lost potential opportunity to breed (see Maynard Smith 1977). Prior temporal investment, under these circumstances, could serve as an indicator of future reproductive potential. Consequently, males should be selected to discard an egg pad as early as possible so that sufficient time remains to remate without loss of a potential mating event (see Mock & Parker 1986). As the time invested in an egg pad increases, the probability of the pad being discarded should decrease. Our observations suggest that male waterbugs are most likely to discard an unhatched pad early ($\leq$ 2 days) in the brooding period. Coincidentally, Smith (1979a) noted that male waterbugs with incomplete pads which have brooded for "a few days" refuse to accept more eggs. Males of this species may therefore have evolved a temporally based decision making process which not only establishes continued investment contingent upon the amount of past investment, but also prevents asynchronous hatching of the eggs in the pad.

The results of Experiment III suggest it is unlikely that small egg pads fall off simply due to increased physical drag. If this were true, small pads should be more likely to fall off later in development, when drag is increased due to the larger surface area of the expanding eggs as they take up water. However, most egg pads, regardless of size, became detached early in the brooding period while the developing eggs were still small. Therefore, it is likely that the egg pads were removed through the actions of the brooding male. Males were observed kicking at viable egg pads with their posterior appendages, apparently causing the pads to become at least partially loosened from the dorsum, as well as using these appendages to actively remove egg pads following hatching of the nymphs.

Males with various portions of their egg pads rendered inviable did not discard in the predicted manner. In such pads, viable and inviable eggs were readily distinguished by visual observation with respect to size within one day of treatment. Inviable eggs remained small while viable eggs in the same pad would become increasingly larger until hatching (due to uptake of water). The results of Experiment IV, however, indicate that inviability of eggs in the pad had no effect on the probability of discarding. It appears that waterbugs have not evolved a mechanism to detect the presence of inviable eggs. This may be the result of the absence of selective pressures in natural populations which could produce such a mechanism (i.e., eggs are rarely inviable under natural breeding conditions). The breeding behavior exhibited by this species makes it unlikely that unfertilized eggs will be oviposited on the backs of males. In addition, although egg pads were observed to rarely become infested with fungus under laboratory conditions (after which they did not hatch), all field captured males bearing eggs were free of fungus. On the rare occasion that an egg pad did become infested with fungus in the laboratory, males continued to brood for extraordinarily long periods and were eventually overwhelmed with fungus and died as a result.

In summary, factors that appeared to affect male parental investment strategies in _Belostoma flumineum_ included both size of an egg pad and the time invested in the pad. Smaller egg pads were more likely to be discarded unhatched than pads which occupied at least 50% of the backspace area. Males were also more likely to discard a pad in which they had little time invested than a pad which they had brooded for at least two days. Finally, male waterbugs appeared incapable of assessing egg viability.

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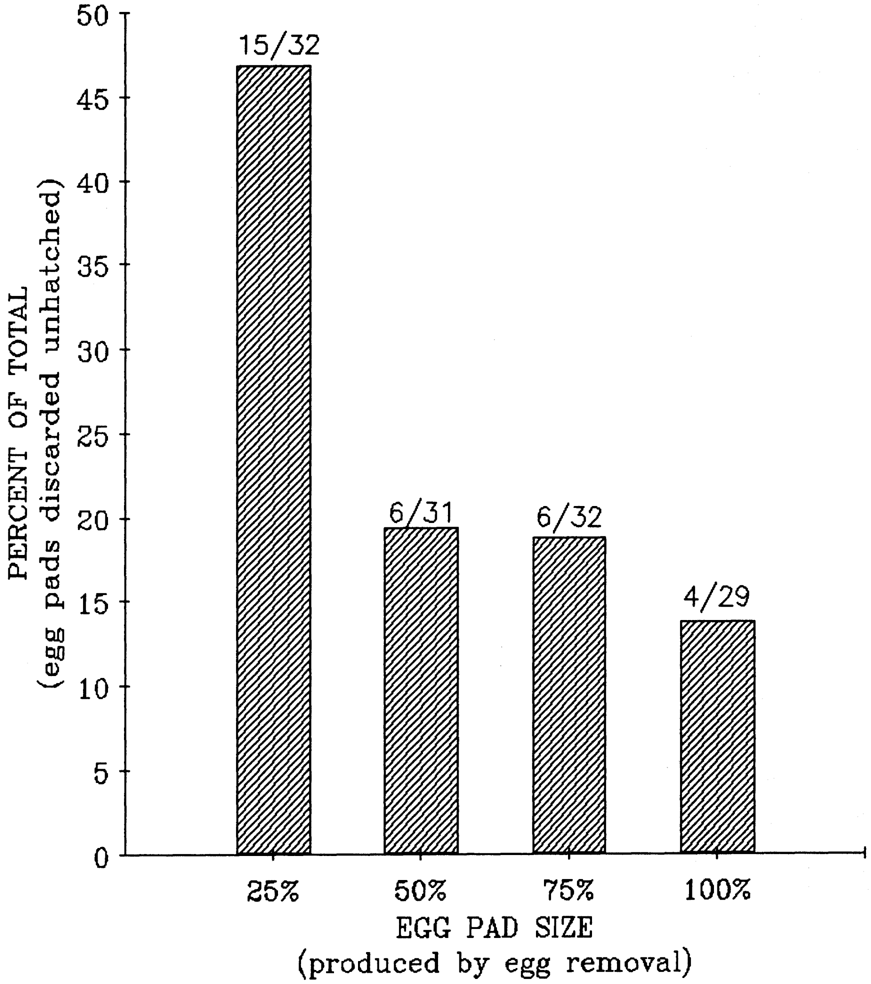
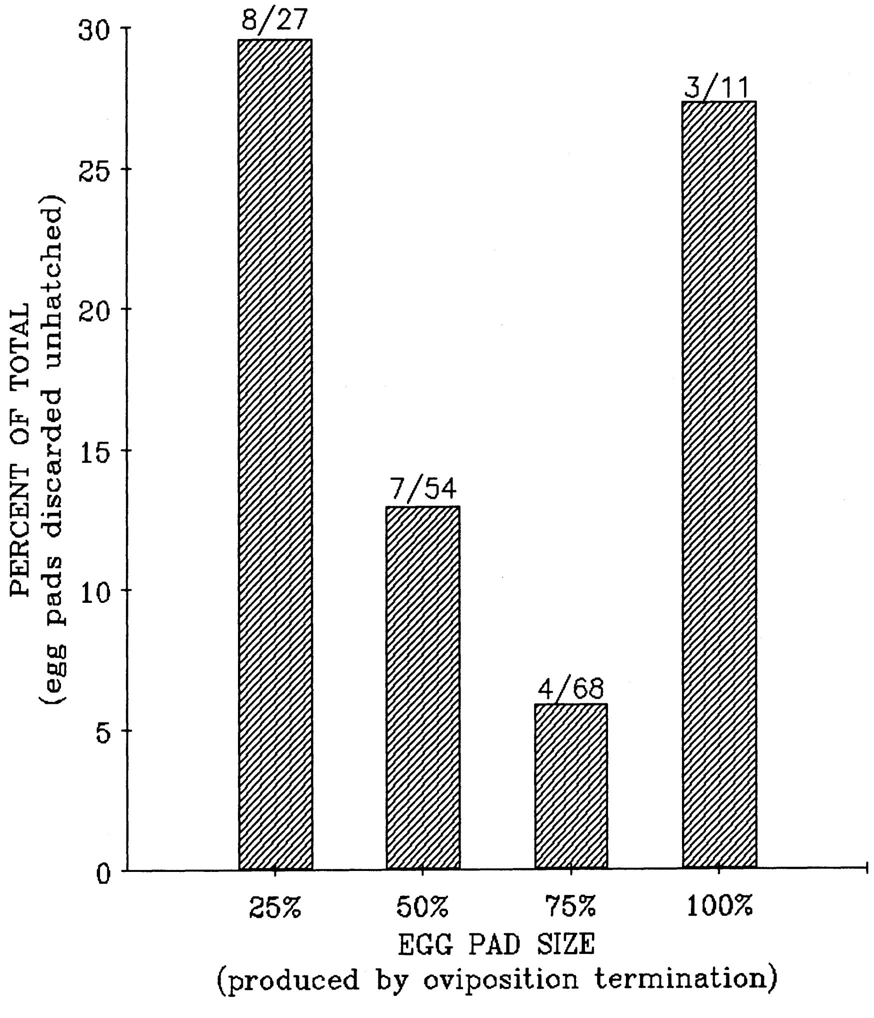
Fig. 1. The relationship of egg pad size (produced by egg removal) to the probability of egg pads being discarded unhatched (percent of total) in male _B. flumineum_. Frequency discarded/total in experiment is found above bars.



PERCENT OF TOTAL
(egg pads discarded unhatched)
50
45
40
35
30
25
20
15
10
5
0
15/32
6/31
6/32
4/29
25%
50%
75%
100%
EGG PAD SIZE
(produced by egg removal)

Fig. 2. The relationship of egg pad size (produced by termination of oviposition) to the probability of egg pads being discarded unhatched (percent of total) in male _B. flumineum_. Frequency discarded/total in experiment is found above bars.



8/27
7/54
4/68
3/11
30
25
20
15
10
5
0
PERCENT OF TOTAL
(egg pads discarded unhatched)
25%
50%
75%
100%
EGG PAD SIZE
(produced by oviposition termination)

Fig. 3. The relationship of egg pad size (produced by egg removal) and time invested to the probability of egg pads being discarded unhatched (percent of total) in male *B. flumineum*. Frequency discarded/total in experiment is found above bars.

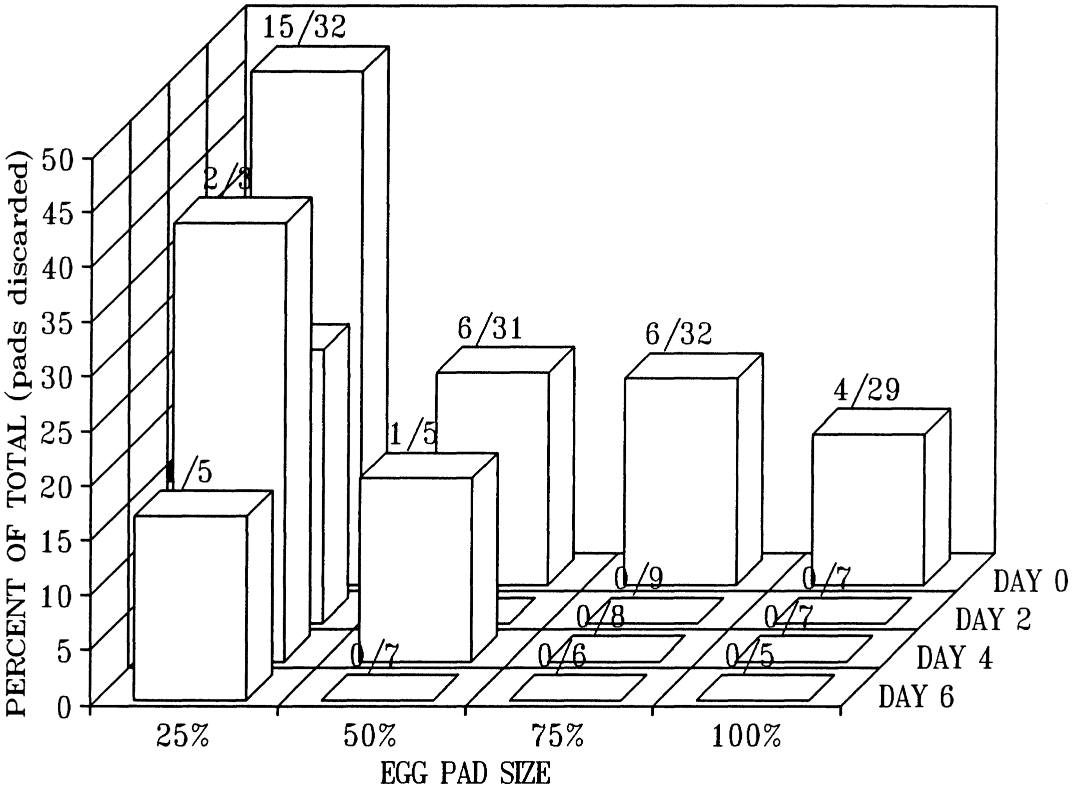

PERCENT OF TOTAL (pads discarded)
50
45
40
35
30
25
20
15
10
5
0
15/32
2/3
1/5
1/5
6/31
6/32
4/29
0/9
0/7
0/8
0/7
0/7
0/6
0/5
DAY 0
DAY 2
DAY 4
DAY 6
25%
50%
75%
100%
EGG PAD SIZE

Fig. 4. The relationship of egg pads with sizes altered before and after 2 days to the probability of egg pads being discarded unhatched (percent of total) in male B. flumineum. Frequency discarded/total in experiment is found above bars.

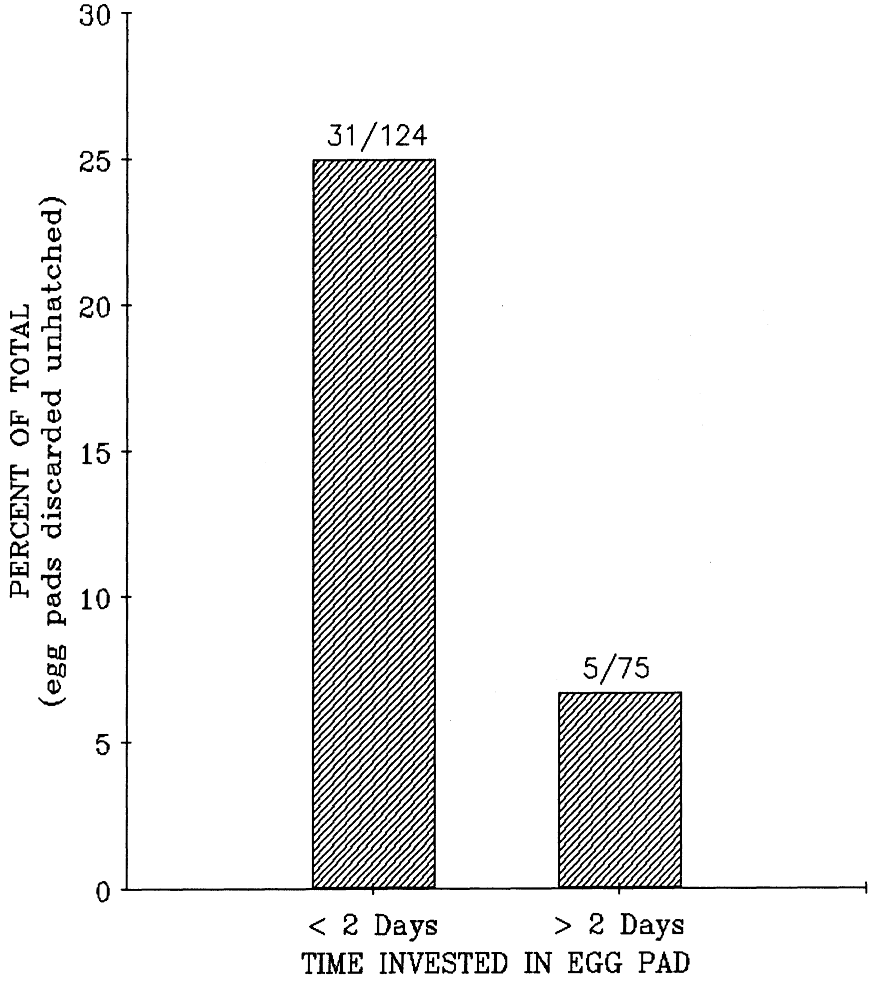

PERCENT OF TOTAL
(egg pads discarded unhatched)
30
25
20
15
10
5
0
31/124
5/75
< 2 Days
> 2 Days
TIME INVESTED IN EGG PAD

Fig. 5. The relationship of egg pads with various degrees of inviability to the probability of egg pads being discarded unhatched (percent of total) in male *B. flumineum*. Frequency discarded/total in experiment is found above bars.

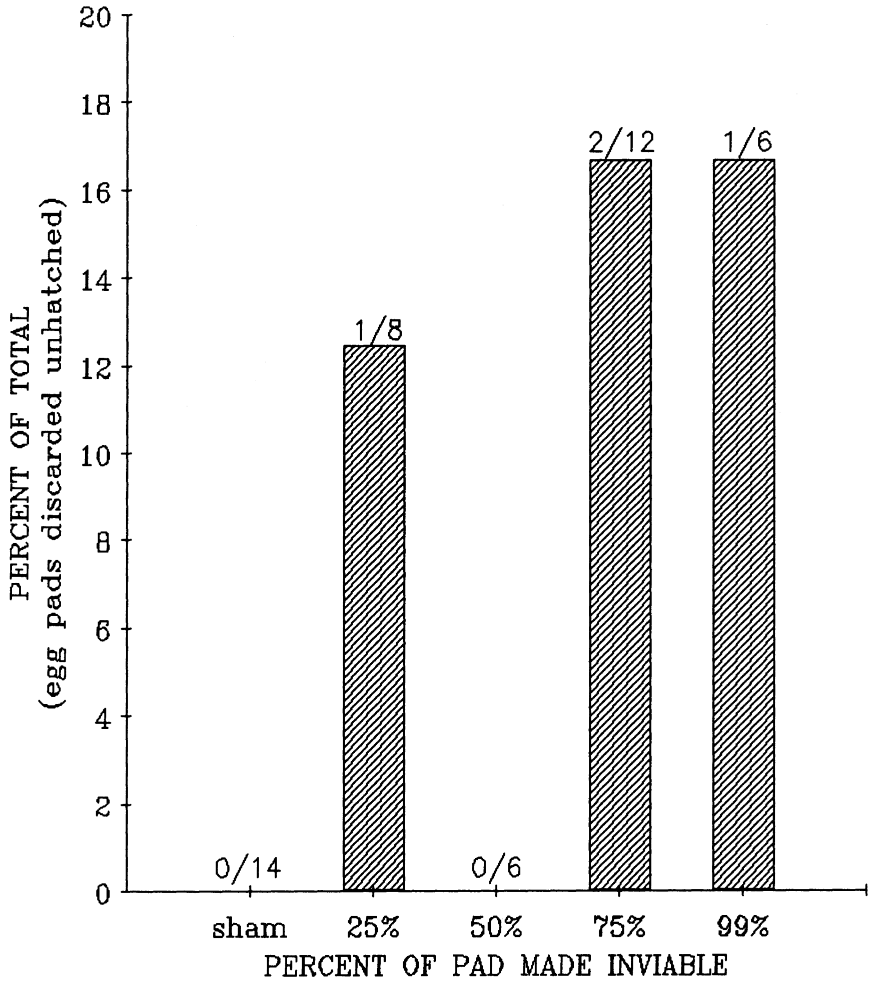

20
18
16
14
12
10
8
6
4
2
0
PERCENT OF TOTAL
(egg pads discarded unhatched)
0/14
1/8
0/6
2/12
1/6
sham
25%
50%
75%
99%
PERCENT OF PAD MADE INVIABLE

Table 1. Time elapsed (days) between treatment administration and discarding of unhatched egg pads. The mean is above the standard deviation; range and sample sizes are in parentheses.

	Treatment Group			
	25%	50%	75%	100%
Experiment I				
	2.8	3.7	3.0	2.0
	2.6	2.7	3.5	2.0
	(1-9)	(1-7)	(1-10)	(1-5)
	(n=14)	(n=6)	(n=6)	(n=4)
Experiment II				
	3.0	2.6	3.3	2.7
	1.6	1.0	1.3	0.6
	(2-6)	(2-4)	(2-5)	(2-3)
	(n=8)	(n=7)	(n=4)	(n=3)
Experiment III				
Day 2	2.0	-	-	-
	-	-	-	-
	-	-	-	-
	(n=1)	-	-	-
Day 4	2.0	1.0	-	-
	1.4	-	-	-
	(1-3)	-	-	-
	(n=2)	(n=1)	-	-
Day 6	1.0	-	-	-
	-	-	-	-
	-	-	-	-
	(n=1)	-	-	-